Dispersal, Habitat Use, and Survival of Native Forest Songbirds in an Urban Landscape

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Abstract

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Because movement between habitat patches isolated by urban development may be necessary for bird populations to remain viable, I examined correlates between land cover, bird survival, habitat use, and mobility during the post-fledging period. I used radio telemetry to measure the movements of 122 fledglings of four species across the urban gradient of the Seattle metropolitan area from 2003-2005. Mortality of post-fledging birds was low, and land cover effects on survival were limited. I observed more mortality in forested areas than in the urban matrix, and independent juveniles often moved into urban areas without increased risk of death. I found little consistency in habitat use within each species, with the exception of American Robins, who used residential areas more so than forested areas. Migratory species were the most mobile, but juvenile mobility was limited in proportion to the imperviousness of the developed landscape. Parts of the urban matrix were permeable to movement and provided consistent food resources to dispersing juveniles.

Because limitation in dispersal of juveniles and adults between years can affect bird population viability, I measured the rates of natal and breeding dispersal, site fidelity, natal philopatry, and dispersal distances of 9 songbird species from 1999-2006. Species, sexes, and age classes differed in their rates of all four movement categories and dispersal distances, which were related to prior breeding success, territory density, and local and landscape forest metrics. I suggest urban growth strategies across multiple scales for maintaining effective bird dispersal in urban ecosystems that focus on maximizing the amount of forest cover and minimizing the amount of impervious urban cover.

The incorporation of science into environmental policy is a concern at many levels of decision making. I interviewed planners and consultants who conducted scientific reviews associated with a Washington State Growth Management Act amendment that requires the inclusion of best available science in protecting critical areas. Jurisdictions of different sizes varied in their definition of best available science and how they dealt with conflicting scientific information. They also differed in the types of science they used and the process by which included science in their land-use policies.

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CHAPTER 1.
SPECIES-SPECIFIC SURVIVAL AND RELATIVE HABITAT USE IN AN URBAN LANDSCAPE DURING THE POST-FLEDGING PERIOD

Introduction

Native habitats are being altered and eliminated by human settlement to an unprecedented extent, primarily due to the needs of growing human populations (Marzluff 2001, Theobald 2005). For example, between 1950-2000 the amount of urban and exurban land cover in the coterminous United States increased by four to five times (Brown et al. 2005). In the central Puget Sound region of Washington state, the population has increased by 2 million people since 1960 (Puget Sound Regional Council 2007), and the demand for new residential development has resulted in large increases in suburban and exurban land cover and decreases in the area of rural areas and wildlands (Robinson et al. 2005). The loss and fragmentation of native land cover types have been recognized as key causes of declining biological diversity worldwide (IUCN 1980, Mönkkönen and Welsh 1994, Fahrig 1999, Czech and Krausman 2001).

Widespread land conversion is closely associated with changes in important wildlife population processes such as reproduction, survival, and dispersal (Turner 1989, Marzluff 2001, Opdam and Wiens 2002, Lampila et al. 2005). Changes in these processes directly affect population persistence and community diversity (Andrén 1994, McKinney 2002, Hansen et al. 2005, Chace and Walsh 2006). Survival influences population growth in many birds (Bradbury et al. 2000, Robinson et al. 2004), underscoring the need for good estimates of adult and juvenile survival and understanding of the factors influencing them for effective bird conservation (Ricklefs 1983, Pulliam and Danielson 1991).

A complex web of direct and indirect factors impact bird survivorship in urban areas, some of which are favorable while others are unfavorable (Marzluff 2001). Collisions with windows, cars, and power lines are common causes of death (Rusz et al. 1986, Codoner 1995, Mannan et al. 2004). Human activities can affect bird survival indirectly, such as disturbance from hiking on trails that results in less time foraging, or directly in the form of persecution. Bird survival can be enhanced by providing bird feeders, water sources, and cover, but birds sometimes risk disease transmission or predation by using feeders (Brittingham and Temple 1986, Dunn and Tessaglia 1994). Growing populations of native and exotic predators in urban areas add pressure to bird survival (Batten 1973, Marzluff et al. 2001a). As land is converted to human uses, birds must be able to adapt to this suite of new pressures or they may be locally extirpated.

Survival may also be influenced by the habitats birds select during each of their life stages. Breeding habitat requirements do not end when the young fledge from the nest, but continue until dispersal of the young. Juvenile birds may require unique habitats while dispersing and searching for a location that allows them to survive over their first winter. This requires at a minimum successfully avoiding sources of mortality and finding food. Many studies have found that juveniles use habitat that has distinct structure and composition from the place they were born (Anders et al. 1998, Vega Rivera et al. 1998, Pagen et al. 2000, Kershner 2001, Cohen and Lindell 2004, Jones and Bock 2005, White et al. 2005, King et al. 2006, Telería and Pérez-Tris 2007).

The goal of this investigation was to understand how post-fledging survival and relative habitat use related to land cover and land use patterns at various spatial scales in a heterogeneous urban landscape. I measured the survival of forest songbird species using radio telemetry along different parts of an urban gradient during the post-fledging period. This period may be the most vulnerable as birds become independent, learn to avoid predators, become self-sufficient, and deal with novel challenges (Snow 1958, Sullivan 1989, Magrath 1991, Anders et al. 1997, Naef-Daenzer et al. 2001, Cohen and Lindell 2004, Kershner et al. 2004, King et al. 2006, Yackel Adams et al. 2006). I tested two hypotheses relating mortality to movement and land cover and two hypotheses concerning relative habitat use in an urbanizing landscape (Table 1.1). I predicted post-fledging survival to decrease with fledgling mobility and the extent of the urban land cover. I expected post-fledging relative habitat use to correlate with the habitat affinities of adults and to reflect the distribution of food resources in urban areas (Table 1.1).

Methods

Study Sites and Species

I measured post-fledging survival of juvenile birds using radio telemetry at sites across the urban gradient of the Seattle, Washington, USA, metropolitan area over a three-year period (2003-2005). I selected 19 forest fragments within a matrix of urban, suburban, exurban, and control (undeveloped forest) landscapes (Marzluff et al. 2001b, Fig. 1.1). Sites were chosen using a stratified random sample of three landscape metrics calculated for a 1 km^2 area containing each study site: mean patch size, contagion, and the percent forest and percent urban land cover (see Donnelly and Marzluff 2004, 2006, Blewett and Marzluff 2005 for details). Forest fragments were primarily coniferous, including western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and western redcedar (*Thuja plicata*), or mixed with deciduous tree species such as red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*) and Oregon ash (*Fraxinus latifolia*, Franklin and Dyrness 1988). Site elevation varied from sea level to 300 m on the lower slopes of the Cascade Range. The four study species are all native songbirds that breed in forests: American Robin (*Turdus migratorius*), Swainson's Thrush (*Catharus ustulatus*), Spotted Towhee (*Pipilo maculatus*), and Song Sparrow (*Melospiza melodia*).

Post-Fledging Survival and Covariates

I radio-tagged 122 recently fledged birds (age 1-~20 days after fledging) and recorded their daily movements until death or transmitter battery expiration. Each transmitter was attached with an elastic thread leg harness (Rappole and Tipton 1991) that was intended to break and fall off the bird after my observations ended. The battery life of radios was proportional to the maximum weight each species could safely carry (<= 3% of body weight, model BD-2, Holohil Systems Ltd., Carp, Ontario, Canada) and was approximately 3 weeks for Song Sparrows, 6 weeks for Swainson's Thrushes, 8 weeks for Spotted Towhees, and 9 weeks for American Robins.

Fledglings were captured either in a hand net shortly after leaving the nest or in mist nets if older, including no more than one young per brood to increase independence of samples. Attempts were made to catch fledglings on their natal territories while still dependent on their parents, but I also caught older juvenile birds which were behaviorally independent at locations unknown relative to their natal territories. I determined age at capture for each bird based on behavior (begging from adults), plumage, and movement patterns (stationary within fragment or actively moving) and classified young birds still dependent on their parents as "fledglings" (N = 57) and older behaviorally independent birds as "juveniles" (N = 65). I analyzed the two age cohorts separately because I viewed them as distinct behavioral periods.

I attempted to relocate each bird daily with an R-1000 telemetry receiver (Communications Specialists, Inc., Orange, CA) and a handheld Yagi antenna. I recorded each location (UTM) using a handheld GPS unit (Garmin 12XL, Olathe, KS, USA) with an accuracy of <10 m estimated position error (GPS EPE). Observers avoided approaching each bird too closely so as to prevent influencing its movement. I recorded only one location per bird per day unless the bird was actively moving while I was tracking it (single movement of >100 m) to maximize my number of samples rather than follow each bird for an extended period of time (Otis and White 1999). When the bird could not be seen, its position was estimated using triangulation. If the signal did not move from the same location for several days, then the bird was detected visually to ensure it was still alive.

In all cases of mortality, the radio was recovered with any evidence of death (e.g. carcass or feathers, above or below ground). If the radio was recovered underground or the radio, harness, or carcass had been chewed, I assumed the predator was a mammal. If the radio harness was cleanly clipped or feathers were cleanly plucked and scattered around an elevated perch, I assumed the predator was avian (Newton and Marquiss 1982). If the signal was absent from the same area as the previous day, then the immediate area around the previously known location was searched in an increasingly larger radius using both a handheld yagi antenna on foot and a roof-mounted omnidirectional antenna while driving. I stopped searching for a missing bird after its battery was expected to have expired. When a radio signal was missing and could not be relocated before the expected date of battery expiration, I believe it is more probable that the bird survived and moved beyond the range of my search area than it is the bird died and the radio was destroyed by a predator, because predators typically broke the radio harness and removed the intact radio from the bird (did not eat the radio). Birds for which the signal was lost had all survived to parental independence. Further, I visually detected a number of birds carrying radios after their batteries had died by searching for them in areas of consistent use (i.e. feeders). Thus, for all analyses I assumed that birds of unknown fate survived (N = 27).

I calculated two aspects of mobility from locations plotted in ArcView GIS 3.3 (ESRI, Redlands, CA, USA). Mean daily speed (m/day) and total distance moved (m) were calculated using the Animal Movements 2.0 extension (Hooge et al. 1999). Mean daily speed is a measure of mobility that is comparable between individuals and species (corrects for differences between species in transmitter battery lives). Total distance is a sum of the total length of all daily movements combined and is suitable for comparisons of individuals within the same species with roughly the same transmitter battery lives. These mobility estimates were used as covariates in a Cox proportional hazards regressions (see below) to relate to survival (Hypothesis 1).

A 2002 Landsat TM satellite image with 30 m resolution was classified into 12 land cover classes (J. Hepinstall et al., In Press a), of which three are examined to test my second hypothesis: medium-heavy urban (>50% impervious surface per pixel, includes pavement, buildings, and lawns), light urban (<50% impervious and >50% forest per pixel), and forest (deciduous, coniferous, regenerating, and mixed). I calculated landscape metrics with the program FRAGSTATS 3.3 (McGarigal et al. 2002) for various buffer sizes around the center of each study site to test for differences in landscape extent on survival (105 m, 250 m, 500 m, 1000 m, 2000 m, 3000 m, and 4000 m). Buffer sizes were determined from the maximum distance moved by each species and extend in a radius around the mean of the UTM coordinates of the capture locations of all birds at each site. The smallest scale was set at 105 m because it encompasses the land cover area of three full pixels in radius surrounding the central pixel (30 m resolution grid) and corresponds with an area roughly equal to that of my smallest study sites (3.5 ha). I calculated the percent cover (the percent of pixels in the landscape of the focal land cover class) for each land cover class. All landscape metrics varied among study sites and spatial scales of analysis (Ch. 2).

To assess the effects of land cover at smaller spatial scales on mortality (Hypothesis 2b), I analyzed the percent land cover at observed versus random points for birds that died. The observed point was the last recorded location per bird. I generated 100 random points by simulating random walk pathways with the same length but varying angles as the observed pathway (site fidelity test, Animal Movements 2.0 extension, Hooge et al. 1999) and creating a point at the end of each pathway. I calculated the percent land cover with a moving window analysis at five scales (75 m, 105 m, 250 m, 500 m, and 1000 m) and attached these values to each point. Then, I ranked the observed point relative to the 100 random points to empirically determine the likelihood that observed ending points were derived from random movements. An observed point was considered significantly more forested than random if its percent forest ranked in the top 5% of random points. An observed point was considered significantly less urban than random if its percent urban ranked in the lowest 5% of random points. Finally, I added up the number of birds whose observed points were significantly more forested or less urban than random and calculated the proportion of significant cases per species, scale, and land cover class out of all possible bird (number died)-scale-class combinations.

I used Cox proportional hazards regressions (Cox 1972) to estimate the probability of survival while incorporating censored cases (those for which death did not occur) and relate survival to land cover. This method of survival estimation is robust to limitation in study design and is subject to less bias than other methods (Murray 2006). I ran separate Cox models for each species, age cohort, and spatial scale to maintain independence of covariates. The odds ratio, exp(B) is reported here, which is the predicted change in the hazard per unit increase in the covariate. When exp(B) < 1 the hazard decreases (survival increases) per unit increase in the predictor. When exp(B) > 1 the hazard increases (survival decreases) per unit increase in the predictor. I used the survival functions resulting from Cox models without covariates as estimates of the daily probability of survival per species. I also estimated the proportion of fledglings surviving to independence and standardized it by dividing it by the mean number of days observed per species. I completed the above statistical analyses using SPSS 13.0 software (SPSS 2004).

Post-Fledging Relative Habitat Use and Covariates

I analyzed relative habitat use within the traveled area by calculating resource utilization functions for each bird that dispersed from its natal patch or the location of capture. Resource utilization functions (RUF) quantify the relative use of resources within an area in a spatially explicit way (Marzluff et al. 2004). First, I used fixed-kernel techniques in the Animal Movements 2.0 extension to ArcView (Hooge et al. 1999) to create the utilization distribution (UD) for each bird using a 30 m cell size to match the resolution of my resource grids (Fig. 1.2). Each cell in the traveled area is assigned a 'use' value based on the continuous, probabilistic measure of space use provided by the UD. The home range boundary was defined as the 99% contour of the fixed-kernel because the 100% boundary is not calculated in Animal Movements. I chose to calculate the smoothing factor or bandwidth (H) using least squares cross validation because it is an objective measure that minimizes error in UD estimation (Kernohan et al. 2001). To determine which birds had a sufficient number of point locations to adequately estimate the fixed-kernel home range, I used an incremental analysis (Marzluff et al. 2004). The minimum number of points at which there was no significant correlation between the number of points (sampling effort) and the size of the minimum convex polygon was twelve ($r = 0.09$, $p = 0.44$), which included 63 birds and 16 study sites.

The resources I related to relative habitat use were the land cover and land use variables of interest (Hypotheses 3-4). I used a classified land use grid derived from 2001-2002 parcel data (Alberti et al. 2005). The residential built land use class included single- and multiple-family neighborhoods and the nonresidential built class included commercial, industrial, office, institutional, parking, and transport. I calculated road density as the length (m) of road per 30 m^2 pixel. To estimate the scale of use by each species, I calculated the mean bandwidth (H) value of the birds in my subsample: American Robin: 210 ± 185 m (N = 16), Song Sparrow: 42 ± 51 m (N = 23), Spotted Towhee: 56 ± 55 m (N = 36), and Swainson's Thrush: 170 ± 205 m (N = 7). Because resource use may be influenced by an area larger than the immediate 30 m^2 pixel, I used a moving window analysis in FRAGSTATS 3.3 (McGarigal et al. 2002) to calculate landscape metrics for each land cover and land use class of interest with the moving window size matching the mean H value per species. To determine which landscape metrics were the least redundant for entering into the RUF multiple regression models, I ran correlations of the percent cover, mean patch area, and aggregation index for each land cover (heavy-medium urban, light urban, forest) and land use (residential built, nonresidential built, road density) variable. I chose the metrics with the lowest R values between resource variables estimated by the same metric: these were the percent cover for Song Sparrows and Spotted Towhees and the aggregation index for American Robins and Swainson's Thrushes. Then, I related the resource values to the 'use' for each home range grid cell in the RUFFIT package in R in separate models for land cover and land use because the classes I tested were not mutually exclusive (Marzluff et al. 2004, available at http://www.csde.washington.edu/~handcock/ruf/). The RUFFIT outputs the maximum likelihood estimates (MLE), which are regression coefficients for each resource variable assuming spatial autocorrelation in the error terms. I calculated both standardized and unstandardized coefficients for each bird's traveled area using the bird's H value as the range of spatial dependence (ρ) and 1.5 as the smoothness of the UD surface (θ). The largest 99% use areas (>5000 rows) were too large to process, so 2000 points were randomly sampled 10 times and regression coefficients and standard errors were averaged. I used one-sample t-tests to determine whether any mean beta values significantly differed from zero. Habitat available was the mean value of each metric for each habitat type calculated with the same moving window size as relative habitat use over the traveled area per bird. I averaged the standardized beta coefficients and habitat available per species and age cohort (including zero values) and tested for differences with ANOVAs and *post hoc* LSD tests.

All percentages were arcsine square root transformed to increase normality and equalize variance (Zar 1999). Means are reported plus or minus one standard deviation unless otherwise noted. Because I proposed specific predictions from my hypotheses (Table 1.1), P values are one-tailed except where noted.

Results

Post-Fledging Survival

Mortality was generally low and concentrated during the time of parental dependence. Overall, only 24 of 122 (20%) birds died while being tracked, and mortality was highest for birds that were still dependent on their parents at the time of capture (16/57, 28% of fledglings; 8/65, 12% of juveniles, $X^2_{(1)} = 4.8$, 2-tailed $p = 0.03$, Table 1.2). Eleven of 57 birds in the fledgling cohort (19.3%) did not survive to parental independence. Of those fledglings that did survive to independence, only 3 died within a week after they became independent and 43 survived beyond this time. Fledglings that left their natal forest patch (35/52, 67%) had a significantly higher survival rate than those that stayed in their natal patch (17/52, 33%, $X^2_{(1)} = 9.3$, 2-tailed $p < 0.01$).

Predation was the most common cause of mortality. It was more frequent (18/24 mortalities) than the only other cause of death I observed, exposure 6/24 ($X^2_{(1)} = 6.0$, 2-tailed $p = 0.01$). Both mortalities that occurred in residential yards (2/24, 8%) were due to predation (and belonged to the juvenile cohort), and the remainder of mortalities (22/24, 92%) occurred in forest fragments ($X^2_{(1)} = 16.7$, 2-tailed $p < 0.01$). Of the predation events for which evidence of the predator type was available (12/18, 67%), half of the individuals were preyed on by avian and half by mammalian predators. Fledglings were mainly preyed on by mammals (5/6, 83%) and juveniles were mainly preyed on by birds (5/6, 83%, $X^2_{(3)} = 9.0$, 2-tailed $p = 0.03$). Avian and mammalian predation was evenly distributed overall (6 cases of each predator type).

Mortality rates differed among species. American Robins died the most (13/26, 50%, $X^2_{(3)} = 21.2$, 2-tailed $p < 0.01$, Table 1.2) and had the most cases of predation (10/18, 56%) and exposure (3/6, 50%). In a Cox proportional hazards model, cumulative survival functions covaried with species ($N = 4$, $p = 0.004$, Fig. 1.3). To eliminate the possible confounding effect of differences in transmitter battery lives between species, I truncated survival to the length of the shortest-lived battery (24 days). Under this scenario, species was still a significant covariate ($N = 4$, $p < 0.01$). All further models were conducted separately for each species. Survival and hazard functions could not be calculated for Swainson's Thrushes because that species had only one mortality. For all ages combined, the mean daily survival probability ranged from 0.62 ± 0.19 for American Robins to 0.94 ± 0.01 for Song Sparrows (Table 1.3).

There was no apparent mortality cost associated with high mobility (Hypothesis 1, Fig. 1.4). American Robin fledglings that moved more quickly (exp(B) = 0.97, N = 20, $p = 0.04$) and a longer total distance (exp(B) = 0.99, N = 20, $p < 0.01$) had a higher daily probability of survival (Table 1.4). Spotted Towhee fledglings that moved a longer distance also had a higher daily probability of survival (exp(B) = 0.99, N = 16, $p = 0.02$, Table 1.4). I found no significant relationships between survival and mobility for Song Sparrows, Swainson's Thrushes, Spotted Towhee juveniles, or American Robin juveniles (Table 1.4).

The probability of survival decreased at highly urban sites, increased at highly forested sites, and increased with forest aggregation for two species (Hypothesis 2a, Fig. 1.5). Spotted Towhees' daily probability of survival decreased with increasing percent medium-heavy urban cover (exp(B) = 4.88, N = 46, $p = 0.05$) and increased with forest aggregation (exp(B) = 0.3, N = 46, $p = 0.04$) at the 105 m scale. The independent effects of these two variables cannot be determined because they are correlated at this scale ($r = -0.63$, $p < 0.01$). Song Sparrows' daily probability of survival increased with the percent forest cover at the 4000 m scale (exp(B) < 0.01, N = 35, $p = 0.05$). No other species-scale combinations showed a significant relationship between the daily probability of survival and percent urban or forest land cover (Fig. 1.5).

Few locations where birds were recovered dead had a greater amount of forest and less urban land cover than expected if movements were random (Hypothesis 2b). Of all possible bird-scale combinations, a small number of nonrandom effects were in areas with greater than random percent forest (N = 5, 4.2%), less than random percent heavy-medium urban (N = 3, 2.5%), and less than random percent light urban (N = 2, 1.7%,

Table 1.5). These 10 significant effects represent only 5 of the 24 (20.8%) birds that died, 3 of which were American Robins. Spotted Towhee mortalities were located at random with respect to land cover types, because none of the 8 deaths were in land covers unexpected by random chance (Table 1.5).

Post-Fledging Relative Habitat Use

At a population-wide level, there was little consistency within each species in the use of land cover and land use classes (i.e. "habitat") by birds that dispersed away from their natal territory or place of capture. Mean standardized beta coefficients of birds that dispersed were generally near zero, had large variance, and differed little from each other despite significant differences in the availability of habitat types (Fig. 1.6). The exception to this was for American Robins, who consistently used heavy-medium urban and residential built cover to a greater extent and forest land cover to a lesser extent than expected based on availability (Fig. 1.6a-c). Among land cover classes, American Robins used heavy-medium urban and light urban areas the most and forested areas the least, despite forest being the most common land cover type (Fig. 1.6a-c). Among land use types, Robins used residential built areas to a greater extent than nonresidential built areas and used areas with high road density least, which was proportional to the availability of each class (Fig. 1.6a-c). American Robins used areas with high road density significantly less than expected as fledglings (Fig. 1.6b) and significantly more than expected as juveniles (Fig. 1.6c). American Robin juveniles also had significantly low use of forested areas and high use of residential built areas, which was inversely proportional to the availability of these habitat types (Fig. 1.6c). The high use by Robins of urban habitats was most pronounced in landscapes where urban land cover was least common (correlation of use of residential areas and percent heavy-medium urban = -0.55, N = 15, 2-tailed p = 0.03; correlation of use of nonresidential built areas and percent light urban = -0.73, N = 15, 2-tailed p < 0.01). Among species, Robins had the largest mean traveled area (259 ± 346 ha) with the highest proportion of residential built cover (46 ± 17%) and highest road density (0.48 ± 0.26 m/m^2, Table 1.6). I found support for my hypotheses of use of land cover (3) and land use (4) by this species.

Relative habitat use by Song Sparrows was inconsistent. Among land cover types, Song Sparrows used forested areas the most, followed by heavy-medium urban areas, and used light urban land cover least, which was in proportion to availability, but not significantly consistent among individuals (Fig. 1.6d-f). Song Sparrows had low use of all three land use classes despite a high availability of residential built areas, but 13 of 16 birds did not have any nonresidential built areas or roads available in their traveled areas (Fig. 1.6d-f). Relative habitat use by Song Sparrows of different ages did not vary between land cover and land use classes, but fledglings had the most consistent use of all three land cover types relative to other species (Fig. 1.6e). Use of residential areas by Song Sparrows was highest where this habitat was most rare (r = -0.59, N = 16, 2-tailed p = 0.03). Among species, Sparrows had the smallest mean traveled area (8 ± 14 ha) with the highest proportion of forest cover (51 ± 26%) and the lowest proportions of residential built (26 ± 24%) and nonresidential built cover (0.15 ± 0.42%, Table 1.6). Differences in Song Sparrows' use of land cover and land use types were not statistically significant, thus my predictions are supported for Hypothesis 3 but not for Hypothesis 4.

Spotted Towhees showed the least consistent use of all habitat types relative to other species (Fig. 1.6g). Among land cover types, Spotted Towhees used forest land cover the most, and used light and heavy-medium urban areas least, in proportion to their availability, but differences in use were not significant (Fig. 1.6g). Spotted Towhee fledglings used forested and heavy-medium urban areas to a significantly greater extent than other habitat types (Fig. 1.6h), but use was equal among habitat types for juveniles (Fig. 1.6i). Spotted Towhees used residential built areas to a greater extent than nonresidential built areas and areas with high road density, but 15 of 26 birds did not have any nonresidential built areas or roads available in their traveled areas (Fig. 1.6g). Use of forested areas by Towhees decreased at more urban sites (correlation between use of forest and percent residential built area = -0.46, N = 26, 2-tailed p = 0.02). Among species, Towhees' traveled areas had the highest proportions of heavy-medium urban (23 ± 22%), light urban (28 ± 13%), and nonresidential built cover (5 ± 12%) and the lowest proportion of forest cover (41 ± 22%, Table 1.6). My predictions are supported for Hypothesis 3 but not for Hypothesis 4 because differences in Spotted Towhees' use of land cover and land use types were not statistically significant.

Swainson's Thrushes used forested and residential built areas the most, and these were the two most common habitat types in their traveled areas (Fig. 1.6j, k). They had the most consistent use of forest of all species, but their relative use did not significantly differ from zero (Fig. 1.6j). Use of heavy-medium urban areas was inversely proportional to the availability of roads (r = -0.83, N = 6, p = 0.04). Among species, Thrushes' traveled areas had the lowest proportions of heavy-medium urban (10 ± 11%) and light urban cover (19 ± 8%) and the lowest road density (0.23 ± 0.16 m/m^2, Table

1.6). I predicted greater relative use of forested than urban areas by Swainson's Thrushes (Hypothesis 3) and greater use of residential than nonresidential built areas and areas with high road density (Hypothesis 4), but found no significant differences in use between habitat types.

Discussion

Post-Fledging Survival

Mortality varied in its location (land cover type) and causal agent. Most mortality occurred in forest fragments, not residential yards, which may be due to the fact that most birds that died did so before they were able to leave their natal forest fragment. Most mortality was caused by predators, as has been consistently reported in other studies of juvenile mortality (Anders et al. 1997, Naef-Daenzer et al. 2001, Kershner et al. 2004, Webb et al. 2004, King et al. 2006, Yackel Adams et al. 2006). Predation was likely due equally to avian and mammalian predators. Accipiters were likely avian predators, which I commonly observed in the study area, and which are important predators of juvenile birds (Newton and Marquiss 1982, Anders et al. 1997, Naef-Daenzer et al. 2001, Yackel-Adams et al. 2001, King et al. 2006). American Robins, Song Sparrows, and Spotted Towhees were all prey items at Cooper's Hawk (*Accipiter cooperii*) nests in Washington (Kennedy and Johnson 1986) and represented the three most frequent prey species of Sharp-shinned Hawks (*Accipiter striatus velox*) at sites across North America (Storer 1986). In Oregon, Cooper's Hawks preyed on juvenile American Robins, Song Sparrows, and Spotted Towhees (Reynolds and Meslow 1984). Of the species I observed, American Robins had the highest mortality rate because they were most often preyed on, and were most likely to fledge from the nest early and die from exposure. Early fledging may occur in response to disturbance, intrabrood competition, wind, or partially successful nestling predation (Marzluff 1985). Mammalian predators were most likely small mammals such as Townsend's chipmunks (*Eutamias townsendi*), because bird remains were often found in small underground burrows. Eastern chipmunks (*Tamias striatus*) depredated the majority of juvenile Ovenbirds (*Seiurus aurocapilla*) in a New Hampshire study (King et al. 2006) and were suspected to be the primary predator of Dark-eyed Junco juveniles (*Junco hyemalis*) in Indiana (Wolf et al. 1988). Only one case of mortality was suspected to be caused by a house cat (*Felis catus*), and I believe cat populations may be limited in this area due to predation by coyotes (*Canis latrans*, Quinn 1997). Different predator types targeted different ages of young birds. Fledglings were most often preyed on by mammals, possibly due to their limited mobility and vulnerability while roosting at night, whereas juveniles were most often preyed on by birds. Eastern chipmunks are a common predator of both nestlings and recent fledglings, which may be attributed to the similarity in behavior between these close developmental stages (King et al. 2006).

Most deaths occurred in younger birds before they moved very far. Birds in the fledgling cohort were twice as vulnerable as those in the juvenile cohort, and one fifth of fledglings did not survive to parental independence. I suspect some of the youngest birds I captured had fledged early from the nest, perhaps in response to a predator at the nest (Marzluff 1985). These very young birds are especially vulnerable because they are unable to fly far (feathers still growing) and behave with low vigilance, and insufficient thermoregulation may have lead to the death of some birds over the first night they were tagged (death by exposure). A peak rate of mortality of birds at this age has been observed in a number of other passerine species including the Yellow-eyed Junco (*Junco phaenotus*, Sullivan 1989), Blackbird (*Turdus merula*, Snow 1958, Magrath 1991), Wood Thrush (*Hylocichla mustelina*, Anders et al. 1997), Great and Coal Tits (*Parus major and P. ater*, Naef-Daenzer et al. 2001), White-throated Robin (*Turdus assimilis*, Cohen and Lindell 2004), Eastern Meadowlark (*Sturnella magna*, Kershner et al. 2004), Ovenbird (*Seiurus aurocapilla*, King et al. 2006), and Lark Bunting (*Calamospiza melanocorys*, Yackel Adams et al. 2006).

Most species show greater survival over time from the nesting to the fledgling and juvenile periods. In this same study area, I estimated nestling mortality of all species to be 52%, which is considerably higher than the 20% fledgling mortality I observed (Marzluff et al. In Press). Mortality rates of American Robins were similar between the nestling (55%) and fledgling (52%) periods, but for the other three species mortality was considerably higher during the nestling period (Song Sparrow nestlings = 33.3%, fledglings = 5.7%; Spotted Towhee nestlings = 44.2%, fledglings = 17.4%; Swainson's Thrush nestlings = 40.4%, fledglings = 6.7%; Marzluff et al. In Press). I was only able to measure mortality during the early part of the post-fledging period due to limited transmitter battery lives, so I do not know if mortality changes during the remainder of the juvenile period. I suspect survival increases over time as birds gain experience and familiarity with the landscape, but they may face new challenges over the winter if food is limited or weather is severe (Brittingham and Temple 1988, Sullivan 1989, Rogers et al. 1991, Robinson et al. 2004). This trend is also consistent with the higher rate of mortality in the younger fledgling cohort compared with the older juvenile cohort I observed. Some studies have shown a second peak of mortality within a week after independence when birds first become nutritionally self-sufficient and may begin dispersing (Sullivan 1989, Anders et al. 1997). I did not observe increased mortality during the week following independence.

Overall, I observed relatively high juvenile survival rates of all species relative to other passerines. Most of the survival rates reported in the literature are lower than those I observed, even after differences in mass between species are accounted for (Fig. 1.7). For example, pre-independence survival of Song Sparrows (standardized by number of days observed) was 0.17 in my study, 0.02 in British Columbia (Smith et al. 1982), and 0.04 in Ohio (Nice 1937). This higher survival could reflect the fact that I only observed fledglings from the time of capture or there could be lower levels of predation in my study area. Although American Robins had the highest mortality rate of the species I studied, I do not believe juvenile survival is a limiting factor for this species in my study area because they commonly attempt multiple nests per year, which may compensate for their losses during the nestling and fledgling phases, and their populations have generally benefited from urbanization (Sallabanks and James 1999). Of the only other studies of juvenile survival in urban areas I am aware of, one reported a lower than expected survival rate (9.4% of Sharp-shinned Hawks survived 110 days post-fledging, Roth et al. 2005), and the other reported a higher than expected survival rate (67% of Cooper's Hawks survived 180 days post-fledging), which was attributed to a high abundance of food (concentration of prey, Mannan et al. 2004). Finally, my survival rates could be overestimates because I assumed missing radio signals were survivors I lost track of. It is possible, but in my opinion unlikely (see Methods), that some of these birds were hit by cars and their transmitters were run over and destroyed.

Inconsistent with my prediction (Hypothesis 1), the daily probability of survival increased with mean daily speed and total distance moved for American Robins and Spotted Towhees. The longer a bird lived, the farther it was able to move. When age cohorts were analyzed separately, only fledgling American Robins and Spotted Towhees with high survival had high mobility. I did not observe a mortality cost for birds that were the most mobile, but rather found the highest mortality in the least mobile, youngest birds. There was no mortality cost for dispersing juvenile Great Tits compared with non-dispersing juvenile tits in a Swedish population (Dhondt 1979). Mortality was unrelated to dispersal distance in Spotted Owls (*Strix occidentalis caurina*, Miller et al. 1997).

There is some support for the hypothesis (2a) that birds have higher survival in landscapes with relatively more forest cover and lower survival in landscapes with relatively more urban land cover, but only for two species at two spatial scales. Although all Spotted Towhee mortalities occurred in forest fragments, there appears to be a negative effect of dense urban development in the larger landscape on juvenile survival in forests. Song Sparrows had higher survival where the percent forest was high at the largest scale I examined, but I only observed two mortalities in this species, one of which I suspect was due to a cat in a suburban yard. As predicted, the probability of survival was unrelated to the amount of light urban land cover, but light urban areas contain an interesting urban-forest interface where there may be added benefits (feeders) as well as risks (cats, people). I did not observe death in the urban matrix due to anthropogenic causes such as cars, kids with guns, or glass windows. Based on the locations of the mortalities I observed, forested areas do not appear to provide refuge from predators as I expected, with the possible exception of Song Sparrows. Higher survival of Spotted Towhees in areas of high forest aggregation may indicate a lower risk of mortality while dispersing through areas with fewer gaps between forest fragments. Blue-breasted Fairy Wrens (*Malurus pulcherrimus*) also had lower rates of dispersal mortality in well-connected neighborhoods (forest fragment clusters, Brooker and Brooker 2002).

I found no support for the hypothesis (2b) that land cover types where birds died were unique. This is consistent with the generalized use of habitat I found for all species except American Robins. Of the three robins with significant land cover effects, two died in areas with a greater than random amount of forest, where their susceptibility to predation was greatest.

Post-Fledging Relative Habitat Use

Use of habitat by dispersing juvenile birds was inconsistent between individuals of the same species, except for American Robins. American Robin matched my predictions based on the relative abundance of adults in my study area, which was higher in the urban matrix than in forest fragments (Ch. 2). The high use by robins of urban habitats was most pronounced in landscapes where urban land cover was least common. The use of urban land cover by adults and juveniles may be at least partially driven by the abundance of food (worms) on expanses of grass lawn in residential and nonresidential built areas. The abundance of breeding American Robins in Toronto increased with the area of lawn (Savard and Falls 2001). Juvenile American Robins may be maximizing their survival in urban landscapes by preferentially using open habitats rich in food resources where ambush by predators is difficult (Roth and Lima 2003, Roth et al. 2006). Their tendency to occur in flocks may also reduce the risk of predation (Roth and Lima 2003, Roth et al. 2006). The shift in use to areas with high road density with age probably reflects the selection by adult robins of areas with fewer roads for breeding, which should be adaptive for raising fledglings with limited flight ability while young. As robin juveniles gain experience and agility, they can safely use areas with high road density and reap the benefits of the urban matrix.

Song Sparrows' relative habitat use was similar to that of Spotted Towhees. For both species, the lack of difference in use between habitat types matches the pattern of relative abundance I observed in adults. One exception was the consistent high use of forested areas by Spotted Towhee fledglings, which may indicate preference for this habitat by nesting adults. Juveniles of both species used forest cover more than light urban cover, which may be a response to the ambush hunting strategy used by Accipiter hawks, which capture most of their prey while feeding on the ground near the edge (Roth and Lima 2003, Roth et al. 2006). Song Sparrows used residential areas the most where this habitat was most rare, which may reflect the importance of such areas as food sources (feeders). Low use could result from low availability of a particular habitat type within the traveled area, such as the absence of nonresidential built cover and roads for most Sparrows and Towhees. Likewise, high use could reflect high availability of habitat, as I observed in Towhees relative to forest cover.

Swainson's Thrushes had the highest use of forest cover among the species I observed, but overall relative habitat use by dispersing Swainson's Thrush juveniles was more generalized than that of breeding adults in this urban ecosystem. Their relative use of forest was probably not significantly different from zero because of the high availability of forest in the landscapes they occupied. Swainson's Thrushes used heavy-medium urban areas where roads were least dense, which may reflect a greater danger of collision with cars than with stationary objects. Like Song Sparrows and Spotted Towhees, Swainson's Thrushes were probably safest from predators in the dense cover of forests, which likely also provided the greatest abundance of fruit. Many studies of juvenile resource use show high use of dense vegetation often in early- or mid-successional habitats (Anders et al. 1988, Vega Rivera et al. 1998, Pagen et al. 2000, Lang et al. 2002, Cohen and Lindell 2004, Jones and Bock 2005, White et al. 2005, King et al. 2006, Telería and Pérez-Tris 2007). Dense vegetation is thought to provide the safest refuge from predators, and many small terrestrial passerines use a woody-cover-dependent escape tactic to avoid predation (Lima 1993). Food abundance may also be greater in densely vegetated areas, especially for fruiting species where tree cover is low, and juveniles of some bird species are able to track fruit as it ripens (Vega Rivera et al. 1998, White et al. 2005, Telería and Pérez-Tris 2007). Patterns of juvenile mobility are consistent with food resource use (Ch. 2).

The low consistency in relative habitat use I observed in most species could be an adaptive response by urban-dwelling species. Flexibility in relative habitat use may be adaptive in highly heterogeneous urban landscapes with associated costs and benefits that vary spatially. Food and cover is likely patchily distributed in forest fragments and at bird feeders, which may necessitate such variation in use. This may promote survival in behaviorally flexible species and help explain the low mortality I observed in these species. The persistence of more specialized, behaviorally rigid species may be threatened if they cannot adapt to the heterogeneity of urban landscapes.

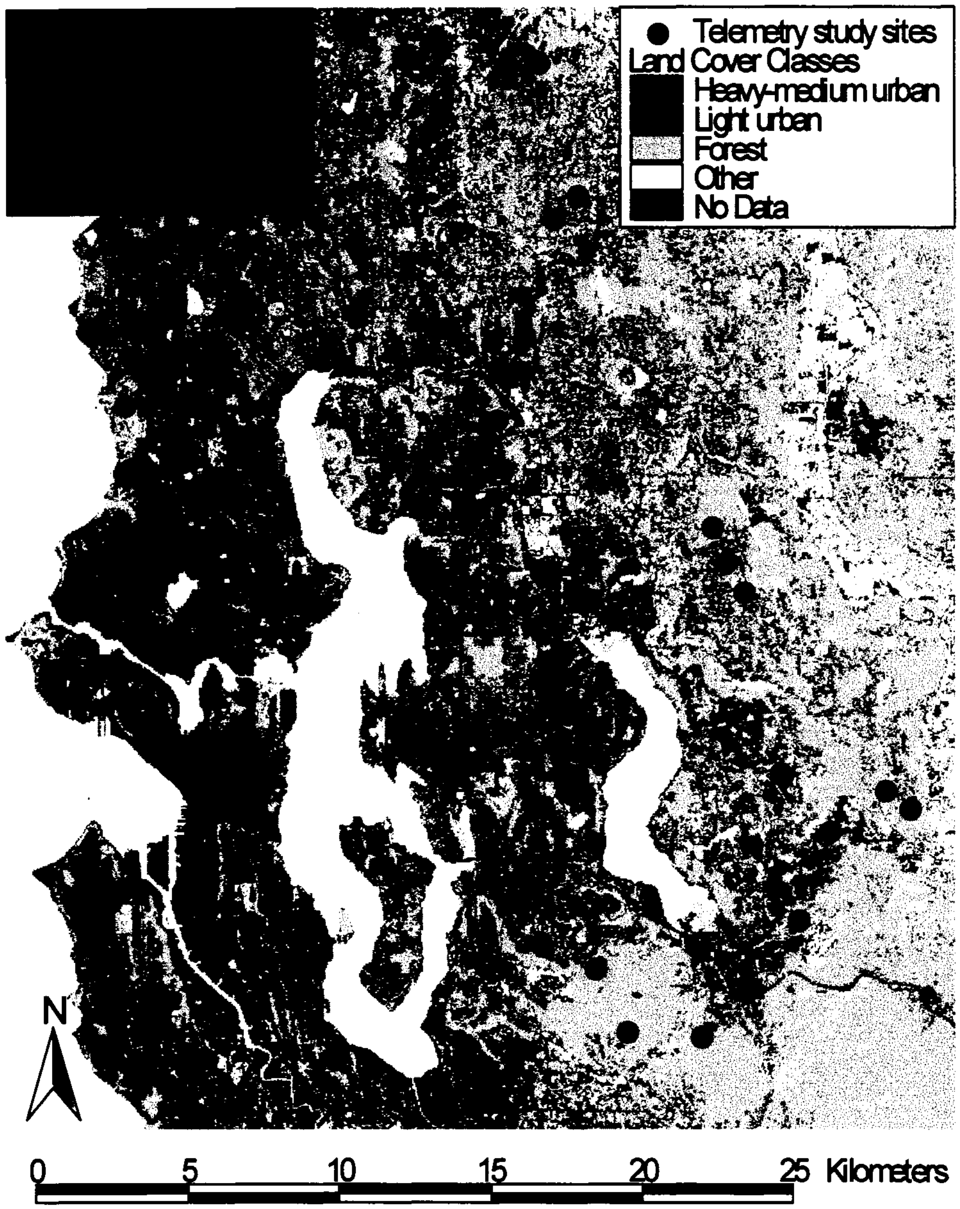


Figure 1.1. The study area included urban, suburban, exurban, and control study sites (black dots) in the Seattle metropolitan area. Land cover classes (from a 2002 LandSat image) are heavy-medium urban (> 50% impervious surface, dark gray), light urban (< 50% impervious surface, medium gray), forest (light gray), and other (white).

Figure 1.2. Movement pathway (black line) of an American Robin juvenile superimposed on its utilization distribution (a) and land cover map (b). Contours of highest use are the lightest color (a).

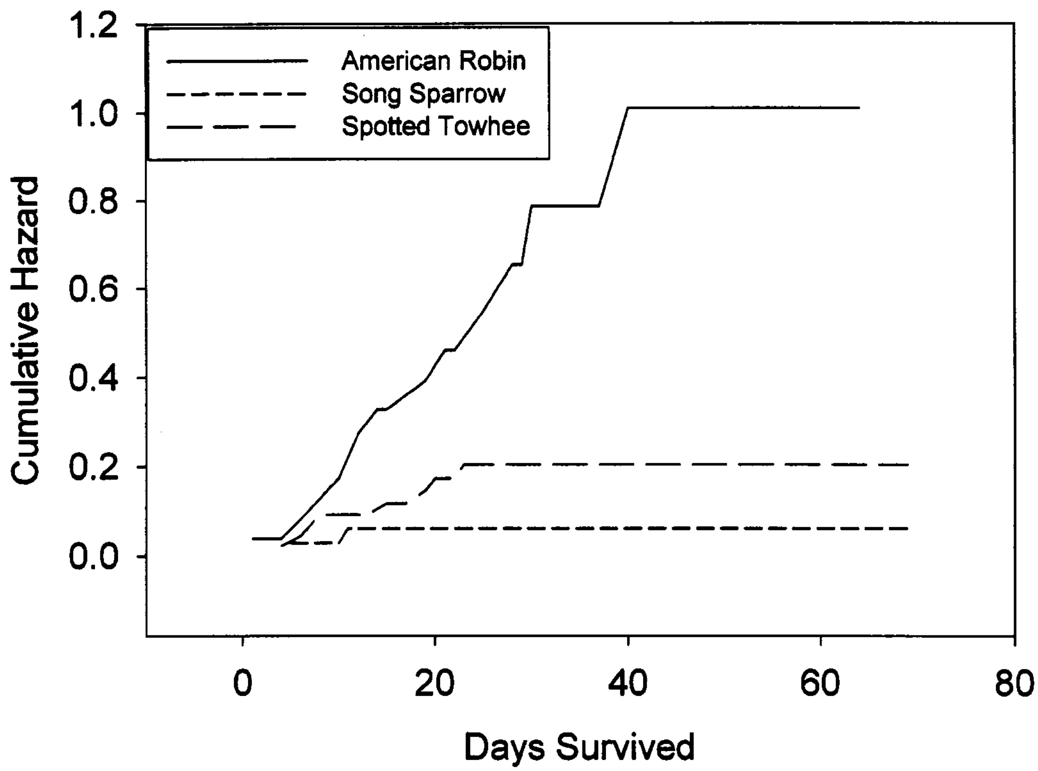


Figure 1.3. Cumulative hazard functions from Cox proportional hazards model for each study species over time (differences between species are independent of differences in transmitter battery lives).

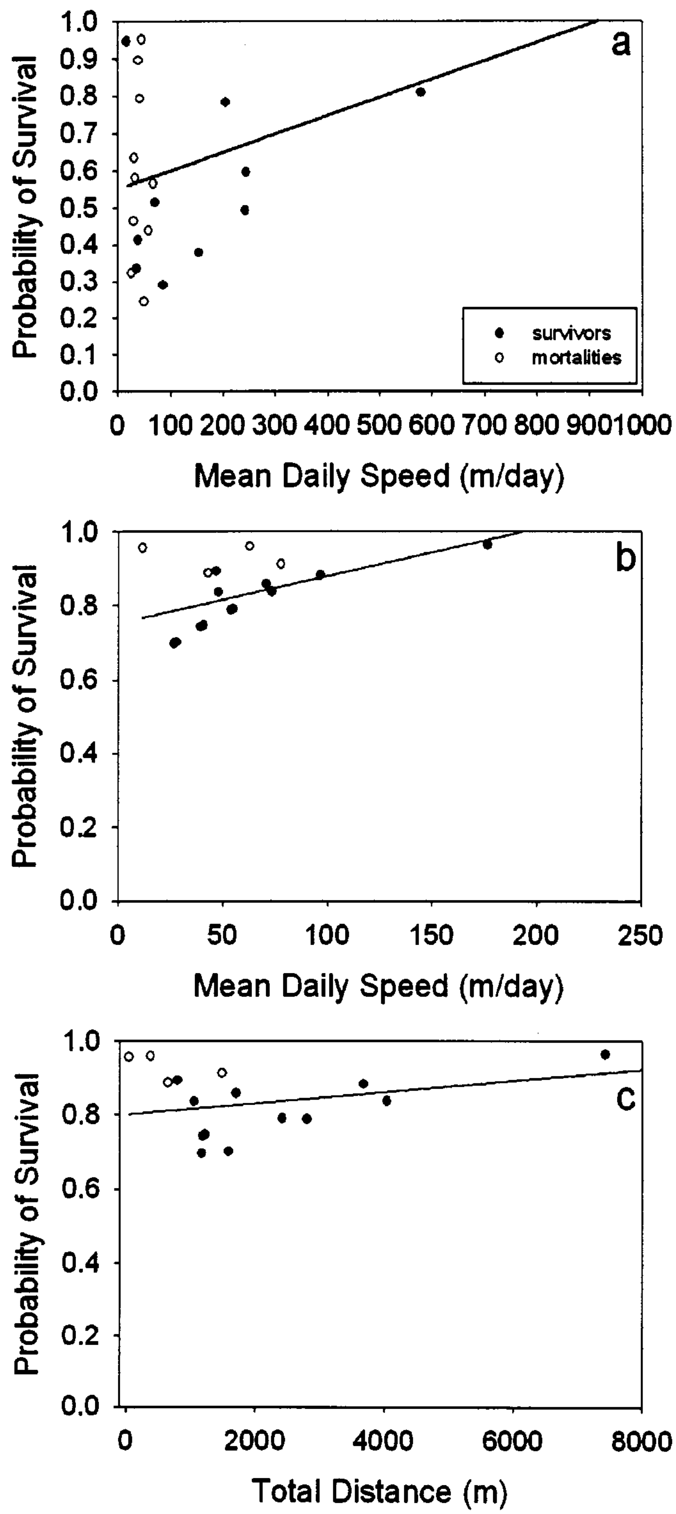


Figure 1.4. The probability of survival increased as mobility increased for American Robin (a) and Spotted Towhee (b,c) fledglings. Open dots are mortalities and closed dots are survivors.

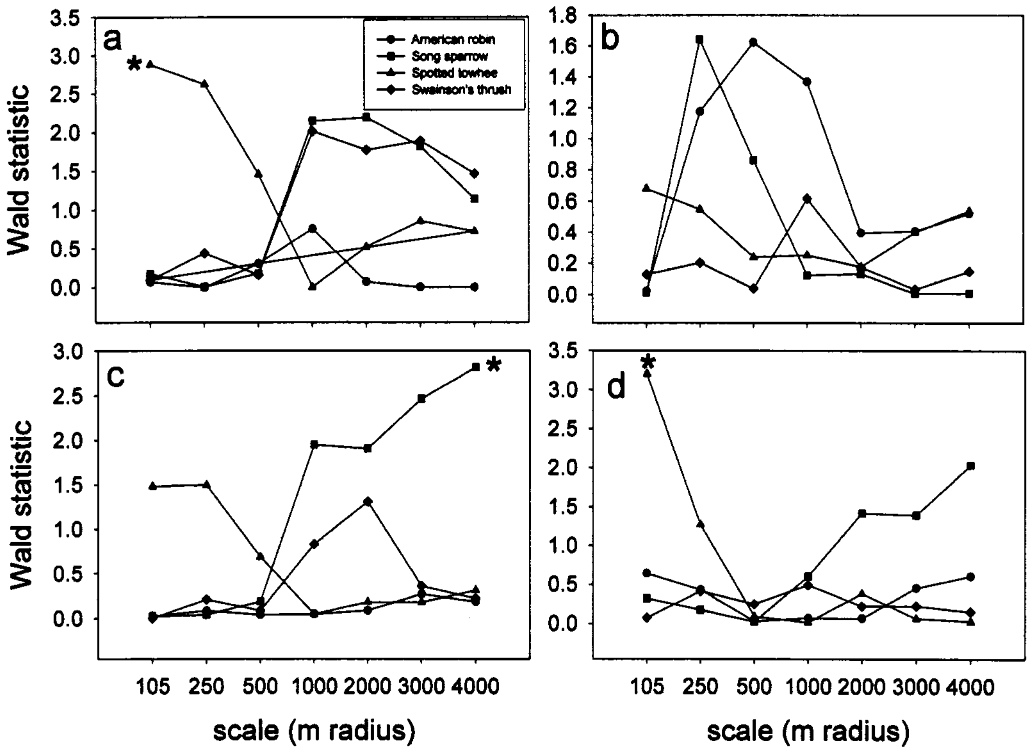


Figure 1.5. Results of Cox proportional hazards models relating the probability of survival to the percent (a) heavy-medium land cover, (b) light urban land cover, (c) forest land cover, and (d) forest aggregation at seven scales. Asterisks indicate significant models ($p < 0.05$; a: negative, c,d: positive).

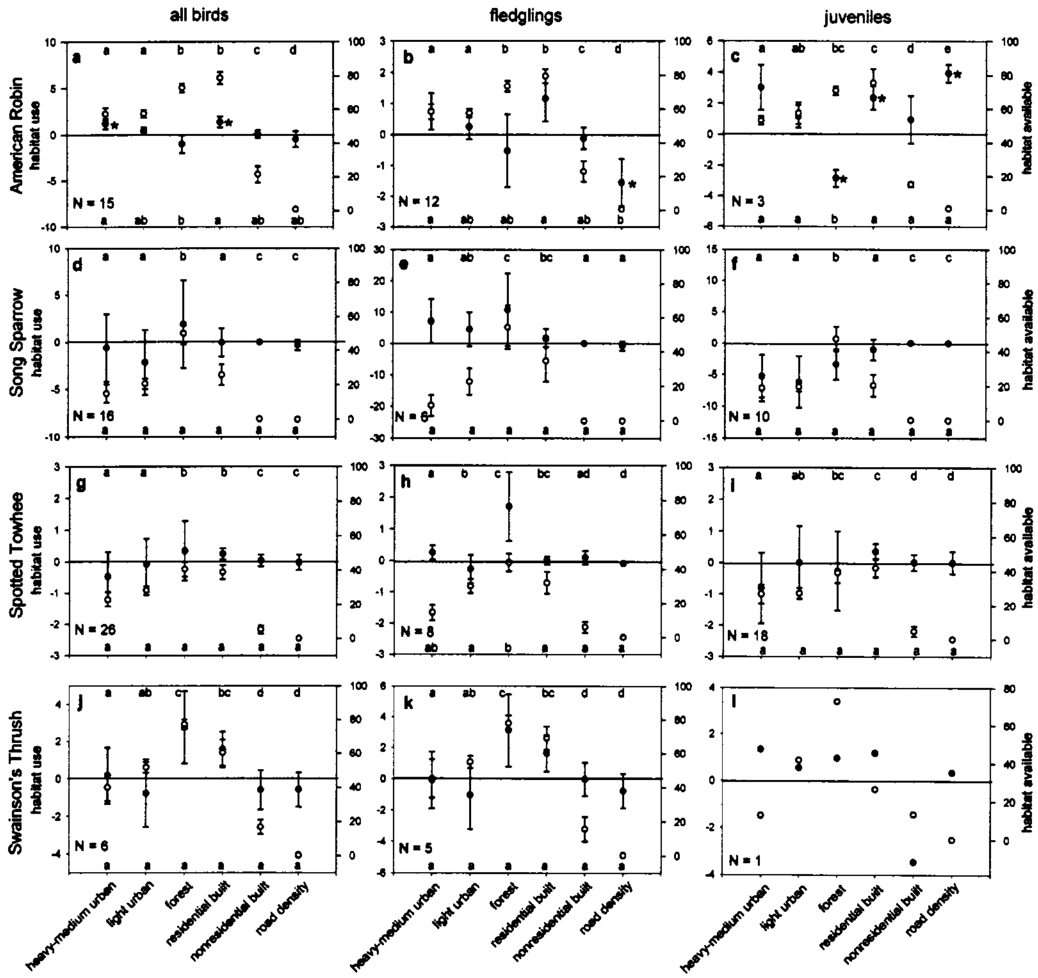


Figure 1.6. Mean standardized beta values from RUF analysis (relative habitat use) and habitat available for birds that dispersed for each land cover and land use type by species and age at capture: (a-c) American Robin, (d-f) Song Sparrow, (g-i) Spotted Towhee, and (j-k) Swainson's Thrush. Metrics of habitat types were the percent cover for Song Sparrows and Spotted Towhees and the aggregation index for American Robins and Swainson's Thrushes. Habitat available (open dots) was the mean value of each metric for each habitat type calculated with the same moving window size as relative habitat use (closed dots). Birds of all ages are included in first column, birds captured as fledglings are in second column, and birds captured as juveniles are in third column. Dots are means with error bars ± 1 SE. Results of LSD post-hoc tests are indicated for habitat available at top of each graph and for relative habitat use at the bottom of each graph. Asterisks indicate mean beta values that were significantly different than zero.

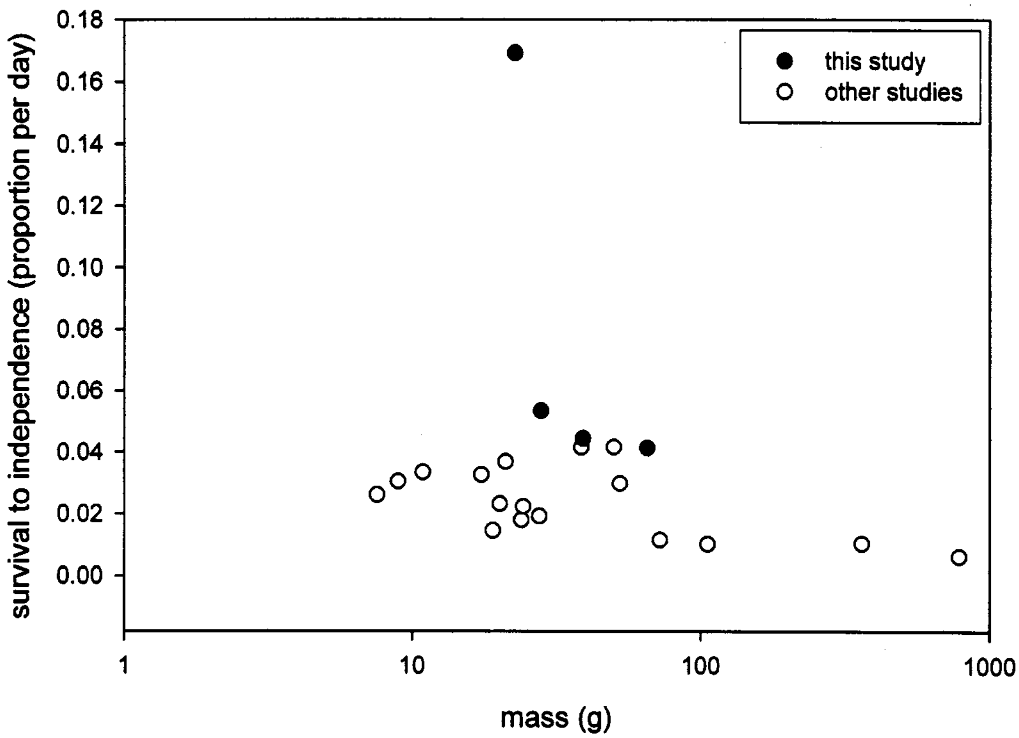


Figure 1.7. The relationship between survival to independence (proportion survived per day) and body size (mass on log scale), illustrating the relatively high survival rates of the species in this study (closed dots) relative to other studies (open dots). When juvenile mass was not available, adult mass was used. When mass estimates were not reported in the same paper as survival estimates, values came from other papers conducted in close geographic proximity. Sources of survival and mass data: Nice 1937, Zimmerman 1965, Smith 1967, Ricklefs 1968, Ricklefs 1975, Nolan 1978, Woolfenden 1978, Post and Greenlaw 1982, Smith et al. 1982, Nolan and Ketterson 1983, Drent 1984, Wolf et al. 1988, Arcese 1989, Sullivan 1989, Marzluff and Balda 1992, Post and Greenlaw 1994, Roth et al. 1996, Vega Rivera et al. 1998, Boarman and Heinrich 1999, Dowling et al. 2003, Kershner et al. 2004, Webb et al. 2004, Withey and Marzluff 2005, Berkeley et al. 2007.

Table 1.1. Hypotheses and predictions.

Hypotheses	Predictions	References
1. There is a mortality cost associated with high mobility. The further a bird disperses, the more hazards it will encounter along its path, and the cost of mortality may outweigh the benefit of dispersing.	The daily probability of survival is negatively related to the mean daily speed and total distance moved.	Dhondt 1979, Miller et al. 1997
2. Survival increases at highly forested sites and decreases at highly urban sites. Forested areas serve as a refuge from predators, whereas urban areas have novel dangers (e.g. cats, cars, kids with guns, glass windows, pollution), and may lack native foods. The risk of death may also increase to the extent that birds have to cross gaps between forest fragments in poorly-connected areas.	a. In landscapes across a range of spatial scales, I predict the probability of survival increases with the percent forest land cover, increases with forest aggregation, is unrelated to the percent light urban land cover, and decreases with the percent heavy-medium urban land cover.	Klem 1989, Brooker and Brooker 2002, Lepczyk et al. 2003
	b. At a local scale, I predict that most mortalities should occur in areas with more urban cover and less forest cover.	Klem 1989, Lepczyk et al. 2003
3. Use of habitat types is proportional to each species level of urban affinity. Breeding bird abundance in forested versus urban parts of the study area should indicate the preferred habitat for dispersing juveniles.	Swainson's Thrushes should use forested areas more than urban areas, American Robins should use urban areas more than forested areas, and Song Sparrows and Spotted Towhees should use forested and urban areas to an equal extent.	Whittaker and Marzluff In Review (Ch. 2)
4. Relative habitat use varies according to the costs and benefits associated with different land use types. Roads are highly dangerous due to the risk of collision. Residential areas contain amenities such as feeders, water sources, and cover. Nonresidential built areas lack these amenities and contain a higher density of dangerous objects (windows, cars).	Relative habitat use should be related negatively to road density. Relative habitat use of residential areas (single- and multiple-family) should be greater than nonresidential built areas (commercial, industrial, office, institutional, parking, transport).	Rusz et al. 1986, Codoner 1995, Mannan et al. 2004

Table 1.2. Proportion of birds by age cohort and fate.

Species	Fledglings Battery died	Radio Recovered	Lost Signal	Died	Juveniles Battery died	Radio Recovered	Lost Signal	Died
American Robin	3	2	5	10	0	0	3	3
Song Sparrow	9	0	1	1	18	1	4	1
Spotted Towhee	9	2	1	4	18	4	4	4
Swainson's Thrush	2	2	5	1	0	1	4	0
All species	23	6	12	16	36	6	15	8

Table 1.3. Daily survival probabilities for each species and age cohort (survival functions resulting from Cox models without covariates). Survival and hazard functions could not be calculated for Swainson's Thrushes because they had only one mortality.

Species	All birds mean	SD	Fledglings mean	SD	Juveniles mean	SD
American Robin	0.623	0.194	0.622	0.197	0.583	0.139
Song Sparrow	0.944	0.009	0.909	0.000	0.957	0.000
Spotted Towhee	0.840	0.044	0.773	0.058	0.873	0.032

Table 1.4. Cox proportional hazards models showed an increase in survival with increasing mobility for American Robin and Spotted Towhee fledglings. When exp(B) < 1 the hazard decreases (probability of survival increases) per unit increase in the predictor. When exp(B) > 1 the hazard increases (probability of survival decreases) per unit increase in the predictor. Bold indicates significance at $p < 0.05$.

		Mean Daily Speed				Total Distance			
Species	age at capture	B	SE	Exp(B)	p	B	SE	Exp(B)	p
American Robin	fledglings	-0.031	0.017	0.970	**0.041**	-0.003	0.001	0.997	**0.006**
	juveniles	-0.002	0.002	0.998	0.201	0.000	0.000	1.000	0.149
Song Sparrow	fledglings	-0.210	0.250	0.811	0.201	-0.008	0.008	0.992	0.184
	juveniles	0.003	0.018	1.003	0.431	-0.001	0.002	0.999	0.348
Spotted Towhee	fledglings	-0.016	0.022	0.984	0.231	-0.005	0.003	0.995	**0.023**
	juveniles	-0.001	0.009	0.999	0.474	-0.001	0.001	0.999	0.066
Swainson's Thrush	fledglings	-0.670	0.801	0.512	0.202	0	0.001	1	0.362
	juveniles								

Table 1.5. Proportion (N) of significant bird-scale-land cover class combinations by species from analysis of percent land cover at observed versus random points for birds that died.

		scale (m)					land cover class			
		75	105	250	500	1000	heavy-medium urban	light urban	forest	subtotal
Species	American Robin	0.026 (1)	0.077 (3)	0 (0)	0 (0)	0.051(2)	0.015 (1)	0.031 (2)	0.046 (3)	0.031 (6)
	Song Sparrow	0 (0)	0 (0)	0 (0)	0 (0)	0.333 (2)	0.1 (1)	0 (0)	0.1 (1)	0.067 (2)
	Spotted Towhee	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	Swainson's Thrush	0 (0)	0 (0)	0 (0)	0.667 (2)	0 (0)	0.2 (1)	0 (0)	0.2 (1)	0.133 (2)
	subtotal	0.014 (1)	0.042 (3)	0 (0)	0.028 (2)	0.056 (4)	0.025 (3)	0.017 (2)	0.042 (5)	0.028 (10)
Land cover class	heavy-medium urban	0 (0)	0 (0)	0 (0)	0.042 (1)	0.083 (2)				
	light urban	0 (0)	0.042 (1)	0 (0)	0 (0)	0.042 (1)				
	forest	0.042 (1)	0.083 (2)	0 (0)	0.042 (1)	0.042 (1)				

Table 1.6. Area used and mean proportion of each land cover and land use class within the traveled area of dispersing juveniles (N = 63).

		American Robin	Song Sparrow	Spotted Towhee	Swainson's Thrush
area traveled (ha)	minimum	1.23	0.52	0.60	0.72
	maximum	1017.16	42.32	337.92	727.03
	mean	258.54	8.48	33.60	209.36
	SD	346.03	13.87	67.99	323.23
heavy-medium urban (%)	mean	15.62	13.93	22.65	10.35
	SD	13.34	20.62	21.62	11.47
light urban (%)	mean	26.86	22.00	28.44	18.83
	SD	8.28	13.17	12.80	7.65
forest (%)	mean	41.09	51.34	40.51	50.83
	SD	11.85	26.45	22.36	17.96
residential built (%)	mean	45.84	25.96	38.59	27.32
	SD	16.84	24.38	21.64	18.17
nonresidential built (%)	mean	2.84	0.15	5.10	3.94
	SD	2.76	0.42	11.90	4.40
road density (m/m^2)	mean	0.48	0.30	0.45	0.23
	SD	0.26	0.29	0.40	0.16

CHAPTER 2.
POST-FLEDGING MOBILITY IN AN URBAN LANDSCAPE

Introduction

Growing human populations are driving land use and land cover change to an unprecedented extent, especially at the urban–wildland interface, or urban fringe, where natural habitats are rapidly being altered and eliminated by human settlement (Marzluff 2001, Theobald 2005). For example, between 1950-2000 the amount of urban and exurban land cover in the coterminous United States increased by four to five times (Brown et al. 2005). This process of urbanization results in a loss and fragmentation of the original native land cover type, which serves as habitat for the native fauna and flora (Collinge 1996, Marzluff and Ewing 2001, Hansen et al. 2005, Robinson et al. 2005). Widespread land conversion is closely associated with changes in important wildlife population processes such as reproduction, survival, and dispersal (Turner 1989, Marzluff 2001, Opdam and Wiens 2002, Lampila et al. 2005) that affect population viability and community diversity (Andrén 1994, McKinney 2002, Hansen et al. 2005, Chace and Walsh 2006). Habitat loss and fragmentation have been recognized as key causes of declining biological diversity worldwide (IUCN 1980, Mönkkönen and Welsh 1994, Fahrig 1999, Czech and Krausman 2001).

Dispersal is an important process that serves many functions, especially in fragmented populations, and population dynamics can be severely disrupted if the rate of dispersal is altered or dispersal is no longer possible due to extreme habitat isolation. For example, dispersal maintains gene flow within and between populations, allows metapopulation survival, and supplements population growth (Levins 1970, Hanski and

Gilpin 1997, Merriam 1991). Dispersal is also a key element in source-sink population models as it contributes to the net gain or loss of individuals through immigration and emigration, respectively, and maintains the existence of sink populations (Pulliam 1988, Pulliam and Danielson 1991). If a species in a given local population is extirpated, the habitat patch may become recolonized by members of the species able to immigrate to the patch (Brown and Kodric-Brown 1977). The viability of forest bird populations after their habitat becomes isolated into separate patches, may hinge on the ability of dispersers to move between habitat remnants. Limitation in dispersal can ultimately lead to extinction in species with few, small populations (Macdonald and Johnson 2001).

Animal movements through fragmented landscapes are affected by both the connectivity of the remaining habitat and the type of matrix that must be traversed. Studies of a number of forest bird species have demonstrated that gaps between forest fragments may or may not be crossable, depending on the size of the gap, the habitat type that must be crossed, and the behavioral preferences of the organism in question (Dunning et al. 1995, Haas 1995, Machtans et al. 1996, Desrochers and Hannon 1997, Rail et al. 1997, St. Clair et al. 1998, Brooker et al. 1999). The landscape matrix serves as a variable filter to interpatch movement depending on the land use or land cover type that must be crossed and the proportion and configuration of original land cover that remains (Trzcinski et al. 1999, Wiens 2001, Castellón and Sieving 2006). For example, a forest bird species may find a rural agricultural area to be more permeable to interpatch movement than a commercial shopping area. Land cover types within an urban landscape mosaic may differ strongly in their permeabilities due to variation in the risk of predation, hazards of novel environments (such as collision with objects), and abundance of food, which may all have especially strong effects during the post-fledging transition from parental care to independence.

The goal of this investigation was to understand how the post-fledging movement process relates to land cover patterns at various spatial scales in a heterogeneous urban landscape. I measured movements of forest songbird species along different parts of an urban gradient during the post-fledging period. During this period, juvenile birds begin the natal dispersal process which is characterized by extensive movement (Greenwood and Harvey 1982). The post-fledging period is disproportionately understudied but deserves more attention as it contributes to bird population stability and persistence (McFadzen and Marzluff 1996).

This study was designed to detect differences between species in perceptions of scale of urban landscapes and the effects of different landscape matrix types on movement patterns. Here I tested the following hypotheses:

1. *Post-fledging mobility is influenced by species' life history strategies.* A species' relative level of mobility in an urban landscape depends on either its migratory strategy (long- or short-distance migrant, resident; Paradis et al. 1998) or its affinity to urban areas (relative abundance, Marzluff 2001). If migratory strategy is most influential, then the mobility of migratory species should be greater than resident species. If urban affinity is most influential, then the mobility of more urban-affiliated species should be greater than less urban-affiliated species.
2. *Birds are more mobile where forest cover is more contiguous.* Dispersal is facilitated where there is less resistance to movement (gaps in habitat). Birds can move farther and faster through landscapes with relatively more contiguous forested habitat

(Dunning et al. 1995, Haas 1995, Desrochers and Hannon 1997, Rail et al. 1997, St. Clair et al. 1998, Brooker et al. 1999).

3. *Birds are more mobile where forest cover is more abundant.* In landscapes with a relatively greater percent of forest cover, birds are able to move with greater speed and distance (Bélisle et al. 2001). Forested land cover should be the most suitable land cover type for the dispersal of post-fledging birds of species that breed in forests.
4. *Birds are less mobile where urban cover is more abundant.* Urban land cover acts as a barrier to bird movement in proportion to its imperviousness (extent paved or built), resulting in relatively lower mobility in highly urban landscapes (Marzluff 2001). The more built an area, the more likely a bird is to encounter dangerous novel objects (cars, windows), novel predators (cats), inhospitable abiotic conditions (water, air, soil, and noise pollution), and disturbance from human activities.
5. *The probability of dispersal from the natal forest fragment is related to local factors such as food availability or territory density.* Dispersal is positively density-dependent due to competition with conspecifics for resources (Matthysen 2005) and negatively dependent on the level of food available in the natal fragment (Arcese 1989, Ims and Hjermann 2001).

Methods

Study Sites and Species

I measured the post-fledging movement patterns of juvenile birds using radio telemetry at sites across the urban gradient of the Seattle, Washington, USA, metropolitan area over a three-year period (2003-2005). I selected 19 forest fragments within a matrix of urban, suburban, exurban, and control (undeveloped forest) landscapes (Marzluff et al. 2001b, Fig. 1.1). Sites were chosen using a stratified random sample of three landscape metrics calculated for a 1 km^2 area containing each study site: mean patch size, contagion, and the percent forest and percent urban land cover (see Donnelly and Marzluff 2004, 2006, Blewett and Marzluff 2005 for details). Forest fragments were primarily coniferous, including western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and western redcedar (*Thuja plicata*), or mixed with deciduous tree species such as red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*) and Oregon ash (*Fraxinus latifolia*, Franklin and Dyrness 1988). Site elevation varied from sea level to 300 m on the lower slopes of the Cascade Range.

The four study species are all native songbirds that breed in forests: American Robin (*Turdus migratorius*), Swainson's Thrush (*Catharus ustulatus*), Spotted Towhee (*Pipilo maculatus*), and Song Sparrow (*Melospiza melodia*). Swainson's thrushes are long-distance neotropical migrants, American Robins are short-distance migrants, and Spotted Towhees and Song Sparrows are year-round residents in this region. To assess their sensitivity to urban land cover (Hypothesis 1), I determined each species' level of urban affinity from relative abundance estimates from point count survey data at all 19 study sites (for methods see Donnelly and Marzluff 2006). I calculated the relative abundance of a given species at a given site as the number of birds per survey point per visit per year from data spanning 1998-2005 and tested for differences between species with analysis of variance and *post hoc* LSD tests. At forested survey points species abundance varied ($F_{3,64} = 10.13$, $p < 0.01$), with American Robins equal to Song

Sparrows and Spotted Towhees, all of which had greater abundance than Swainson's Thrushes (LSD test, all $p < 0.01$, Table 2.1). At urban matrix survey points abundance also varied between species ($F_{3,52} = 33.95$, $p < 0.01$), with American Robins more abundant than Song Sparrows, which were equal to Spotted Towhees, and all were more abundant than Swainson's Thrushes (LSD test, all $p < 0.01$, Table 2.1). In paired-t tests of the relative abundance between point types for each species, American Robins were more abundant at matrix than forest points ($t = -4.0$, $p < 0.01$) and Swainson's Thrushes were more abundant at forest than matrix points ($t = 2.42$, $p = 0.03$), whereas Song Sparrows and Spotted Towhees were equally abundant in both areas, though slightly more abundant in forests (Table 2.1). I used this information to rank American Robins as the most urban-affiliated species followed by less, but equally urban Song Sparrows and Spotted Towhees. Swainson's Thrushes were the least urban-affiliated species.

Post-Fledging Movements and Covariates

I radio-tagged 122 recently fledged birds (age 1–~20 days after fledging) and recorded their daily movements until death or transmitter battery expiration. Each transmitter was fixed with an elastic thread leg harness (Rappole and Tipton 1991) that was designed to break and fall off the bird after my observations ended. The battery life of radios was proportional to the maximum weight each species could safely carry (<= 3% of body weight, model BD-2, Holohil Systems Ltd., Carp, Ontario, Canada) and was approximately 3 weeks for Song Sparrows, 6 weeks for Swainson's Thrushes, 8 weeks for Spotted Towhees, and 9 weeks for American Robins.

Fledglings were captured either in a hand net shortly after leaving the nest or in mist nets if older, including no more than one young per brood to increase independence of samples. Attempts were made to catch fledglings on their natal territories (where they were born) while still dependent on their parents, but I also caught older juvenile birds which were behaviorally independent at locations unknown relative to their natal territories. I determined age at capture for each bird based on behavior (begging from adults) and movement patterns (stationary within fragment or actively moving) and classified young birds still dependent on their parents as "fledglings" (N = 57) and older behaviorally independent birds as "juveniles" (N = 65). Movement pathways of fledglings typically included parts of the periods both before and after parental independence. I analyzed the two age cohorts separately because I viewed them as two somewhat distinct behavioral periods in which birds may respond differently to the same land cover patterns, and combining the two cohorts may confound or obscure any meaningful relationships unique to one cohort or the other.

I attempted to relocate each bird daily with an R-1000 telemetry receiver (Communications Specialists, Inc., Orange, CA) and a handheld Yagi antenna. I recorded each location (UTM) using a handheld GPS unit (Garmin 12XL, Olathe, KS) with an accuracy of <10 m estimated position error (GPS EPE). Observers avoided approaching each bird too closely so as to prevent influencing its movement. I recorded only one location per bird per day unless the bird was actively moving while I was tracking it (single movement of >100 m) to allow me to maximize the number of samples rather than follow each bird for an extended period of time (Otis and White 1999). When the bird could not be seen, its position was estimated using triangulation. If the signal did not move from the same location for several days, then the bird was detected visually to ensure it was still alive. In all cases of mortality, the radio was recovered with any evidence of death (e.g. carcass or feathers). If the signal was absent from the same area as the previous day, then the immediate area around the previously known location was searched in an increasingly larger radius using both a handheld yagi antenna on foot and a roof-mounted omnidirectional antenna while driving. Searching for an absent signal ceased after the date the expected battery life of the transmitter had passed.

I calculated several metrics of mobility from locations plotted in ArcView GIS 3.3 (ESRI, Redlands, CA). Mean daily speed (m/day) and total distance moved (m) were calculated using the Animal Movements 2.0 extension (Hooge et al. 1999). Mean daily speed is a measure of mobility that is comparable between individuals and species (corrects for differences between species in transmitter battery lives). Total distance is a sum of the total length of all daily movements combined and is suitable for comparisons of individuals within the same species with roughly the same transmitter battery lives. To estimate the total distance displaced, I created a 'displacement' metric that equals the hypotenuse of the triangle made by the differences between the maximum and minimum X and Y coordinate locations for each individual. I also conducted a site fidelity test for each bird to assess whether their movement pathway was random, more dispersed than random, or more constrained than random pathways (Animal Movements 2.0 extension, Hooge et al. 1999). This test compares the observed movement pattern with 100 random walks using a Monte Carlo simulation and parameters from the original data.

To estimate dispersal probability, I classified each bird as a 'disperser' (left the capture site and did not return) or a 'local' (stayed at or returned to the capture site) during each bird's transmitter battery life (as late as mid-September). Only birds that survived until the battery expired or died after parental independence were included in this analysis. I did not include birds that died early (before independence), whose transmitters fell off before the battery died and they could leave the site, or whose fate was unknown (signal lost without leaving the site). Not all sites had sufficient replications of each species for a full analysis, so relationships within each species were limited to a subset of sites. At this subset of sites, the dispersal probability per site ranged from 0-1.0 ($N = 8$, mean ± SD = 0.53 ± 0.32) for Song Sparrows, 0.2-1.0 ($N = 7$, mean ± SD = 0.58 ± 0.29) for Spotted Towhees, and 1.0 ($N = 2$, mean ± SD = 1.0 ± 0) for Swainson's Thrushes. The probability of dispersal pooled for all species varied from 0-1.0 ($N = 19$, mean ± SD = 0.76 ± 0.3).

Territory density was calculated for each site from spot-mapping data from 2005 as the number of territories within a designated polygon (for spot-mapping methods see Marzluff et al. In Press). Spot-mapping is not an appropriate technique for estimating American Robins' territory density due to bias in observations of non-territorial behaviors at communal foraging grounds, so this species is excluded from this analysis. Territory density per site (territories per ha) ranged from 0.1-4.4 (mean ± SD = 1.6 ± 1.1) for Song Sparrows, 0.3-4.1 (1.2 ± 0.8) for Spotted Towhees, and 0-1.7 (0.6 ± 0.4) for Swainson's Thrushes. I used a combined territory density of all three species for comparison with the pooled dispersal probability estimate. Territory density for all species combined ranged from 0.87-7.29 territories per ha (3.4 ±1.6).

I estimated food availability from the percent shrub cover at two vegetation survey points within each study site (calculated from the most recent year of available data). A shrub was defined as anything < 13 cm diameter at breast height and woody in nature. Percent cover of shrub canopy (from above) was estimated within an 8 m radius circle around each survey point (see Donnelly and Marzluff 2006 for details). A total of 44 shrub and sapling species were observed at forest survey points included in this analysis. The most common species (in decreasing order of abundance) were salmonberry (*Rubus spectabilis*), red elderberry (*Sambucus racemosa*), vine maple (*Acer circinatum*), red huckleberry (*Vaccinium parvifolium secunda*), trailing blackberry (*Rubus ursinus*), salal (*Gaultheria shallon*), indian plum (*Oemleria cerasiformis*), and Oregon grape (*Mahonia aquifolium*), all of which bear fruit. Percent shrub cover varied from 12.5-90% (mean ± SD = 0.48 ± 0.25) per site.

Land Cover Analyses

A 2002 Landsat TM satellite image with 30 m resolution was classified into 12 land cover classes (J. Hepinstall et al., In Press a), of which three are examined to test my hypotheses: medium-heavy urban (>50% impervious surface, includes pavement, buildings, and lawns), light urban (<50% impervious), and forest (deciduous, coniferous, and mixed). I calculated landscape metrics with the program FRAGSTATS 3.3 (McGarigal et al. 2002) for various buffer sizes around the center of each study site to test for differences in landscape extent on movement patterns (105 m, 250 m, 500 m, 1000 m, 2000 m, 3000 m, and 4000 m, Table 2.2). Buffer sizes were determined from the maximum distance moved by each species and extend in a radius around the mean of the UTM coordinates of the capture locations of all birds at each site. The smallest scale was set at 105 m because it encompasses the land cover area of three full pixels in radius surrounding the central pixel (30 m resolution grid), it was the minimum size at which the aggregation index (below) was estimated consistently at each site, and corresponds with an area roughly equal to that of my smallest study sites (3.5 ha). I calculated the percent cover (the percent of pixels in the landscape of the focal land cover class) for each land cover class and the aggregation index (the frequency with which different pairs of patch types appear side-by-side on the map, taking into account only the like adjacencies involving the focal land cover class) for the forest land cover class. All landscape metrics varied among study sites and spatial scales of analysis (Table 2.1, Fig. 2.1).

Statistical Analyses

I tested for differences between species in post-fledging mobility with one-way ANOVAs and *post hoc* LSD tests. I log transformed mean daily speed, total distance, and displacement due to unequal variances (Zar 1999). Relationships between land cover and movement variables for each species and age cohort were assessed with Pearson correlations run separately at each of the seven site scales. Percent forest, percent urban, forest aggregation, dispersal probability, and percent native shrub cover were arcsine square root transformed to meet assumptions of normality and equal variances (Zar 1999). Pearson correlations were also used to relate dispersal probability to territory density and percent native shrub cover. Means are reported plus or minus one standard deviation. The significance level (alpha) was 0.05. P values are 2-tailed for the test of the hypothesis without *a priori* predicted direction (Hypotheses 1) and one-tailed for tests of hypotheses with *a priori* predicted directions (Hypotheses 2-5). I completed all statistical analyses using SPSS 13.0 software (SPSS 2004).

Results

Post-fledging mobility varied between species, which may reflect differences in species' life history strategies (Hypothesis 1). Mean daily speed ($F_{3,118} = 5.86$, $p < 0.01$, Fig. 2.2a) and the net distance displaced differed among species ($F_{3,118} = 5.84$, $p < 0.01$, Fig. 2.2c). All species moved with greater speed and displaced significantly farther than Song Sparrows (LSD tests, all $p < 0.03$, Fig. 2.2a,e). American Robins and Swainson's thrushes showed greater variability in all mobility metrics than Song Sparrows and Spotted Towhees (Fig. 2.2a,c,e). I found an allometric affect on mobility for mean daily speed ($R = 0.4$, $N = 106$, $p < 0.01$), total distance ($R = 0.35$, $N = 106$, $p < 0.01$), and displacement ($R = 0.36$, $N = 104$, $p < 0.01$) measured from log-log power functions of all species (Peters 1983). Using standardized residuals of the log of each mobility metric and log mass, many of the species differences were eliminated. The mean daily speed (Fig. 2.2b) and displacement (Fig.2.2f) of Swainson's Thrushes relative to their body size was significantly greater than all other species, but total distance was equal for all four species (Fig. 2.2d). A test of site fidelity revealed predominantly random movement by American Robins (80%) and Swainson's Thrushes (77%) and primarily constrained movement by Song Sparrows (49%) and Spotted Towhees (59%, Table 2.3).

Some birds were more mobile where forest cover was more contiguous (Hypothesis 2). American Robin juveniles showed a higher speed of movement at sites where forest cover was more aggregated at the 250 m (adj. $R^2 = 0.45$, $N = 6$, $p = 0.04$, Fig. 2.3a, 2.4a) and 500 m scales of analysis (adj. $R^2 = 0.91$, $N = 6$, $p < 0.01$, Fig. 2.4a). American Robin juveniles also showed a greater distance moved at sites where forest cover is more aggregated at the 250 m (adj. $R^2 = 0.69$, N = 6, p = 0.01, Fig. 2.4b) and 500 m scales of analysis (adj. $R^2 = 0.82$, N = 6, p < 0.01, Fig. 2.4b). Forest aggregation does not appear to be factor influencing fledgling movements for any other species-age cohort combination at any of the scales measured (Fig. 2.4a,b).

Some birds were more mobile where forest cover was more abundant (Hypothesis 3). American Robin juveniles moved more rapidly at sites with greater percent forest at the 105 m (adj. $R^2 = 0.61$, N = 6, p = 0.02, Fig. 2.4c), 250 m (adj. $R^2 = 0.67$, N = 6, p = 0.02, Fig. 2.3b, 2.4c), and 500 m scales (adj. $R^2 = 0.91$, N = 6, p < 0.01, Fig. 2.4c). They also moved a greater total distance in sites with greater forest cover measured at the 105 m (adj. $R^2 = 0.72$, N = 6, p = 0.01, Fig. 2.4d), 250 m (adj. $R^2 = 0.82$, N = 6, p < 0.01, Fig. 2.4d), and 500 m scales (adj. $R^2 = 0.82$, N = 6, p < 0.01, Fig. 2.4d). Mobility was unrelated to the percent forest cover for any other species or American Robin fledglings (Fig. 2.4c,d).

Some post-fledging birds were less mobile where urban cover was more abundant (Hypothesis 4). The strongest negative effects of heavy-medium urban land cover were shown by Swainson's Thrush juveniles and American Robin juveniles (Fig. 2.4e,f). Swainson's Thrush fledglings' and Song Sparrow juveniles' mobility was also reduced at sites with high percent heavy-medium urban cover, but to a lesser extent. No other species-age cohort combinations showed a significant relationship between mobility and the percent of heavy-medium urban land cover at any scale (Fig. 2.4e,f). The strongest negative effect to light urban land cover was shown by American Robin juveniles (Fig. 2.4g,h) and weaker effects were shown for the fledgling cohort of Song Sparrows, Spotted Towhees, and American Robins. No significant relationships were found between mean daily speed and percent light urban cover for Spotted Towhee juveniles or Swainson's Thrush fledglings or juveniles (Fig. 2.4g). The total distance moved was unrelated to the percent light urban cover for American Robin fledglings, Song Sparrow fledglings, Spotted Towhee juveniles, or Swainson's Thrush fledglings or juveniles (Fig. 2.4h).

A number of birds showed the opposite trend as predicted and had higher mobility at sites with abundant light urban land cover (Hypothesis 4). Song Sparrow juveniles' mobility showed the strongest positive effects at larger spatial scales (Fig. 2.4g,h). American Robin fledglings and juveniles showed a weaker positive response to light urban land cover (Fig. 2.4g,h). I fail to reject the null hypothesis of no effect for all of the above cases due to my one-tailed prediction.

Dispersal probability per site was unrelated to measured environmental variables in the natal patch (Hypothesis 5). I was able to assess these relationships for each species at a subset of sites (where I followed at least 2 birds of a species each). Dispersal probability was not related to percent shrub cover for Song Sparrows (adj. $R^2 = -0.01$, $N = 8$, $p = 0.18$, Fig. 2.5a), Spotted Towhees (adj. $R^2 = 0.15$, $N = 7$, $p = 0.11$, Fig. 2.5c), or Swainson's Thrushes ($N = 2$, statistics not computable, Fig. 2.5e). Dispersal probability was also unrelated to territory density for Song Sparrows (adj. $R^2 = -0.08$, $N = 8$, $p = 0.25$, Fig. 2.5b), Spotted Towhees (adj. $R^2 = 0.01$, $N = 7$, $p = 0.17$, Fig. 2.5d), and Swainson's Thrushes ($N = 2$, statistics not computable, Fig. 2.5f). Song Sparrows (7/35 birds = 20%) and Spotted Towhees (27/46 birds = 59%), were frequently observed at feeders. Of these birds, Song Sparrows spent an average of 19.9 (±12.9)% of the total days tracked at feeders (range: 1-25 days), and Spotted Towhees spent an average of 15.2

(±9.6)% of the total days tracked at feeders (range: 1-17 days). Feeder use was probably underestimated due to limited visibility or access to private yards. In contrast, American Robins and Swainson's Thrushes moved widely to ephemeral food sources (fruiting trees and shrubs, invertebrate concentrations, pers. obs.).

Discussion

Post-fledging mobility appeared to be influenced by species' migratory strategies more than their level of urban affinity (Hypothesis 1). If migratory strategy is most influential, then the mobility of migratory species should be greater than resident species (Swainson's Thrush > American Robin > Spottee Towhee = Song Sparrow). If urban affinity is most influential, then the mobility of more urban-affiliated species should be greater than less urban-affiliated species (American Robin > Spotted Towhee = Song Sparrow > Swainson's Thrush). The observed relative mean daily speed among species (American Robin = Swainson's Thrush = Spotted Towhee > Song Sparrow, Fig. 2.2a) changed when mobility was corrected for body size (Swainson's Thrush > American Robin = Spotted Towhee = Song Sparrow, Fig. 2.2b). This suggests that migratory ability influenced juvenile mobility more than urban affinity. In a study of 75 terrestrial bird species in Great Britain, Paradis et al. (1998) found a positive allometric relationship between body size and natal and breeding dispersal distances, which eliminated most effects of dispersal distance with various life history traits. They also found that migratory species dispersed farther than resident species regardless of body size (Paradis et al. 1998). The two resident species I studied (Spotted Towhees and Song Sparrows) were the least mobile, have a moderate level of urban affinity, and showed much less variability in all measures of mobility than American Robins and Swainson's Thrushes. I may have observed the beginning of the migratory period for a few Swainson's Thrushes who made relatively large southward movements before disappearing from the study area, but this occurred infrequently and should not have confounded my estimates of mobility.

In addition to the effect of migratory guild, I suspect these species differences in post-fledging movements may also be driven by variation in foraging requirements. Song Sparrows and Spotted Towhees commonly used bird feeders in residential yards, whereas American Robins and Swainson's Thrushes often moved more widely to ephemeral food sources (fruiting trees and shrubs, invertebrate concentrations, pers. obs.). Consistent with these observations, American Robins and Swainson's Thrushes exhibited predominantly random movement pathways and Song Sparrows and Spotted Towhees exhibited primarily constrained movement pathways (Table 2.3). I observed a mixture of fast, linear movements and slow, pulsed movements, which I suspect may have been driven by differences in food resource availability across the landscape. Sallabanks and James (1999) reported that in autumn and winter American Robin juveniles and adults track sources of berries in large flocks. White et al. (2005) found that habitat use of juvenile Swainson's Thrushes in central coastal California was best predicted by fruit abundance variables. Habitat use by juvenile Wood Thrushes (*Hylocichla mustelina*) in the Virginia Piedmont was best described by the optimal foraging hypothesis (Vega Rivera et al. 1998). The movement patterns of juvenile Eastern Meadowlarks (*Sturnella magna*) also seemed to be driven by immediate needs for food resources (Kershner et al. 2004). I suggest that life history differences between frugivores and granivores influence the extent of movement during the post-fledging period, relative to the spatial pattern of food resources in the urban matrix. Grains provided at feeders were an important driver of spatial food patterns in my study area, suggesting one factor important to birds that is unique to human-dominated landscapes.

Post-fledging mobility varied with all land cover patterns examined, but species and age cohorts showed considerable differences in the landscape metrics and scales at which their movements responded. Movements of the juvenile age cohort were far more sensitive to land cover patterns than the fledgling cohort with three times as many significant effects, but this is to be expected due to the criteria for group definition (pre- versus post-parental independence at the time of capture). The movement patterns of American Robins showed more significant effects than all other species combined and the strongest effects overall (all $p <= 0.01$). I found significant effects for land cover patterns at all scales considered, but the most consistently important scales were at 250-500 m radii around study sites (Fig. 2.4). American Robins showed strong support for the hypotheses (2-3) that forest contiguity and abundance enhanced their mobility at small scales (105-500 m), but post-fledging birds showed a more widespread response in their mobility to urban than to forest land cover patterns (more than twice the number of significant effects). This offers support for the hypothesis (4) that abundant heavy-medium urban land cover may inhibit bird movement for some species at some spatial scales (for American Robins at medium scales and for Song Sparrows and Swainson's Thrushes at medium-high scales). Other studies have demonstrated reduced dispersal ability of birds in response to habitat gaps or in landscapes with very low amounts of habitat remaining such as agricultural areas (Haas 1995, Brooker et al. 1999, Martin et al.

2006) or forest clearcuts (Dunning et al. 1995, Machtans et al. 1996, Desrochers and Hannon 1997, Rail et al. 1997, St. Clair et al. 1998, Castellón and Sieving 2006), but this is the first study to my knowledge to measure the effects of urban landscape patterns on bird dispersal.

In contrast with heavy-medium urban, the light urban land cover class appeared to enhance movement in some cases and inhibit it in others (Fig. 2.4g,h), which offers support for the hypothesis (4) that urban land cover acts as a barrier to bird movement in proportion to its imperviousness. For example, at large scales, American Robin fledglings and juveniles and Song Sparrow juveniles were more mobile where light urban land cover was abundant. In contrast, American Robin juveniles were less mobile (at small scales) and Song Sparrow juveniles and Spotted Towhee fledglings were less mobile (at large scales) where light urban land cover was abundant. The light urban land cover class (< 50% impervious surface) characterizes the ecotone between forest fragments and residential yards (where supplemental food is often found). I suspect that abundant light urban land cover may lead to low mobility if bird feeders or fruiting trees and shrubs are common or high mobility if light urban land cover is safer from predation than forest cover. This is consistent with my observations of feeder use by juveniles in residential yards and observations of the locations of depredation. Only 8% (N = 2/24) of depredation events occurred in residential yards, and the remaining 92% (N = 22/24) of depredations occurred in forest fragments (Ch. 1).

Efforts made by home owners to attract birds to their yards did not go unnoticed by the juvenile birds I followed. Yards offering feeders commonly also contained water sources (birdbaths, ponds) and native landscaping, all of which were used by birds, including American Robins. It seems that the greater the diversity of resources provided in yards, the greater the diversity of bird species that can be attracted. By providing bird feeders, planting more fruiting trees and shrubs, and reducing imperviousness in their yards, home owners may be able to shift more of the matrix into light urban land cover and ameliorate some of the negative effects of heavy-medium urban land cover on juvenile mobility. According to my observations, the benefits of bird feeders to young birds of consistent, supplemental food resources seem to outweigh the costs such as depredation or disease transmission. Full investigation of the effects of feeders requires understanding how they affect survival of juveniles over the winter and later as adults.

Post-fledging mobility appears to be more sensitive to the amount of forest land cover than to its spatial pattern of occurrence (Fig. 2.4a-d). Similar results were found in a study of bird communities conducted at the same sites as this study, in that habitat quantity and structure (percent land cover) were stronger predictors of species presence or absence than were habitat pattern variables (patch size and aggregation, Alberti and Marzluff 2004, Donnelly and Marzluff 2006). Surveys of forest breeding bird presence or absence in southwest Ontario and Quebec, Canada (Traczinski et al. 1999) and Oregon (McGarigal and McComb 1995), also showed a stronger effect of forest abundance than forest fragmentation on species richness. It is important to note that the landscape metrics I included in this study were highly correlated at the scales considered, so the individual effects of different landscape metrics cannot be clearly separated. I interpret these results cautiously because the percent and aggregation of forest may interact to affect movement (Andrén 1994). For example, my study sites average 47(±5)% forest cover with 81(±6)% aggregation (Table 2.2), and aggregation may not be a significant factor until the amount of forest drops below a critical threshold level. Results of a linked spatially explicit land use and land cover change - ecological process model predict that the amount of forest in this region will drop from 60% in 2003 to 38% in 2027 (Hepinstall et al. In Press b), largely due to increasing urban cover. My sites are most representative of suburban and exurban landscapes, so my results may have differed had I measured patterns of bird movement at the more urban end of the gradient. Future studies can be designed to sample populations from more distinctive landscapes to better tease apart the independent effects of various landscape patterns on bird movements.

The probability of dispersal from the natal forest fragment was not related to local factors such as food availability or territory density (Hypothesis 5, Fig. 2.5). Birds may exhibit condition-dependent dispersal in response to environmental cues such as a shortage of food or absence of suitable breeding sites (Ims and Hjermann 2001, Matthysen 2005, Ch. 3). In a study of resident Song Sparrows in British Columbia, dispersal increased as competition for food increased and the number of territorial adults in the autumn increased, and food supplementation experiments led to an increase in the rate of philopatry (Arcese 1989). If there was an effect of food abundance or territory density in my study, I may not have detected it due to my study design. For example, the area I surveyed for shrub cover may have been too small or not representative of the entire natal fragment. Insects are also an important food source, but I did not measure insect abundance. Due to transmitter battery lives of only weeks, I was unable to track birds along their full dispersal pathways to breeding territories, and may have underestimated the number of birds that left their natal fragments if they dispersed later in the year.

A number of parameters contribute to population viability, including reproduction, survival, and dispersal, which often vary in the strength of their effects on population persistence. Dispersal can be an important limiting factor of population persistence (Brooker and Brooker 2002), but in this urban landscape, the birds I studied during the post-fledging period are dispersing and surviving well. Juvenile movements were limited in highly urban areas for some species, but low mobility in some species may be explained by the abundance of patchy food resources. I observed only 20% mortality of radio-tracked birds during the post-fledging period (Ch. 1). These and other native forest songbird species have average levels of reproductive success (52% of nests and 49% of territories successful, Marzluff et al. In Press). I suspect that adult survival may be a more important factor limiting bird population persistence in this urbanizing region. Of the species in this study, Swainson's Thrushes have the lowest relative abundance, were the least urban-affiliated species, and did not breed at some of my study sites. Yet their young are highly mobile and survive the post-fledging period well (7% or 1/15 mortalities, Ch. 1). Dispersal does not appear to limit their populations. The species I chose to measure in this study may be less sensitive to urban land cover than other less abundant or specialized species, so it would be inappropriate to extrapolate my results to all species.

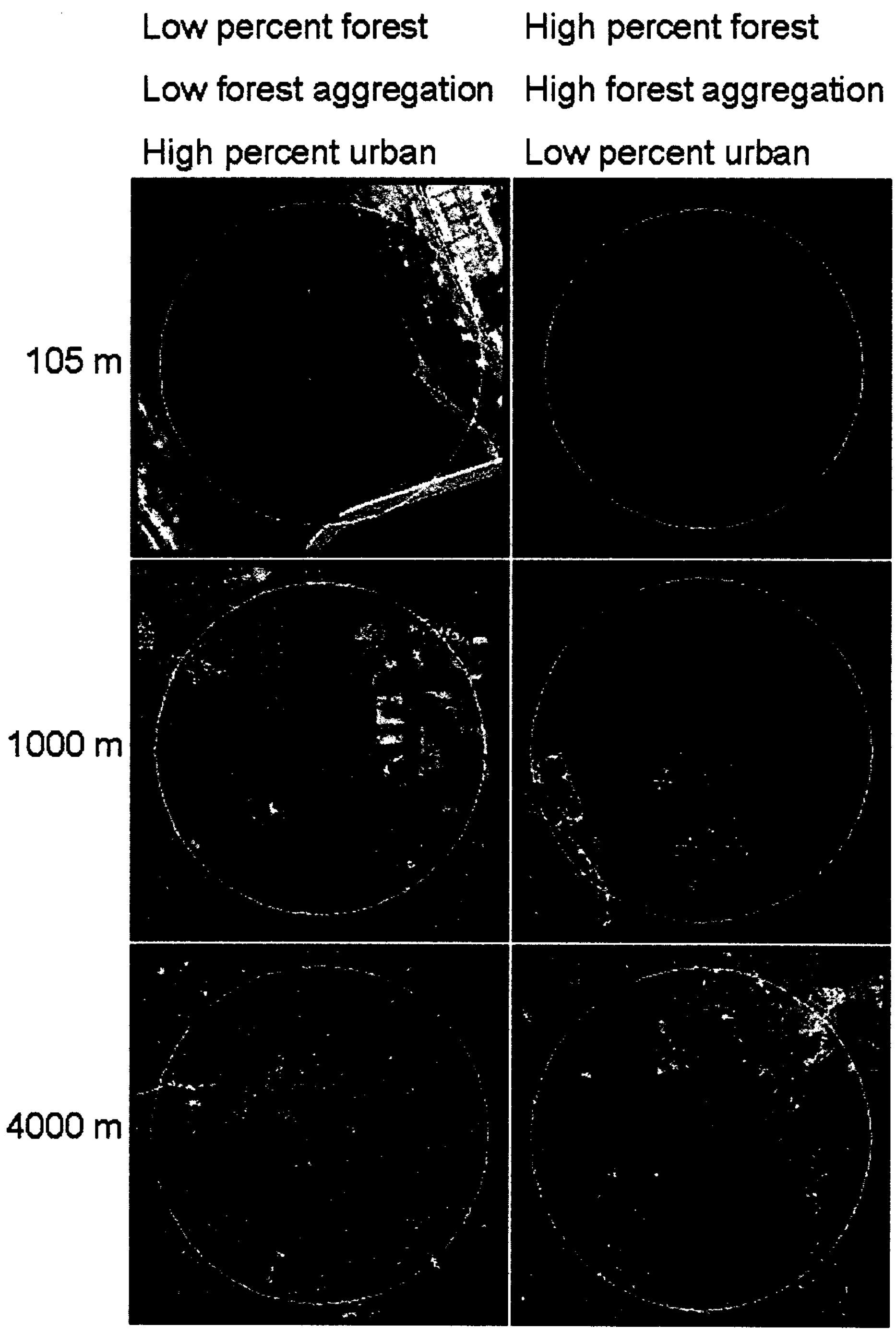


Figure 2.1. Aerial orthophotos of a subset of study sites illustrating variation in land cover patterns with scale (top row: 105 m radius, middle row: 1000 m radius, bottom row: 4000 m radius). Left column shows sites with low percent forest, low forest aggregation, and high percent urban. Right column shows sites with high percent forest, high forest aggregation, and low percent urban. All three landscape metrics are highly correlated at all site scales. For full range of metric values across sites, see Table 2.1.

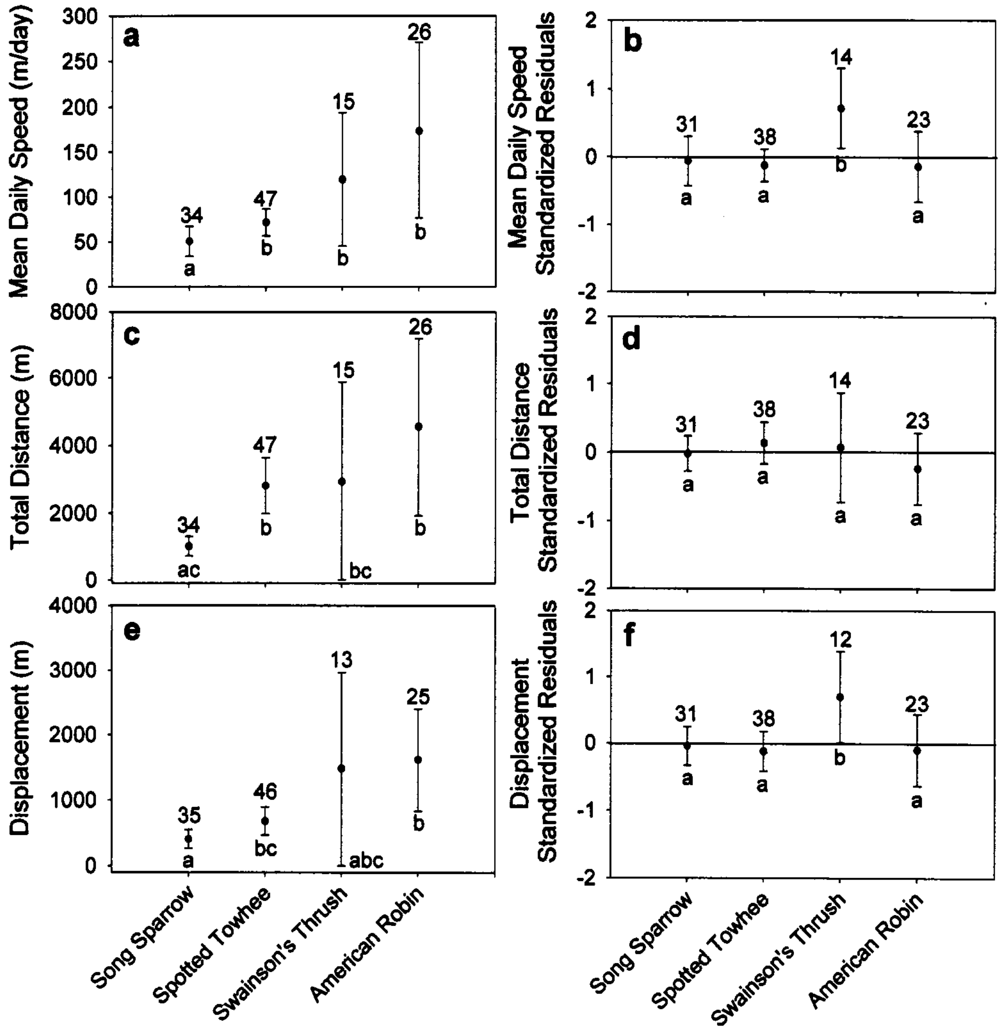


Figure 2.2. Species differed in measures of post-fledging mobility: (a) mean daily speed (m/day), (c) total distance (m), and (e) net distance displaced (m). Species differences were weaker after accounting for variation in body size measured from log-log power functions of all species, shown as standardized residuals of the (b) mean daily speed, (d) total distance, and (f) net distance displaced. Points are means ± 95% CI. Numbers above bars indicate sample sizes. Letters below bars indicate results of *post hoc* LSD tests.

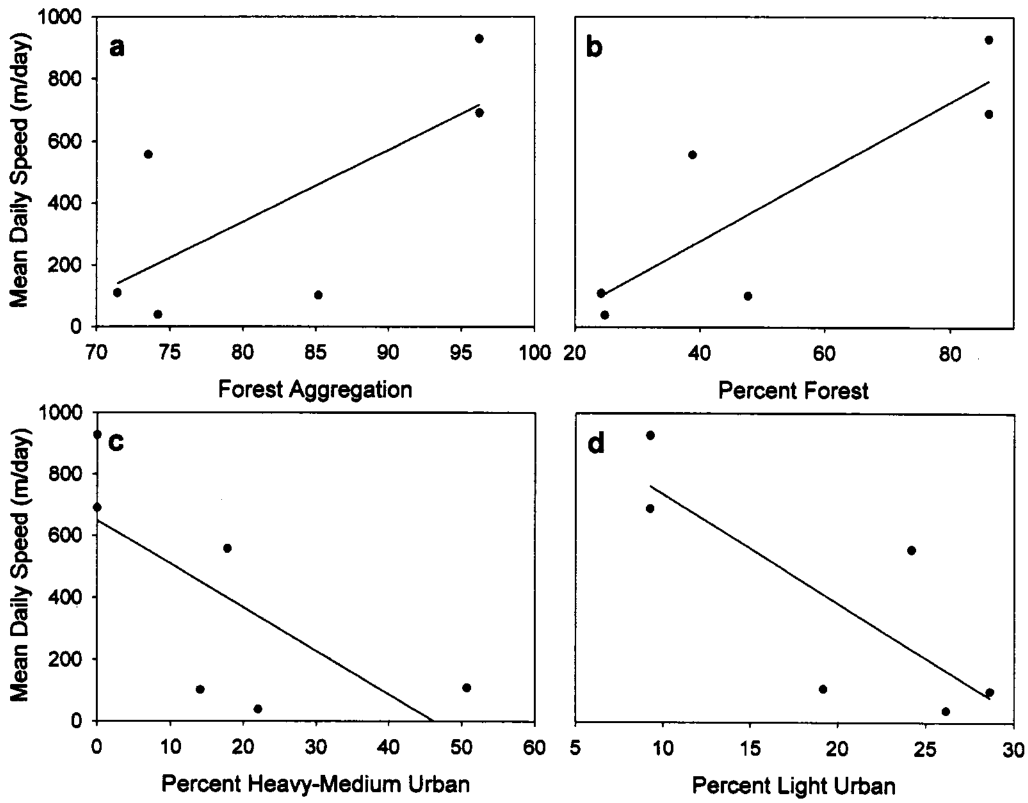


Figure 2.3. At the 250m scale, American Robin juveniles moved at a greater speed at sites where forest cover was more aggregated (a) and more abundant (b); they moved at a slower speed at sites with a greater percent heavy-medium urban (c) and percent light urban (d) land cover. Lines are least squares linear regressions.

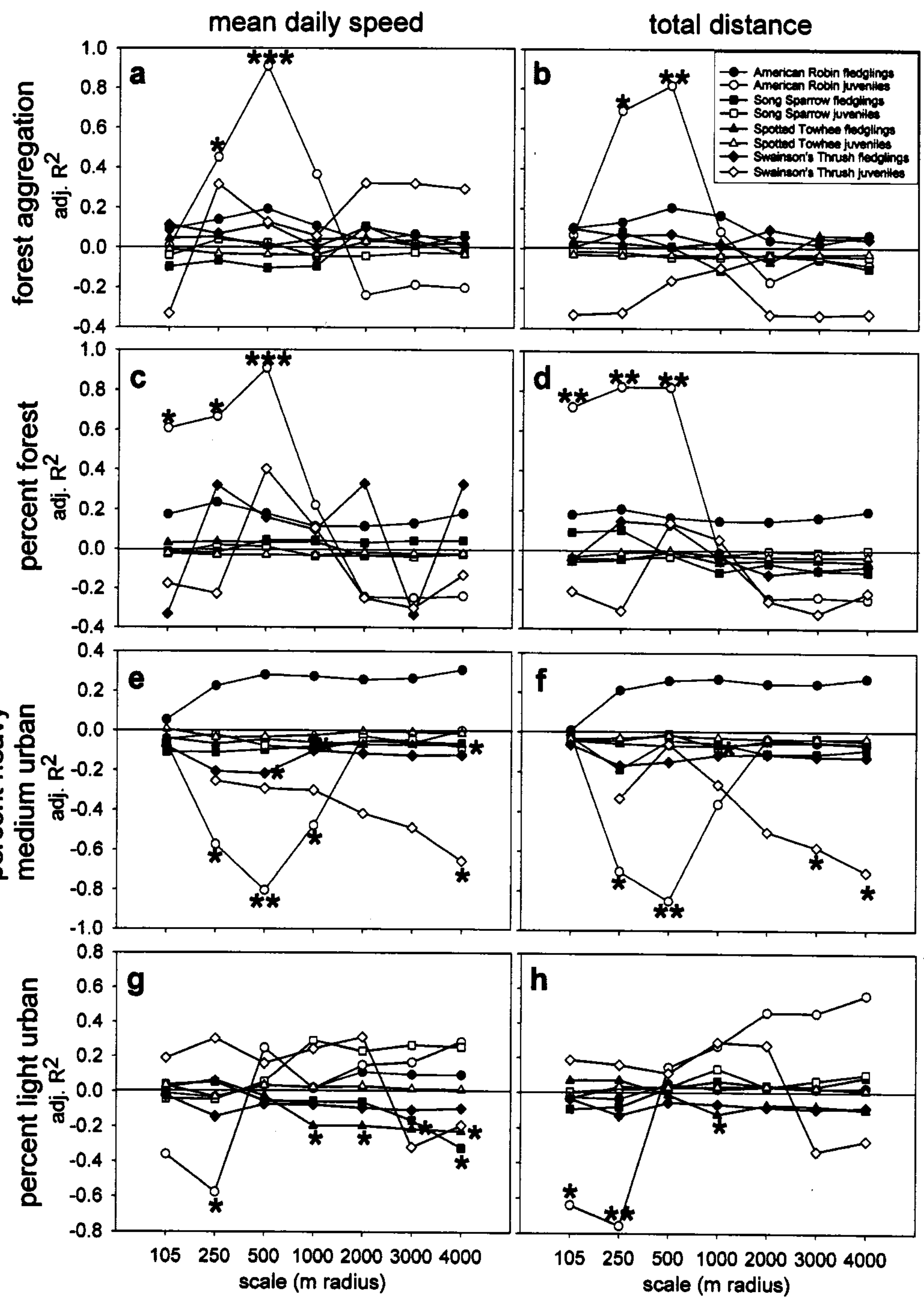


Figure 2.4. Results of Pearson correlations for each species at multiple spatial scales: (a) mean daily speed and forest aggregation (b) total distance and forest aggregation, (c) mean daily speed and percent forest, (d) total distance and percent forest, (e) mean daily speed and percent heavy-medium urban, (f) total distance and percent heavy-medium urban, (g) mean daily speed and percent light urban, and (h) total distance and percent light urban. Asterisks indicate significant relationships: ***p <= 0.001, **p <= 0.01, *p <= 0.05.

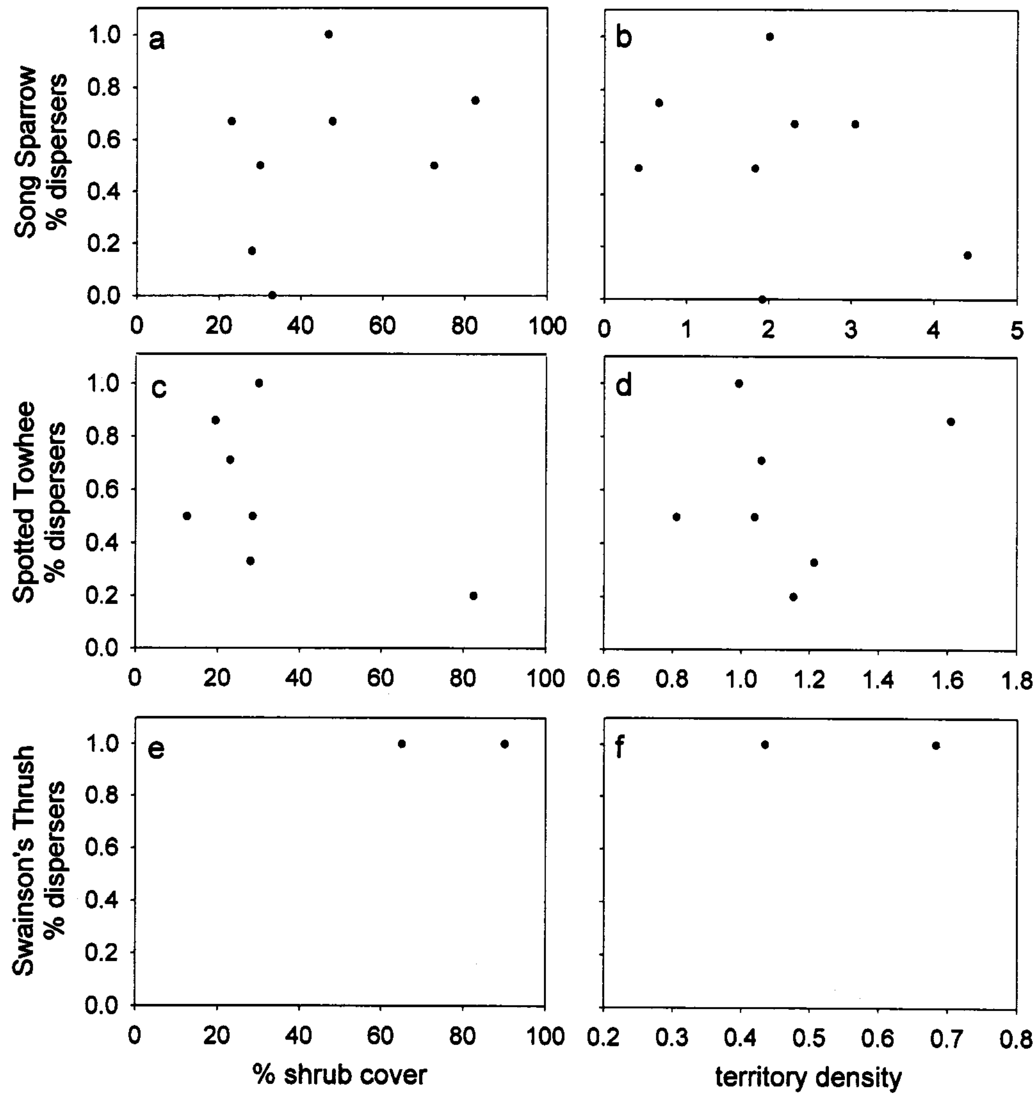


Figure 2.5. The probability of dispersal from the natal site during the tracking period was not related to food availability (percent shrub cover; a,c,e) or territory density (b,d,e) for Song Sparrows (a,b), Spotted Towhees (c,d), or Swainson's Thrushes (e,f).

Table 2.1. Relative abundance (RA) and variation (SD) estimates per species at survey points in forest fragments or the urban matrix.

Species	forest	forest	matrix	matrix		
	RA	SD	RA	SD	paired-t	p (2-tailed)
American robin	0.707	0.195	0.851	0.107	-3.995	0.002
Song sparrow	0.647	0.221	0.564	0.191	0.936	0.366
Spotted towhee	0.722	0.162	0.664	0.153	1.187	0.256
Swainson's thrush	0.335	0.222	0.229	0.202	2.418	0.031

Table 2.2. Summary statistics of landscape metric values across all spatial scales of analysis. Scales represent radii around the center of each study site. All metrics on 0-100 scale.

Scale	Landscape metric	Minimum	Maximum	Mean	SD
105 m	% heavy-medium urban	0	58.62	11.07	19.73
	% light urban	0	41.38	21.23	14.60
	% forest	3.45	100	58.08	28.83
	forest aggregation	0	93.62	74.48	23.50
250 m	% heavy-medium urban	0	51.14	17.47	16.67
	% light urban	0.91	35.62	19.74	9.85
	% forest	12.79	96.80	52.58	27.01
	forest aggregation	59.57	97.72	82.04	11.70
500 m	% heavy-medium urban	0	56.68	21.50	19.24
	% light urban	9.23	32.14	21.33	7.91
	% forest	16.30	87.10	47.36	24.52
	forest aggregation	65.77	94.23	82.63	9.69
1000 m	% heavy-medium urban	1.09	64.58	22.89	19.86
	% light urban	7.98	40.55	22.36	8.17
	% forest	9.67	87.56	44.94	22.28
	forest aggregation	60.79	95.61	81.43	9.35
2000 m	% heavy-medium urban	2.44	63.74	23.97	17.78
	% light urban	8.95	39.78	21.45	7.12
	% forest	12.06	82.93	42.37	19.50
	forest aggregation	61.08	95.36	81.77	8.56
3000 m	% heavy-medium urban	3.70	57.25	23.08	16.38
	% light urban	12.28	38.02	21.91	7.74
	% forest	8.59	74.39	41.83	17.78
	forest aggregation	68.94	93.59	82.17	7.76
4000 m	% heavy-medium urban	5.27	48.78	22.24	14.74
	% light urban	10.41	37.31	22.18	7.19
	% forest	6.22	65.49	40.81	16.10
	forest aggregation	66.69	92.50	81.94	7.32
overall	% heavy-medium urban	0	64.58	20.32	1.94
	% light urban	7.11	37.83	21.46	8.94
	% forest	3.45	100	46.85	4.77
	forest aggregation	0.00	97.72	80.92	5.64

Table 2.3. The proportion of individuals (N) of each species assigned to each movement category by the site fidelity test. Test result categories indicate whether a bird's movement pathway was random, more dispersed, or more constrained than 100 random pathways.

Species	Constrained	Dispersed	Random
Song Sparrow	0.49 (17)	0.26 (9)	0.26 (9)
Spotted Towhee	0.59 (27)	0.07 (3)	0.35 (16)
Swainson's Thrush	0.15 (2)	0.08 (1)	0.77 (10)
American Robin	0.12 (3)	0.08 (2)	0.80 (20)
All species	0.41 (49)	0.13 (15)	0.46 (55)

CHAPTER 3. CORRELATES OF NATAL AND BREEDING DISPERSAL AND SITE FIDELITY IN URBAN FOREST FRAGMENTS

Introduction

Dispersal is an important process that serves many functions, and population dynamics can be severely disrupted if the rate of dispersal is altered or dispersal is no longer possible due to extreme habitat isolation. For example, dispersal maintains gene flow within and between populations, allows metapopulation survival, and supplements population growth (Levins 1970, Hanski and Gilpin 1997, Merriam 1991). Dispersal is also a key element in source-sink population models as it contributes to the net gain or loss of individuals through immigration and emigration, respectively, and maintains sink populations (Pulliam 1988, Pulliam and Danielson 1991). If a species in a given local population is extirpated, the habitat patch may become recolonized by members of the species able to immigrate to the patch (Brown and Kodric-Brown 1977). The viability of forest bird populations after their habitat becomes isolated into separate patches, may hinge on the ability of dispersers to move between habitat remnants. Limitation in dispersal can ultimately lead to extinction in species with few, small populations (Macdonald and Johnson 2001).

The ability of birds to move between remnant patches of native vegetation in urban landscapes is poorly known. It is important to measure movement patterns in urban areas because cities are dynamic and ephemeral environments to which species respond positively or negatively (Marzluff 2001), and urban land cover is expanding rapidly (Brown et al. 2005, Robinson et al. 2005). If recruitment into the local population via dispersal is limited, then urban bird population persistence may be threatened. The goals of this study are to describe the processes of dispersal and philopatry (lack of dispersal) in several native forest songbird species and to relate these processes to various landscape variables. I test the following hypotheses:

1. Across study sites (forest fragments):
   a. dispersal rate and distance are positively related (and philopatry negatively related) to body size (Paradis et al.1998) because dispersal may be more costly in smaller species with shorter lifespans and thus reproductive potential,
   b. males show higher rates of site fidelity and natal philopatry, lower rates of breeding and natal dispersal, and shorter dispersal distances than females (Greenwood and Harvey 1982),
   c. natal dispersal distances are greater than breeding dispersal distances (Greenwood and Harvey 1982),
   d. and dispersal rate and distance are negatively related to breeding success the previous year because it may pay to disperse to a higher quality territory if the ability to produce young on the current territory is limited (Greenwood and Harvey 1982).
2. Between study sites:
   a. the rate of site fidelity is negatively related (and rate of dispersal positively related) to territory density due to competition for resources (Matthysen 2005),
   b. the rate of site fidelity is higher (and rate of dispersal lower) within larger forest fragments with a lower perimeter:area ratio because site quality increases with size and decreases with the amount of edge,

c. the rate of site fidelity is higher (and rate of dispersal lower) where the surrounding landscape has low percent forest and forest aggregation because adequate cover and food are needed for successful dispersal and survival (Haas 1995, Brooker and Brooker 2002), and

d. the rate of site fidelity is proportional (and rate of dispersal inversely proportional) to the extent of urban development activity in the landscape, because dispersal is hindered by direct habitat disturbance (clearing and building).

Methods

Data Collection

I banded, recaptured, and resighted birds at sites across the urban gradient of the Seattle, Washington, USA, metropolitan area over a nine-year period (1998-2006). Thirty forest fragments were selected within a matrix of urban, suburban, exurban, and undeveloped forest landscapes (Marzluff et al. 2001b, Fig. 3.1) using a stratified random sample of three landscape metrics calculated for a 1 km^2 area containing each study site: mean patch size, contagion, and the percent forest and percent urban land cover (see Donnelly and Marzluff 2004, 2006, Blewett and Marzluff 2005 for details). Forest fragments were primarily coniferous, including western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and western redcedar (*Thuja plicata*), or mixed with deciduous tree species such as red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*) and Oregon ash (*Fraxinus latifolia*, Franklin and Dyrness 1988). Site elevation varied from sea level to 300 m on the lower slopes of the Cascade Range. The nine study species are all native songbirds that breed in forests: American Robin, Bewick's Wren, Oregon Junco, Pacific-slope Flycatcher, Song Sparrow, Spotted Towhee, Swainson's Thrush, Wilson's Warbler, and Winter Wren.

I captured birds at each site using standard mist nets. From 1998-2001, netting was conducted systematically with 10 nets open for 5-6 hours, 4 times per site per year. From 2002-2006, netting was done with fewer nets that were focused on particular birds on their territories with song and call playbacks and decoys to lure them towards the nets. I recorded the species, age, and sex of each captured bird and gave each bird 4 bands: one USFWS aluminum band with a unique number (readable in hand) and 3 colored plastic bands in a unique sequence (readable with binoculars). Only metal bands were put on Pacific-slope Flycatchers because they are difficult to detect visually in the forest canopy and Wilson's Warblers due to their short tarsi.

I resighted color-banded birds using a number of methods. I spot mapped each site once per week, which entailed mapping the behaviors of birds of all focal species on their territories (for details see Marzluff et al. In Press). I recorded the color band combinations of any color-banded birds and determined breeding success based on behavioral indicators (Vickery et al. 1992). If a pair fledged any young within a given year, they were considered successful breeders that year. American Robin behavior is not conducive to spot mapping due to bias in observations of non-territorial behaviors at communal foraging grounds, so for this species I relied on banding records. I also found and monitored nests of all species, which yielded some additional color-banded bird sightings each year. To detect banded birds that had dispersed outside of the study sites, I systematically searched forest fragments and neighborhoods concentrated within 500-

1000 m around each site. If a territorial bird was not visible, I played recorded song and calls of that species and made other noises (pishing, squeaking) to bring the bird into view. I searched public areas or private areas that I had been granted permission to enter.

Additional movements were measured from banding and recovery data provided by the USGS Bird Banding Laboratory. This included records of the birds banded by the Marzluff lab in the study area (from 1998-2006) and recovered elsewhere, plus birds of the same target species originally banded in western Washington and recovered later. Locations of banding and recovery were provided as 10-minute lat-long blocks. I included only birds that were captured and recovered during the breeding season of different years in this analysis to restrict the data set to dispersal movements (not migratory movements).

Data Analysis

Each resighted or recaptured bird was placed into one of four categories based on their pattern of movement (Greenwood and Harvey 1982). "Site fidelity" included birds that bred at the same site (if banding record) or same territory (if mapping record) between two years. "Breeding dispersal" included birds that bred at a different site (if banding record) or different territory (if mapping record) between two years. To determine the minimum distance moved that classified as a move to a new territory, I measured the average distance to the nearest neighboring territory and averaged this distance across sites for each species. "Natal philopatry" included birds that bred at the same site as that where they were caught as juvenile the previous year. "Natal dispersal" included birds that bred at a different site than where they were caught as juvenile the previous year. If a bird was detected at the same site in two or more nonconsecutive years, I assumed it was present at that site in intermediate years and went undetected.

I calculated the rate at which each movement category occurred for each unique study sites, species, age, sex, and year combination. For banding data from 1998-2002, each recapture rate was the number of recaptured birds in a given year divided by the total number of birds banded the previous year. For mapping data from 2003-2006, each resighting rate was the number of resighted birds in a given year divided by the total number of birds mapped the previous year. Movements between sites were detectable within all years, but movements between territories were only detectable on spot maps from 2003-2006. For a subset of birds (N = 277), at least two pairs of coordinate locations were recorded, from which I calculated the straight-line distance moved. In all analyses of distance moved I used only movements of these color-banded birds, not movements by radio-tracked juveniles nor long-distance movements of recovered birds.

Territory density was calculated for each site, species, and year from spot-mapping data as the number of territories per hectare within a designated polygon (Table 3.1). Rates of dispersal or site fidelity were compared with the territory density from the previous year.

A 2002 Landsat TM satellite image with 30 m resolution was classified into 12 land cover classes (J. Hepinstall et al., In Press a) including four forest types (deciduous, coniferous, regenerating, and mixed) which I combined into one class. I calculated landscape metrics with the program FRAGSTATS 3.3 (McGarigal et al. 2002) at various spatial scales around the center of each study site to test for differences in landscape extent on dispersal (105 m, 250 m, and 500 m). Scale sizes were those that were significantly related with the mobility of dispersing juvenile birds (Ch. 2) and extend in a radius from the center of each site. The smallest scale was set at 105 m because it encompassed the land cover area of three full pixels in radius surrounding the central pixel (30 m resolution grid), it was the minimum size at which the aggregation index (below) was estimated consistently at each site, and corresponds with an area roughly equal to that of my smallest study sites (3.5 ha). I calculated the percent cover (the percent of pixels in the landscape) and the aggregation index (the frequency with which different pairs of patch types appear side-by-side on the map, taking into account only the like adjacencies involving the focal land cover class) for the forest land cover class. Both landscape metrics varied among study sites and spatial scales of analysis (Ch. 2). I measured the patch area and perimeter of each study site from color aerial orthophotos taken in 2002. I also classified each study site as either pre-post (urban development actively occurring), suburban-exurban (development occurred in the past), or reserve (control forests) to compare rates of dispersal and philopatry between landscape types.

I tested for differences between species, sexes, and ages in dispersal rates and distances with independent t-tests, one-way ANOVAs, and *post hoc* LSD tests. The proportion of birds recaptured or resighted, percent forest, and forest aggregation were arcsine square root transformed to meet assumptions of normality and equal variances (Zar 1999). Pearson correlations were used to relate dispersal rates to territory density, patch size, perimeter:area ratio, percent forest, and forest aggregation. Means are reported plus or minus one standard deviation. The significance level (alpha) was 0.05. P values are 2-tailed unless otherwise stated. I completed all statistical analyses using SPSS 13.0 software (SPSS 2004).

Results

Species differed significantly in their rates of site fidelity and breeding dispersal (Hypothesis 1a, both 2-tailed $p < 0.01$), but not in their rates of natal philopatry or natal dispersal (both 2-tailed $p > 0.16$, Fig. 3.2). Song Sparrows consistently had the highest rates of site fidelity (mean: 0.11 ± 0.08, $N = 29$) and breeding dispersal (0.01 ± 0.02, $N = 29$, Fig. 3.2). Contrary to predicted, adult mass was significantly positively correlated with the rate of site fidelity ($r = 0.25$, $N = 242$, 2-tailed $p < 0.01$) but not with the rate of breeding dispersal ($r = 0.01$, $N = 238$, 2-tailed $p = 0.97$). Juvenile mass decreased with increasing natal philopatry as predicted ($r = -0.16$, $N = 131$, 1-tailed $p = 0.03$), but was unrelated to rates of natal dispersal ($r = 0.01$, $N = 131$, 2-tailed $p = 0.96$). Species differed in the distance moved by adults ($F_{6,244} = 2.2$, 2-tailed $p = 0.04$), but not by natal dispersers ($F_{4,23} = 0.2$, 2-tailed $p = 0.94$, Table 3.2). When only color-banded bird resight or recapture data is included (above tests), Spotted Towhee juveniles (mean: 7430 ± 12438 m, $N = 3$) and American Robin adults (10906 ± 0 m, $N = 1$) moved the farthest. When the total distance moved by radio-tracked juveniles was added (Ch. 2), American Robin juveniles moved the farthest (4714 ± 6467 m, $N = 26$, Table 3.2).

Sexes differed in their rates of dispersal and philopatry (Hypothesis 1b). With all species combined, males had significantly higher rates of site fidelity than females as predicted ($t_{495} = -2.09$, 1-tailed $p = 0.02$), but no other rates differed between sexes (all 2-tailed $p > 0.05$). When each species was considered separately, males had higher rates of site fidelity than females in Song Sparrows ($t_{55} = -3.45$, 1-tailed $p < 0.01$), Swainson's Thrushes ($t_{56} = -1.69$, 1-tailed $p = 0.05$), and Winter Wrens ($t_{29} = -2.88$, 1-tailed $p < 0.01$,

Fig. 3.3), consisted with my prediction. Song Sparrow males also had significantly higher rates of natal philopatry than females, which also consisted with my prediction (t_{39} = -1.83, 1-tailed p = 0.04, Fig. 3.3). With all species combined, the distance moved did not differ between males and females (t_{230} = -0.39, 1-tailed p = 0.35). The distance moved did not differ between sexes for any individual species (Table 3.2).

Dispersal rates varied by age class (Hypothesis 1c). Rates of natal dispersal were significantly lower than rates of breeding dispersal for Dark-eyed Juncos (t_{56} = 1.39, 2-tailed p = 0.04), Song Sparrows (t_{143} = 2.02, 2-tailed p = 0.04) and Swainson's Thrushes (t_{79} = 1.79, 2-tailed p = 0.03, Fig. 3.2b,d), but these rates did not differ for any other species or for all species combined. With all species combined, adults dispersed marginally farther than juveniles (t_{277} = 2.78, 2-tailed p = 0.06), but age classes did not differ for any individual species (Table 3.2). All of these significant effects were the opposite as I had predicted.

Rates of dispersal and philopatry were related to prior breeding success (Hypothesis 1d). As predicted, birds that had fledged young the previous year had a significantly higher rate of site fidelity than birds that did not fledge young the previous year for all species combined (t_{656} = -2.95, 1-tailed p , 0.01), Song Sparrows (t_{99} = -2.03, 1-tailed p = 0.02), and Spotted Towhees (t_{103} = -1.86, 1-tailed p = 0.03, Fig. 3.4). Contrary to predicted, birds that had fledged young the previous year also had a significantly higher rate of breeding dispersal than birds that did not fledge young the previous year for all species combined (t_{707} = -1.88, 2-tailed p < 0.01) and for Song Sparrows (t_{99} = -1.78, 2-tailed p = 0.04). Breeding success the year prior to movement was unrelated with the distance moved for all species combined ($t_{193} = -0.06$, 1-tailed $p = 0.48$) or for each species considered separately (all 1-tailed $p > 0.18$).

Territory density was related to some measures of dispersal and philopatry (Hypothesis 2a). With all species combined, territory density increased with rates of site fidelity ($r = 0.30$, $n = 579$, 2-tailed $p < 0.01$) and breeding dispersal ($r = 0.30$, $n = 579$, 2-tailed $p < 0.01$), but was unrelated to rates of natal philopatry ($r = 0.08$, $n = 126$, 1-tailed $p = 0.18$) and natal dispersal ($r = 0.09$, $n = 126$, 1-tailed $p = 0.17$). When each species was analyzed separately, rates of site fidelity increased with territory density for Dark-eyed Juncos ($r = 0.29$, $n = 69$, 2-tailed $p = 0.02$) and Spotted Towhees ($r = 0.21$, $n = 94$, 2-tailed $p = 0.05$, Fig. 3.5), contrary to predicted. Rates of breeding dispersal also increased with territory density for Bewick's Wrens ($r = 0.20$, $n = 66$, 1-tailed $p = 0.05$), Dark-eyed Juncos ($r = 0.44$, $n = 69$, 1-tailed $p < 0.01$), Song Sparrows ($r = 0.31$, $n = 89$, 1-tailed $p < 0.01$), and Spotted Towhees ($r = 0.17$, $n = 94$, 1-tailed $p = 0.05$, Fig. 3.5) consistent with my prediction.

Movement and philopatry rates were related with forest patch size and perimeter:area ratio (Hypothesis 2b). The only correlation consistent with my prediction was for Swainson's Thrush natal philopatry, which increased with patch size ($r = 0.42$, $N = 20$, 1-tailed $p = 0.03$, Fig. 3.6a). The remaining correlations were opposite as predicted. Rates of breeding dispersal increased with patch size for Dark-eyed Juncos ($r = 0.56$, $N = 26$, 2-tailed $p < 0.01$, Fig. 3.6a). For Song Sparrows, site fidelity decreased with increasing patch size ($r = -0.55$, $N = 27$, 2-tailed $p < 0.01$, Fig. 3.6a) and natal philopatry increased with the forest patch perimeter:area ratio ($r = 0.4$, $N = 26$, 2-tailed $p = 0.04$, Fig. 3.6b).

Forest landscape metrics correlated with rates of dispersal and philopatry (Hypothesis 2c). With all species combined, natal philopatry increased with decreasing percent forest at the 105 m scale as predicted ($r = -0.17$, $N = 138$, 1-tailed $p = 0.03$). Bewick's Wrens' rate of natal philopatry was highest at sites with low percent forest ($r = -0.56$, $N = 15$, 1-tailed $p = 0.01$, Fig. 3.7c) and low forest aggregation ($r = -0.88$, $N = 15$, 1-tailed $p < 0.01$, Fig. 3.8c) both at the 105 m scale. Similarly, Song Sparrows had a higher rate of natal philopatry at sites with low percent forest (105 m scale: $r = -0.34$, $N = 26$, 1-tailed $p = 0.05$; 250 m scale: $r = -0.37$, $N = 26$, 1-tailed $p = 0.03$; 500 m scale: $r = -0.37$, $N = 26$, 1-tailed $p = 0.03$, Fig. 3.7c) and forest aggregation (250 m scale: $r = -0.41$, $N = 26$, 1-tailed $p = 0.02$; 500 m scale: $r = -0.45$, $N = 26$, 1-tailed $p = 0.01$, Fig. 3.8c). Sparrows also showed higher rates of breeding dispersal at sites with low percent forest at the 500 m scale ($r = -0.41$, $N = 26$, 1-tailed $p = 0.05$, Fig. 3.7b) contrary to predicted. For Winter Wrens, the rate of breeding dispersal increased with increasing percent forest (250 m scale: $r = 0.35$, $N = 25$, 1-tailed $p = 0.04$; 500 m scale: $r = 0.37$, $N = 25$, 1-tailed $p = 0.03$, Fig. 3.7b) and forest aggregation ($r = 0.35$, $N = 25$, 1-tailed $p = 0.05$, Fig. 3.8b), consistent with my prediction. Spotted Towhees showed the only significant correlation with natal dispersal, which increased with decreasing percent forest ($r = -0.49$, $N = 21$, 2-tailed $p = 0.02$, Fig. 3.7d) and forest aggregation ($r = -0.47$, $N = 21$, 2-tailed $p = 0.03$, Fig. 3.8d) at the 105 m scale, contrary to predicted.

Rates of movement and philopatry varied with the level of active urban development for one species (Hypothesis 2d). Swainson's Thrushes showed significantly higher site fidelity at pre-post sites ($F_{2,26} = 3.63$, 2-tailed $p = 0.04$) and higher natal philopatry at reserve sites ($F_{2,17} = 3.61$, 2-tailed $p = 0.05$) compared with other landscape types (Fig. 3.9). No other rates of movement or philopatry varied between site categories for any other individual species or for all species combined (all 2-tailed $p > 0.16$).

Discussion

Species differed in their dispersal rates and distances, but not consistently relative to their body size (Hypothesis 1a). Song Sparrows had the highest rates of both site fidelity and breeding dispersal, and their mass was 4th highest among species (mean: 23.3 ± 2.5 g, N = 1242). Part of this effect may be explained by the relatively high detectability of Song Sparrows, which were easiest to catch and resight among species in this study area. The least detectable species (Pacific-slope Flycatchers and Wilson's Warblers) were not color-banded (had metal band only), were among the smallest of species, and had the lowest rates of all four movement categories among species. As predicted, juveniles of smaller species had the highest rates of natal philopatry, but adults of smaller species had the lowest rates of site fidelity (contrary to predicted). Only adults differed between species in the distance moved, and the largest species (American Robin, mean: 83.9 ± 11.8 g, N = 387) moved the farthest (Fig. 3.10). The distance dispersed increased with body size in a large sample of British bird recoveries (Paradis et al. 1998). Any allometric effect among these species was inconsistent and differences in rates of dispersal between species may depend more on other life history or environmental variables (below). For example, migratory strategy was the strongest variable related to juvenile mobility after a positive allometric effect was corrected for (Ch. 2).

Sexes differed in their rates of dispersal and philopatry, but not in the distance moved (Hypothesis 1b). Consistent with many other passerines (Darley et al. 1977, Greenwood and Harvey 1982, Gavin and Bollinger 1988), males had higher rates of site fidelity and natal philopatry than females in a number of species. Females were expected to have higher rates of breeding and natal dispersal and to move a farther distance than males, but these movement types were more difficult to detect and were probably underestimated for both sexes. If females moved off-site more often than males, and were thus more difficult to detect, then their dispersal rates were underestimated relative to males. The sample of females (N = 53) in this analysis was less than a third as large as the sample of males (N = 183), so a more balanced sample may have yielded different results.

Rates and distances of breeding dispersal were greater than natal dispersal, contrary to predicted (Hypotheis 1c). Natal dispersal was detected in only four species, compared with breeding dispersal recorded for seven species. Higher rates of breeding dispersal may also occur if adults tend to disperse between territories within a study site and juveniles tend to disperse outside of study sites where they are less likely to be detected again. In most passerines, natal dispersal distances are greater than breeding dispersal distances (Greenwood and Harvey 1982), but I found the opposite to be true. One caveat to this analysis is that it included only resight and recapture data primarily from my study sites, which does not reflect the distance moved by juveniles that leave the study sites (Ch. 2). Juvenile dispersal distances were farther in several species when telemetry data was included (Fig. 3.10), which is more representative of actual natal dispersal patterns, even though it underestimates the total dispersal distance because birds were only tracked until their transmitter batteries died (prior to reaching the place they bred the next spring).

Movement rates by adults were related to breeding success the previous year (Hypothesis 1d). Rates of both site fidelity and breeding dispersal were higher in birds that successfully fledged young the previous season. A number of passerines show higher site fidelity the year after a successful breeding attempt (Darley et al. 1977, Gavin and Bollinger 1988, Haas 1997). Birds that had failed to produce young and dispersed may have been underrepresented in this sample if they moved outside of my study sites and went undetected. For those birds that did disperse after a breeding attempt, there was no effect of prior breeding success on dispersal distance. The decision whether to stay on a territory or leave probably depends on factors other than previous breeding success, such as mate choice, competition for space, or a sudden change in habitat characteristics (clearing or urban development on or near the territory).

Movement rates were related to territory density (Hypotheis 2a). Rates of both site fidelity and breeding dispersal increased with territory density in a number of species. Most cases of breeding dispersal were movements between territories within the same study sites, within which territory density was presumably the same, so territory density is probably not driving breeding dispersal in most cases I analyzed. Then again, there may be benefits to staying at a site that has high territory density, such as kin cooperation and familiarity with local conditions, but these benefits must be weighed against the costs of increased competition for resources (Lambin et al. 2001). A review of density-dependent dispersal studies showed a mixture of positive and negative density-dependence in studies that compared dispersal rates between sites that varied in density (Matthysen 2005), which may explain the equivocal results of this analysis. Dispersal decisions are most likely made according to multiple factors, one of which may be territory density.

Local forest metrics were related to rates of movement in some cases (Hypothesis 2b). The only relationship consistent with my prediction was for Swainson's Thrushes, which indicates that larger forest fragments are of higher quality for this species. In contrast, Song Sparrow adults tended to stay in smaller patches, juveniles tended to stay in edgy patches, and Dark-eyed Juncos dispersed from larger patches. These species seem to be less dependent upon interior forest conditions and better able to exploit edge habitats for breeding.

Variation in the amount and configuration of forest in and around study sites was associated with variation in rates of movement and fidelity (Hypothesis 2c). As predicted, natal philopatry in Bewick's Wrens and Song Sparrows was inversely related with the percent forest and forest aggregation among sites, which may indicate a tendency for juveniles of these species to stay in the forest fragment where they were born because their ability to disperse from it safely is limited or the benefits of staying are high. Lower rates of dispersal in poorly-connected landscapes have been observed in other species (Haas 1995, Brooker and Brooker 2002). Dispersal by Winter Wren adults seems to be facilitated by forest cover, which is expected for this forest-interior-associated species. Contrary to my prediction, dispersal by Spotted Towhee juveniles and Song Sparrow adults was higher at sites with a lower percent and aggregation of forest, which may indicate limited resource availability (food, cover, breeding territories) as well as the ability of these species to disperse into areas with little forest (Ch. 1). Based on the relative number of significant effects, dispersal by juveniles appears to be more sensitive to forest cover in the landscape than dispersal by adults, and the amount of forest is more important to dispersing birds than forest connectivity.

Variation in movement rates among sites with different levels of development activity was limited (Hypothesis 2d). Swainson's Thrush adults were most site faithful to pre-post sites, which was surprising given this species was most mobile and forest-associated during the post-fledging period (Ch. 1-2). Pre-post sites were the most dynamic in land cover, and high site fidelity most likely occurred prior to the urban development of these sites. Swainson's Thrush juveniles were most philopatric to reserve sites, which is expected due to the large size and presumably high quality of these sites for this species.

My methods (capture-mark-recapture or resight) were limited in that I was unable to distinguish between birds that dispersed from a study site and were not observed again from birds that died. One solution to this problem is to use radio telemetry (Ch. 1), but with limited resources it is only practical to use this method for a much smaller sample of individuals. Program MARK (White and Burnham 1999) would be more appropriate for analyzing the encounter and survival rates of birds not seen again and relating these rates to the ecological covariates of interest.

MANAGEMENT STRATEGIES

Life in an urban landscape certainly complicates the tradeoffs affecting bird dispersal, survival, and relative habitat use, but the species I studied appear to be adapting well to this dynamic environment. Conditions in the natal forest patch where birds are naïve and vulnerable appear to be more important to juvenile survival than conditions in the urban matrix, which is used when they are older and more experienced. Predation pressure on juvenile songbirds seems to be low in the urban ecosystem I investigated and is dominated by native predators in forests, not exotic predators in the urban matrix. Despite the fact that most mortality occurred in forest fragments, the mortality rate was still quite low relative to other studies, and native predators do not appear to be exerting too much predation pressure on juvenile songbirds in this urban ecosystem. The species that was under the most predation pressure (American Robin) is in fact one of the most abundant and widespread species in this study area (Donnelly and Marzluff 2004, 2006). Maintenance of urban coyote populations will benefit many birds to the extent that they control house cat populations.

During the post-fledging dispersal stage, juvenile birds of the species I studied benefit from a number of landscape elements. They used a mixture of habitat types within the heterogeneous urban landscape, not strictly breeding habitat. My sites were most representative of suburban and exurban landscapes, and my results may have differed had I measured patterns of bird movement at the more urban end of the gradient. All species used areas with dense cover while dispersing, which must be retained in forested and urban parts of the landscape. American Robins depended on dense cover less than all other species, and instead found safety in groups in more open, developed areas. The positive effects these species are currently experiencing could easily be negated if the level of danger increases or resources decrease with more cars, windows, people, and pets in this urban landscape. Although the species I studied are adapting well to urban life, other native species may be more sensitive to urban development in their vulnerability to predation and resource requirements, and be forced out of increasingly larger areas of former habitat as cities grow. The amount of forest in this region is expected to drop from 60% in 2003 to 38% in 2027 (Hepinstall et al. In Press b), largely due to increasing urban cover. Juvenile birds in this study used landscapes with 41-51% forest cover and 29-51% (heavy-medium and light) urban cover (Table 1.6). These figures are in line with those suggested by Donnelly and Marzluff (2004) for maintaining high species richness of breeding birds (> 46% forest cover and <52% urban cover). We must strive to maintain this level of forest cover if we want to maintain bird dispersal, survival, and population viability in this dynamic urban ecosystem. Forest contiguity appears to be less important to bird dispersal and survival than does the amount of forest cover, at least from the perspective of the species I studied.

I suggest several strategies for maintaining effective bird dispersal in an urban ecosystem that focus on maximizing the amount of forest and minimizing the amount of impervious urban cover. This can be achieved through either the restoration of degraded, fragmented habitat in developed areas or the maintenance of existing forest cover and connectivity during future urban development. The latter alternative allows for the most flexibility in design and the least potential conflict with existing land uses. In either scenario, the goal is to maximize the retention of native vegetation and to encourage native landscape plantings to make the matrix conditions more like those of the native habitat fragments (Marzluff and Ewing 2001). This may take the form of stepping stones (intact forest patches), corridors (linear strips of forest connecting patches), or maintaining forest cover in the urban matrix whether it be residential, commercial, or industrial (Beier and Noss 1998, Bennett 1999). Preserving forest fragments in close proximity (< 1 km apart) will be most important to the least mobile species, which tend to be small resident species like Song Sparrows. The most consistently important landscape scales in this study were at 250-500 m radii around study sites, which corresponds to roughly the area of a small subdivision (20-80 ha). Landscape patterns at the 500 m radius (or 1 km^2) scale were also related to bird species richness in this area (Donnelly and Marzluff 2004, 2006, Blewett and Marzluff 2005). A multi-scaled approach is most appropriate because no single strategy will meet the requirements of all species in heterogeneous urban landscapes with differences in the scale, habitat specificity, and mobility between species (Lindenmayer and Franklin 2002, Opdam and Wiens 2002). Because species varied widely in their rates of dispersal and philopatry relative to forest cover metrics, I recommend a range of forest fragment shapes and sizes be maintained in landscapes with existing and future urban developments. For example, large contiguous forest patches are needed by strongly forest-associated species such as Swainson's Thrushes and Winter Wrens, whereas smaller forest patches with more edge are needed by edge-associated species such as Song Sparrows and Dark-eyed Juncos. Providing landscape heterogeneity through a variety of different settlement and open space configurations is needed to conserve the full diversity of native bird species (Donnelly and Marzluff 2004, Blewett and Marzluff 2005, Donnelly and Marzluff 2006).

Multiple strategies by diverse stakeholders are available to achieve these conservation goals. For example, policy makers such as city and county councils and state legislators can enact zoning regulations, critical area ordinances, tax incentives, and open space acquisition measures to help retain forest cover (Miller 1984, Bradley 1991, Gillham 2002). When planning new developments, landscape architects can play a direct role in the design of landscape patterns such as the amount and shape of native habitat remnants that are conducive to animal movements (Collinge 1996). Large-scale developers can build clustered residential areas which retain a larger proportion of contiguous forest than sprawling, low density developments (Arendt 1999). Homeowners can enhance bird dispersal by enhancing the conditions of the matrix in their yards and maximizing tree and shrub cover while minimizing impervious cover (lawn, built, and paved areas), and may be able to enhance bird survival by providing supplemental food, water, and cover. By managing our forests across multiple scales utilizing multiple strategies, we can facilitate the effective dispersal of birds and maintain viable bird populations in urban ecosystems.

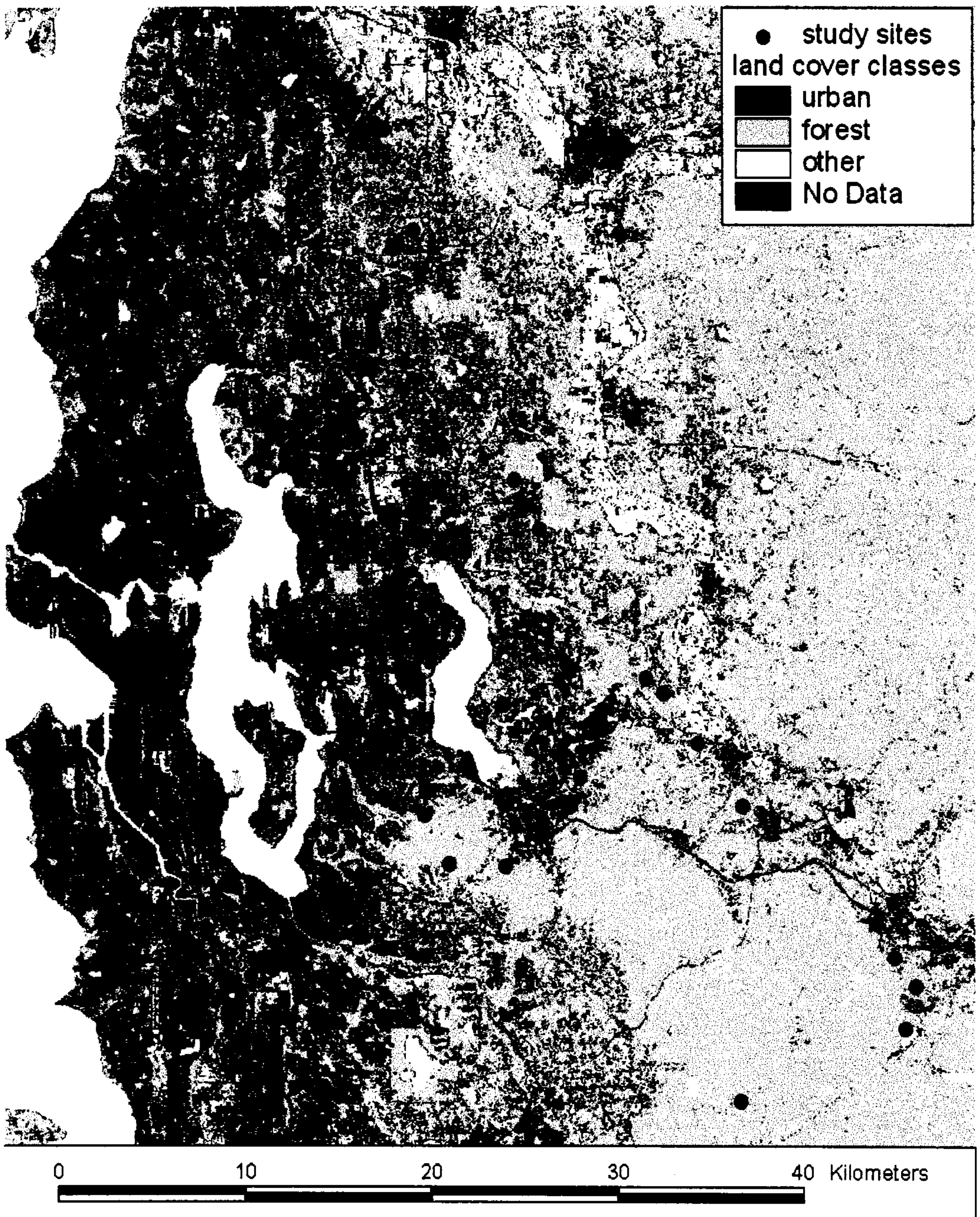


Figure 3.1. The study area included urban, suburban, exurban, and control study sites (black dots) in the Seattle metropolitan area. Land cover classes (from a 2002 LandSat image) are urban (dark gray), forest (light gray), and other (white).

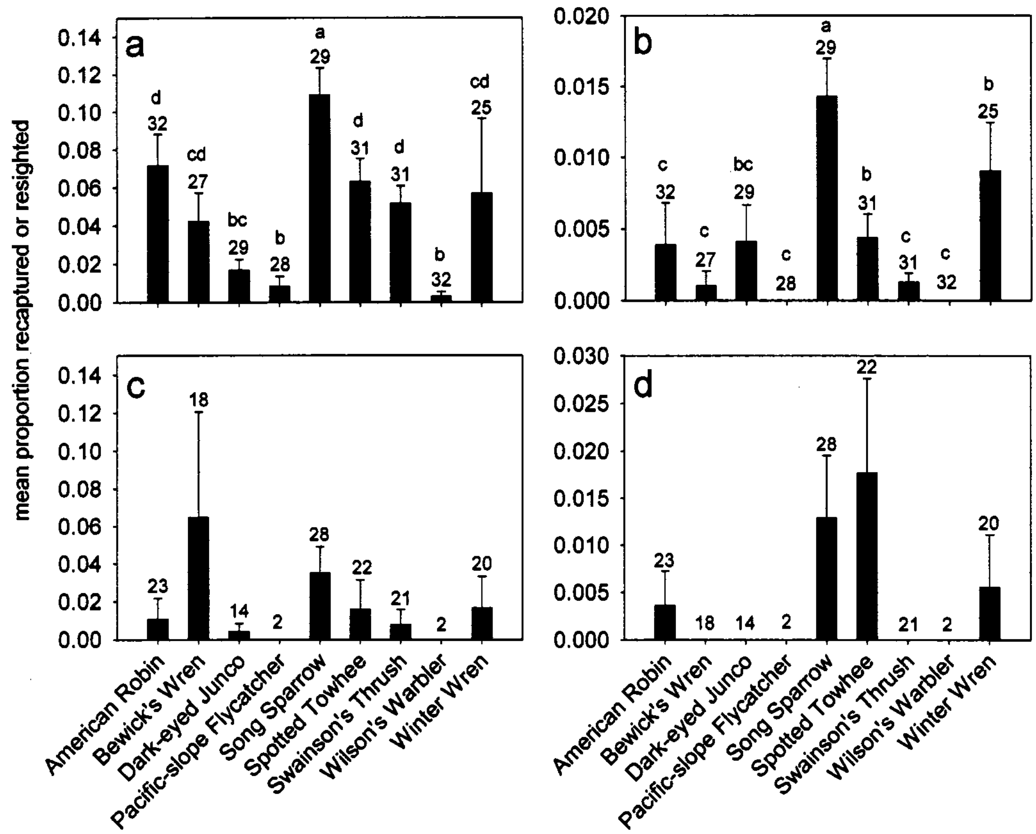


Figure 3.2. Mean proportion of recaptured or resighted birds by species and movement category: a) site fidelity, b) breeding dispersal, c) natal philopatry, and d) natal dispersal. Numbers above error bars (±1 SE) indicate sample size (number of study sites). Letters above error bars indicate results of *post hoc* LSD tests for significant models only (a, b). The total number of birds banded or mapped across all years was: American Robin: 360 adults, 89 juveniles; Bewick's Wren: 438 adults, 77 juveniles; Dark-eyed Junco: 599 adults, 57 juveniles; Pacific-slope Flycatcher: 528 adults, 3 juveniles; Song Sparrow: 1678 adults, 321 juveniles; Spotted Towhee: 1446 adults, 132 juveniles; Swainson's Thrush: 963 adults, 69 juveniles; Wilson's Warbler: 447 adults, 2 juveniles; Winter Wren: 828 adults, 49 juveniles.

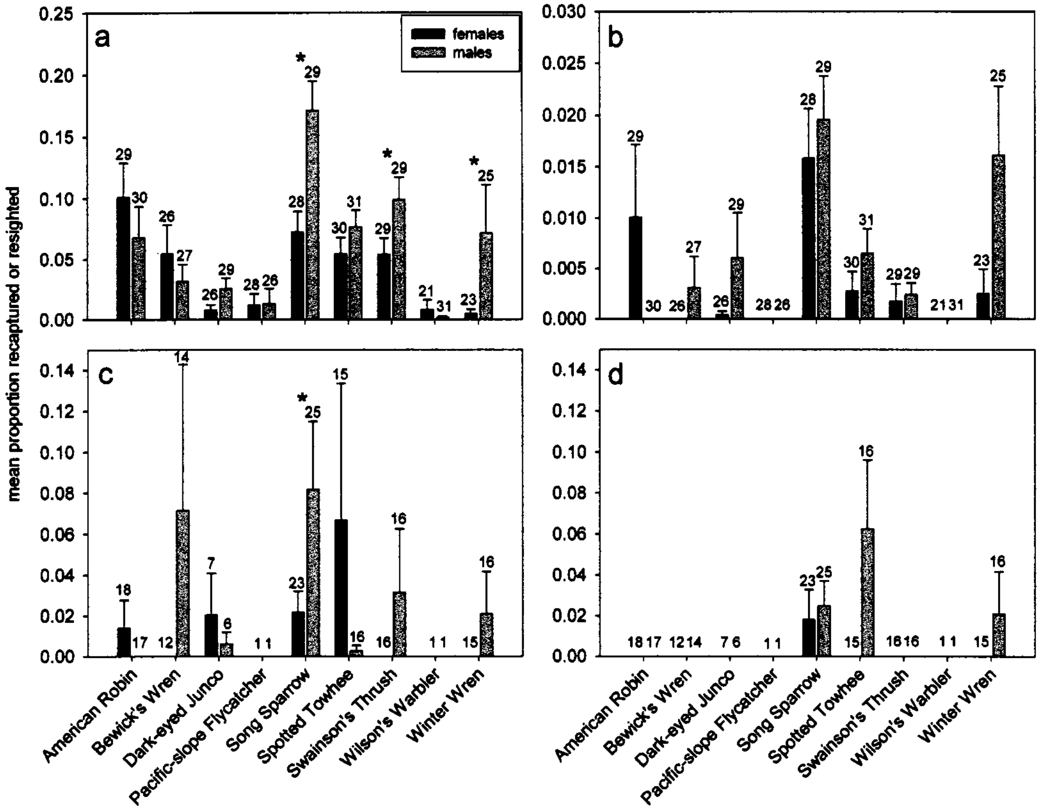


Figure 3.3. Mean proportion of recaptured or resighted birds by species, sex, and movement category: a) site fidelity, b) breeding dispersal, c) natal philopatry, d) natal dispersal. Numbers above error bars (±1 SE) indicate sample size (study sites). Asterisks above error bars indicate significant differences between sexes (1-tailed $p < 0.05$). The total number of birds banded or mapped across all years was: American Robin: 163 females, 189 males; Bewick's Wren: 175 females, 214 males; Dark-eyed Junco: 255 females, 343 males; Pacific-slope Flycatcher: 203 females, 304 males; Song Sparrow: 689 females, 954 males; Spotted Towhee: 632 females, 810 males; Swainson's Thrush: 339 females, 522 males; Wilson's Warbler: 98 females, 345 males; Winter Wren: 308 females, 515 males.

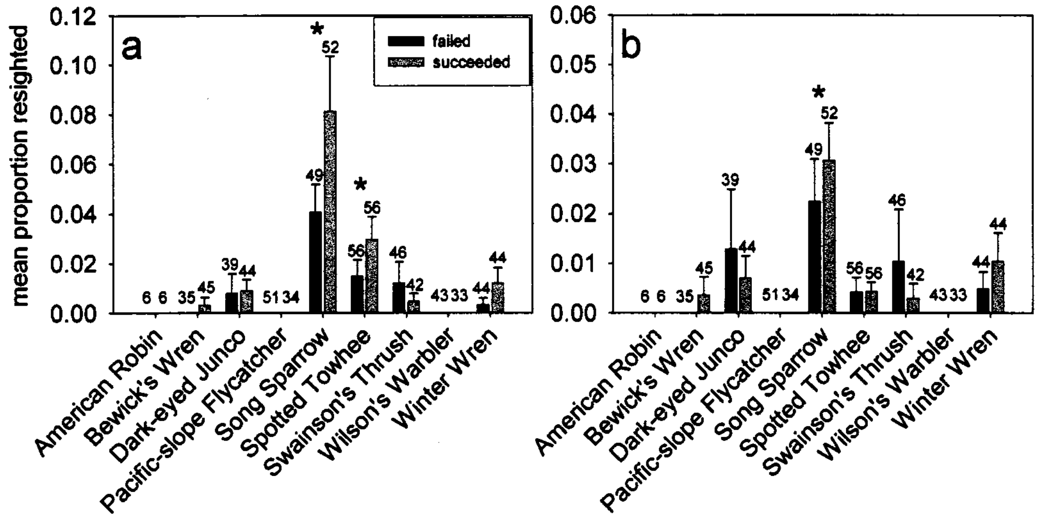


Figure 3.4. Mean proportion of resighted birds by breeding success the previous year, species, and movement category: a) site fidelity and b) breeding dispersal. Numbers above error bars (±1 SE) indicate sample sizes (site-species-sex-breeding success combinations). Asterisks above error bars indicate significant differences between groups (1-tailed $p < 0.05$).

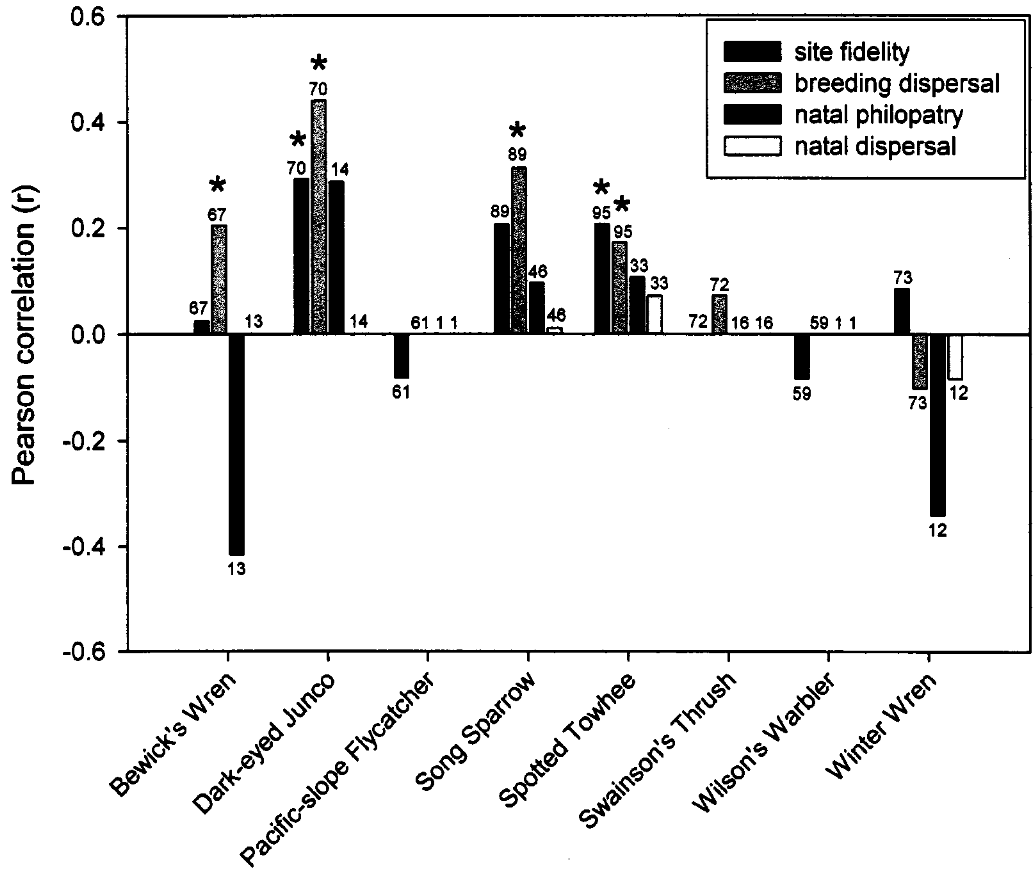


Figure 3.5. Results of Pearson correlations between territory density and each movement category. Sample sizes (site-year-species combinations) are given with each bar. Asterisks indicate correlations significantly different than zero.

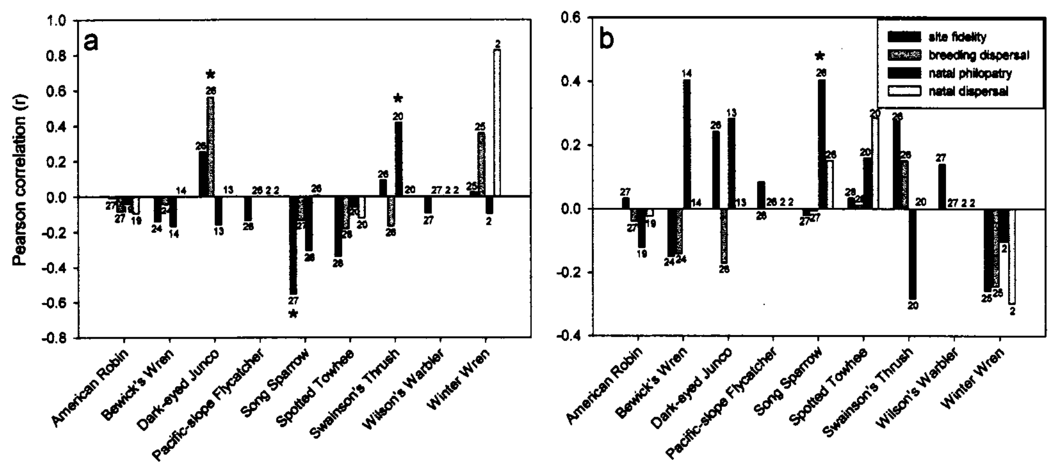


Figure 3.6. Results of Pearson correlations between rates of dispersal and philopatry and a) patch size and b) perimeter:area ratio. Sample sizes (site-species combinations) are given with each bar. Asterisks indicate correlations significantly different than zero.

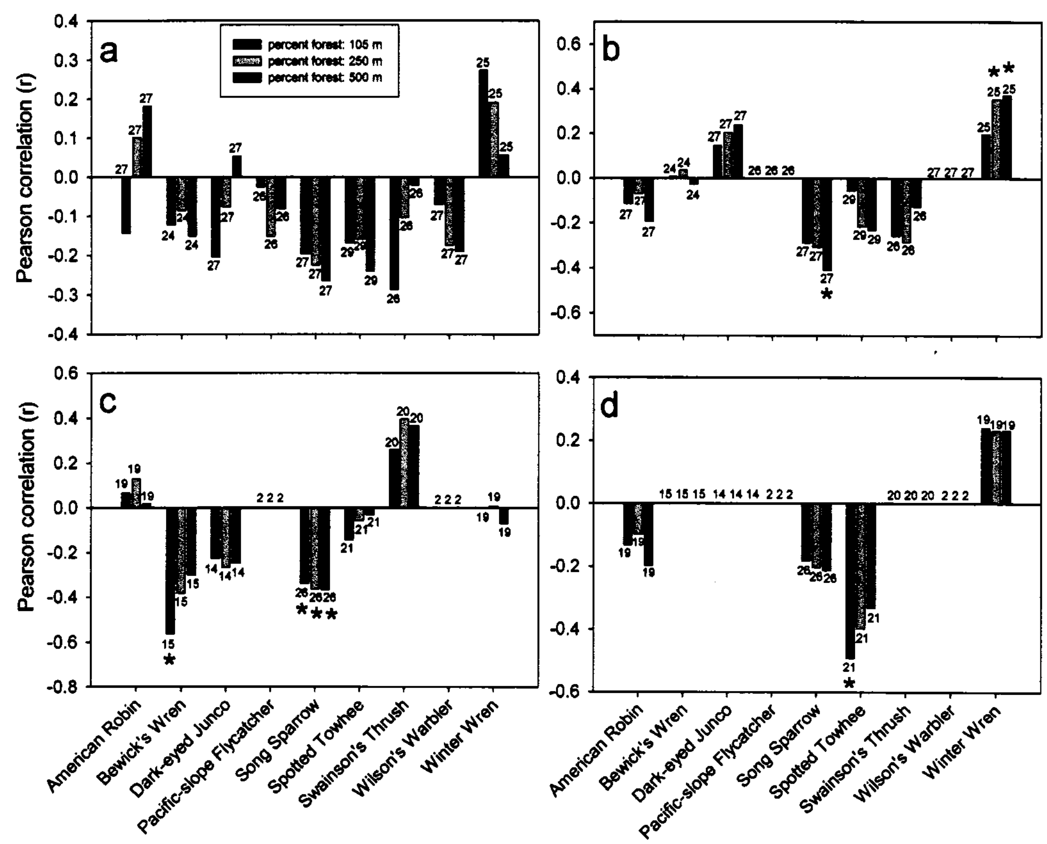


Figure 3.7. Results of Pearson correlations between percent forest and rates of: a) site fidelity, b) breeding dispersal, c) natal philopatry, d) natal dispersal. Numbers above bars indicate sample size (study sites). Asterisks above error bars indicate significant difference from zero (2-tailed $p < 0.05$).

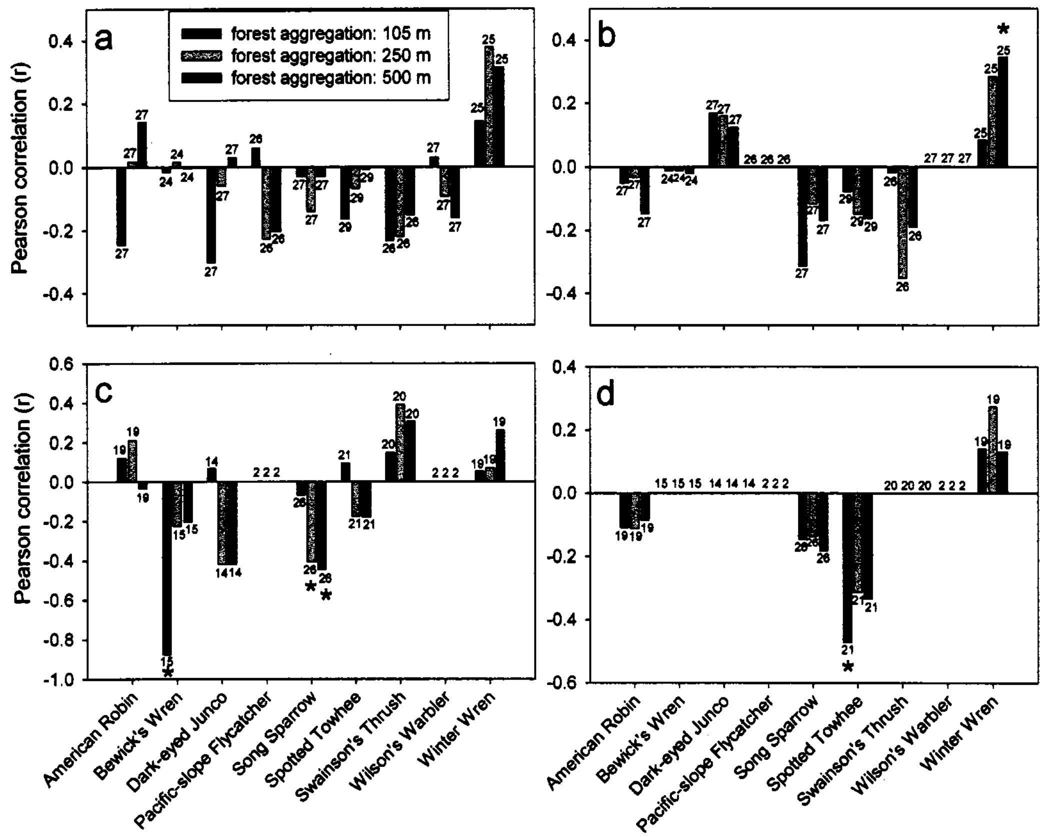


Figure 3.8. Results of Pearson correlations between forest aggregation and rates of: a) site fidelity, b) breeding dispersal, c) natal philopatry, d) natal dispersal. Numbers above bars indicate sample size (study sites). Asterisks above error bars indicate significant difference from zero (2-tailed $p < 0.05$).

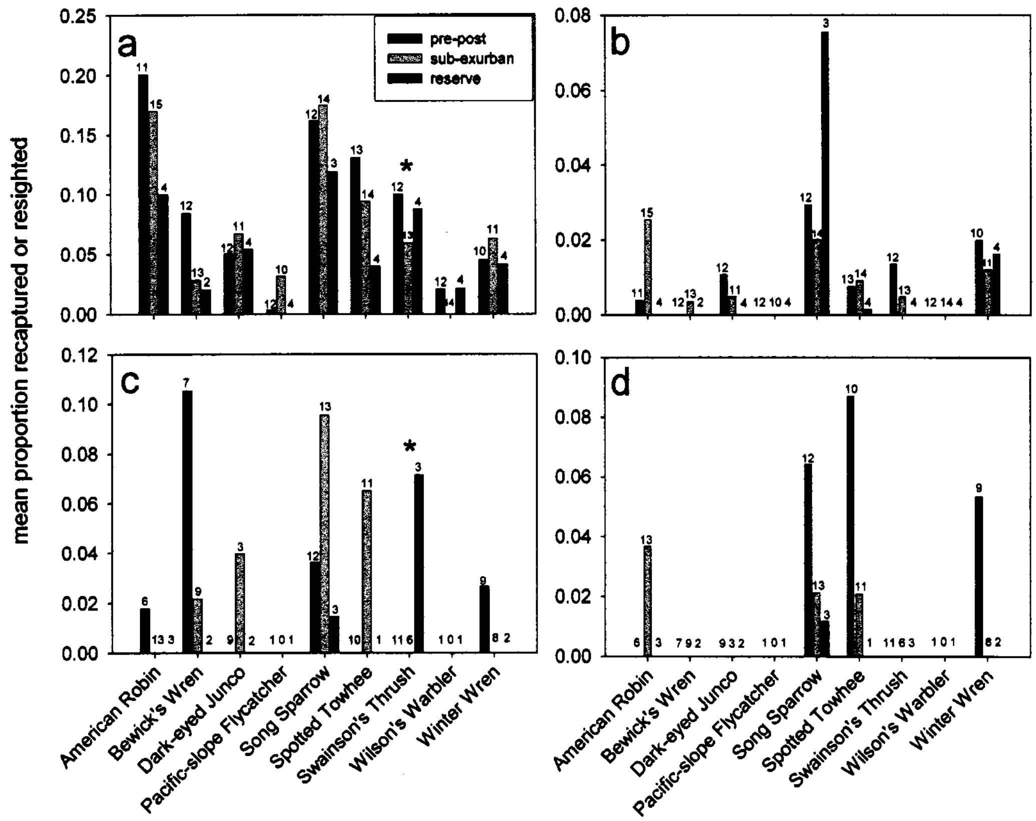


Figure 3.9. Mean proportion of recaptured or resighted birds by species and site category: a) site fidelity, b) breeding dispersal, c) natal philopatry, d) natal dispersal. Numbers above bars indicate sample size (study sites). Asterisks above bars indicate significant differences between sexes (2-tailed $p < 0.05$).

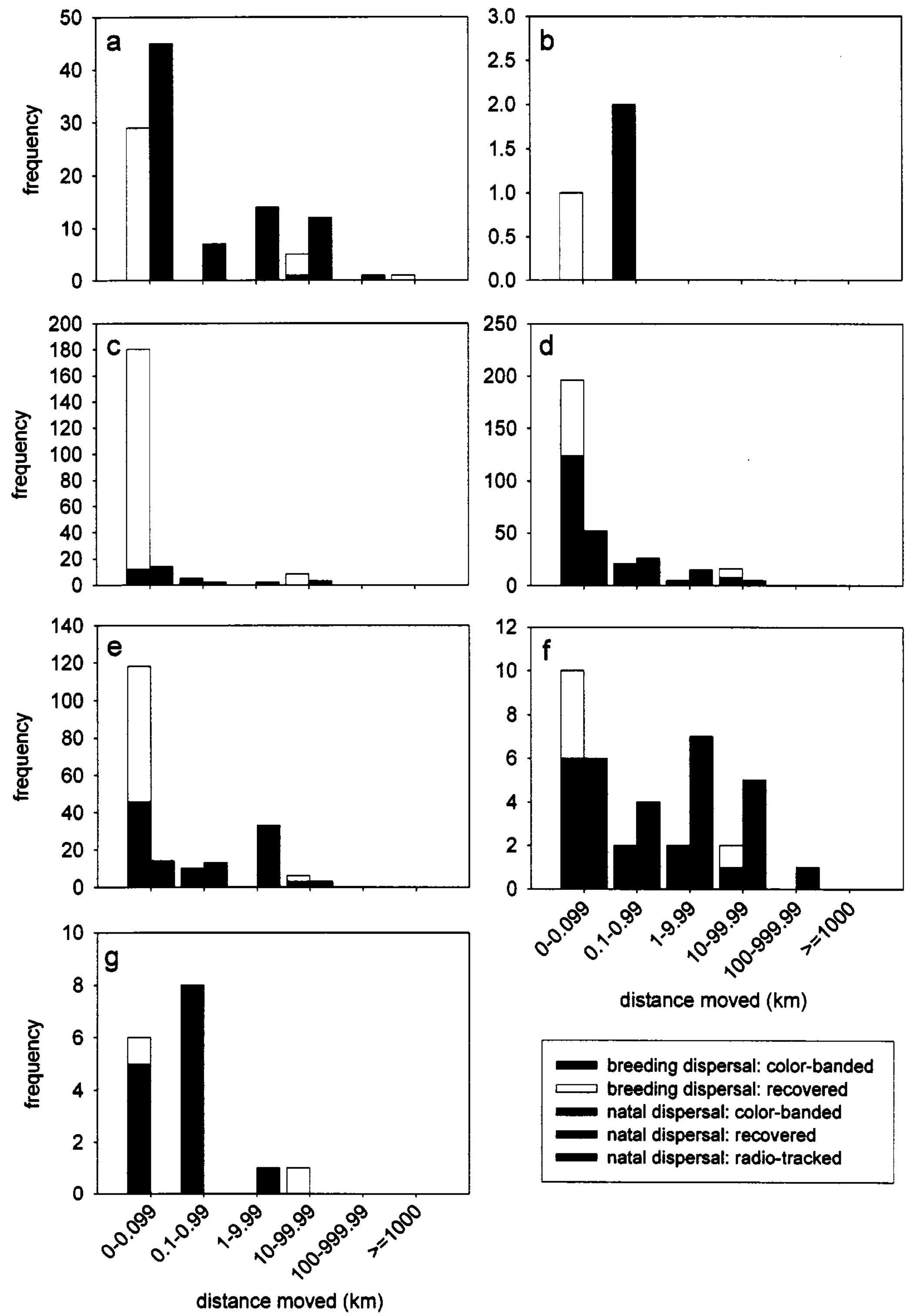


Figure 3.10. Frequency distribution of breeding and natal dispersal distances (km) by species and data source: a) American Robin, b) Bewick's Wren, c) Dark-eyed Junco, d) Song Sparrow, e) Spotted Towhee, f) Swainson's Thrush, and g) Winter Wren. Note log scale on x-axis.

Table 3.1. Territory density by species.

Species	average	SD	minimum	maximum
Bewick's Wren	0.50	0.39	0	1.76
Dark-eyed Junco	0.62	0.55	0	2.00
Pacific-slope Flycatcher	0.71	0.61	0	3.64
Song Sparrow	1.42	1.10	0	4.40
Spotted Towhee	1.05	0.70	0	3.34
Swainson's Thrush	0.83	0.69	0	4.65
Wilson's Warbler	0.50	0.48	0	1.93
Winter Wren	0.79	0.58	0	2.25

Table 3.2. Mean dispersal distances (m) of birds recaptured, resighted, or radio-tracked (juveniles only) by species, sex, and age.

	females			males			juveniles			adults			total		
species	mean	SD	N	mean	SD	N	mean	SD	N	mean	SD	N	mean	SD	N
American Robin	10906	0	1				4714	6467	26	10906	0	1	4944	6453	27
Bewick's Wren				138	0	1				144	8	2	144	8	2
Dark-eyed Junco	49	70	6	155	139	7	0	0	1	119	127	14	111	126	15
Song Sparrow	850	3559	28	1629	5923	116	2278	5167	51	1364	5302	158	1587	5271	209
Spotted Towhee	60	58	13	59	55	43	3092	3871	49	59	55	56	1475	3038	105
Swainson's Thrush	2234	2771	2	78	43	7	3380	5581	13	4109	10813	11	3714	8199	24
Winter Wren	181	75	3	156	190	9	3900	0	1	156	160	13	424	1012	14
total	770	2999	53	1064	4767	183	3107	5062	141	1094	4810	255	1811	4989	396

CHAPTER 4.
INCORPORATING SCIENCE INTO THE ENVIRONMENTAL POLICY PROCESS: A CASE STUDY FROM WASHINGTON STATE

Introduction

The use of science in environmental policy is a primary goal of resource management and conservation that is relevant to issues at global, national, and local scales. Explicit calls for the inclusion of science in policy decisions are found at levels ranging from the United Nations to city governments. The relationship between science and policy has been the topic of special issues of scientific journals, e.g., a 1995 supplement to BioScience, issue 51(6) of BioScience in 2001, an Ecological Society of America symposium in 1999, and countless national and international meetings involving scientists, policy makers, and natural resource managers. The debate about the use of science in policy has recently been highlighted by a report charging the White House with distorting the process by which scientific information is used to develop policy (UCS 2004). However, there is little empirical information about how science is actually used in formulating environmental policy at any scale.

The debate about the relationship between science and policy centers on questions related to how scientific information is incorporated into public policy. It is largely believed that there are inherent differences between the fundamental structures and traditions of science and policy. Correctly or not, the scientific process is assumed to be objective and logical compared with the policy process, which is often described as nonlinear and chaotic (Norse and Tschirley 2000). Alternate views describe the scientific method as limiting and inflexible, and inappropriate for use in environmental policy

(Tarlock 2002). Ultimately, gaps between science and policy probably exist because of their different stated values and goals (Collingridge and Reeve 1986, Policansky 1998, Kinzig and Starrett 2003).

Communication of science represents one of several key barriers to the use of science in policy (Policansky 1998, Weber and Word 2001, Kinzig and Starrett 2003), for example, when scientific arguments are used to mask a debate over values (Policansky 1998, Kinzig and Starrett 2003). Scientific uncertainty itself may also pose a major barrier to the effective use of science in policy (Lubchenco 1995), in part as a result of the difficulties in quantifying uncertainty (Kinzig and Starrett 2003). Furthermore, ecological research has traditionally excluded humans, which may have contributed to the gaps between science and public policy, especially in urban areas (Alberti et al. 2003).

Over the past decade, environmental policies have been amended to require that decisions be based on "best science" or "best available science" (BAS). These terms are often invoked to indicate the existence of some standard against which the scientific information collected and used by policy makers will be judged. In addition, requiring that decisions be based on BAS ensures that a record exists of the decision-making process that can be challenged and defended later. This requirement is applied to policies at all levels of decision making, including the United Nations Environmental Programme (UN 1992), the U.S. strategic policy on global climate change (CCSP 2003), the U.S. Endangered Species Act (ESA), the Washington State Salmon Recovery Program (JNRC 1999), and Washington State's Growth Management Act (36 R.C.W. § 70A.172). The BAS standard is controversial, as evidenced by legal action (Bogert 1994) as well as a report by the U.S. General Accounting Office (GAO) on the effectiveness of the BAS tenet of the U.S. Fish and Wildlife Service (USFWS) in the ESA (Brennan et al. 2003, GAO 2003). The GAO expressed concerns over the adequacy and function of the data used by the USFWS to designate critical habitat, suggesting that there were some disconnects between the science and its application in the ESA. The meaning of BAS is ambiguous, and its principle is often invoked without accompanying definitions or prescriptions for use (Bisbal 2002). Despite the widespread requirement that environmental policies be based on BAS, to date there have been few empirical studies on how decision makers include science in policy (but see Eliasson 2000).

Washington State's Growth Management Act (GMA) requires cities and counties to include BAS as part of the planning process for protecting critical areas. Critical areas include wetlands, fish and wildlife habitat conservation areas, aquifer recharge areas, geologically hazardous areas, and frequently flooded areas (Ousley 2003). The GMA requires that critical areas be protected before other planning requirements are fulfilled while acknowledging that other considerations are part of the decision-making process about land use. A technical work team assembled to interpret the GMA concluded that, by requiring the inclusion of science in critical areas ordinances, the state aims to "protect the functions and values" of critical areas (Ousley 2003). In addition, they acknowledged that some development may occur within designated critical areas, and that not all critical areas must be protected to the same degree (Ousley 2003). The work team also recognized that, before jurisdictions can include BAS, they must accomplish two tasks: (1) they must identify and collect the BAS relevant to their critical areas, and (2) they must interpret the assembled information to determine its validity and applicability to their local characteristics.

Washington State's Department of Community Trade and Economic Development (DCTED) has provided some guidance to jurisdictions in accomplishing these tasks (Ousley 2003), but has left much of the decision-making process up to local discretion. For example, the DCTED developed definitions of BAS, including the types of scientific information and associated characteristics that are considered by the state to be the BAS (Ousely 2003). Despite such efforts by state government, and because local governments must balance the protection of critical areas with other GMA goals such as increasing housing density within the urban growth boundary, it is likely that the various methods by which jurisdictions collect, interpret, and incorporate BAS mediate the influence of scientific information on the development of policy related to critical areas and, ultimately, their protection. Attention to jurisdictional characteristics such as population size, degree of urbanization, or resource base, as opposed to policies aimed at blanket solutions such as requiring the BAS, may be more effective in achieving policy goals.

In this study, we aim to provide some of the first empirical data addressing the major outstanding questions related to how science informs policy decision making. For example, how do policy makers determine what is the "best" available science? What gaps, if any, actually exist between science and policy? To answer these questions, we interviewed local policy makers in western Washington about how they used BAS to update critical areas ordinance (CAO), i.e., the local policy that governs land-use decisions in critical areas. Specifically, we present results related to how planners and others define, collect, and interpret BAS. Our study addresses four key questions: (1) How do jurisdictions define BAS? (2) How extensive was the review of BAS? (3) What were the major steps in the process for updating the CAO, and at what stage was scientific information incorporated? (4) How do jurisdictions make policy when they encounter what they perceive as conflict within BAS?

Where policy makers are required by law to incorporate science into policy, it is extremely useful to describe this process, not only for the purposes of adapting science to meet the needs of policy, but also for informing the interactions between policy makers and researchers. The results of our study provide much-needed information to ecologists who aim their research toward informing environmental management decisions. Our general goal here is to provide a case study lending insight into the process by which scientific information is incorporated into land-use planning policy at local scales, the resolution that is particularly relevant to issues of urbanization in the United States and across the globe.

Methods

Critical Areas Ordinance Update Process

Washington State's Growth Management Act (GMA) was updated in 1995 to require cities and counties, as part of the planning process, to include best available science (BAS) in designating and protecting the functions and values of critical areas. In addition, jurisdictions must "give special consideration to conservation or protection measures necessary to preserve or enhance anadromous fisheries" (Ousley 2003). Typically, jurisdictions designate and protect their critical areas in a policy document called a critical areas ordinance (CAO). In 2002, the GMA was further amended to require jurisdictions to update their CAOs every 7 yr, and the first jurisdictions were due to complete their updates by December 2004. Thus, our study was motivated in part by the fact that most western Washington jurisdictions would be incorporating BAS into their CAOs for the first time in 2004. It is the duty of the jurisdiction to justify its decisions about designating and protecting critical areas through its review of BAS. CAOs are subject to a public hearings process, and objections to the designation and protection of critical areas may be filed with the Western Washington State Growth Management Hearings Board, which then rules on the appropriateness of the ordinance.

Study Sample and Design

Our study area included the nine counties in Washington State mandated to update their CAOs by this first deadline (Fig. 4.1). We studied the cities and counties that had completed at least half of the BAS review associated with the update as of early 2003; their status was determined by phoning each jurisdiction. We contacted the planning or other departments responsible for the ordinance update of all 112 cities and nine counties in the study area. Our study sample included 21 cities and six counties, or 23% of all possible jurisdictions updating their CAOs by 2004. In addition, we focused exclusively on the sections of each jurisdiction's CAO that dealt with the biological critical areas: wetlands and fish and wildlife habitat, which also typically incorporated the "special consideration" for anadromous fisheries.

Following standard qualitative research methods, we used an interview strategy for data collection. Our approach involved an exploratory phase during which we conducted preliminary interviews, followed by the use of a semistructured interview protocol (Miles and Huberman 1994). In the preliminary interviews conducted over the phone, jurisdictions were queried about their general impressions of the requirement to include BAS in their CAOs. We used the information gathered during the preliminary interviews to develop the semistructured interview protocol (Miles and Huberman 1994). We pretested the protocol on planners in jurisdictions outside of our sample and on other local government employees involved in the implementation of the GMA amendment.

From December to May of 2003 we conducted 43 structured interviews, representing 27 jurisdictions, with city and county planners in lead positions for the CAO update process in their jurisdictions, as well as with any consultants they had hired to conduct the BAS review. In those cases in which the responsibility for the BAS review was specific to a particular type of critical area, we selected interviewees who had focused specifically on wetlands and fish and wildlife habitat conservation areas, because of the concern over threatened salmonid species and habitat in this region. We conducted face-to-face interviews with the majority of our respondents (n = 40), but, for logistical reasons, three were interviewed by telephone. The interviews consisted of a mixture of open-ended, fixed-response, i.e., yes/no, and scale questions, with the majority being open-ended. Interviewers were closely familiar with the interview guide and occasionally used prompts to clarify the intent of the question or to elicit a more detailed response. The interviews lasted 60–90 min and were taped and later transcribed. The four major themes that are the focus of this study are as follows:

- How did the jurisdiction define BAS, and what types of scientific information did they consider to be BAS?
- What was the extent (breadth, scope) of the review of BAS by the jurisdiction? Where did it get its scientific information?

- What were the major steps taken by the jurisdiction in the process of updating its CAO?
- How did the jurisdiction make decisions when there was contradictory scientific information?

The complete interview guide is found in Appendix 1.

Data Analysis

We developed an approach for analyzing interview data according to the principles of content analysis (Glaser 1967, Strauss and Corbin 1990), which describes an iterative process of breaking down, conceptualizing, and restructuring textual data. We imported entire interview transcripts into Atlas.ti (Scientific Software Development, Berlin, 1997), a qualitative data analysis software package for organizing and coding interview data. Codes, or descriptive labels, were applied to selections of text from the interviews to organize responses into categories for analysis. These codes were developed using both a priori (Miles and Huberman 1994) and inductive coding techniques (Strauss and Corbin 1990), such that some categories of responses were developed in advance based on our preliminary research, and some were developed based on what was said by the interviewees. The coding process is iterative and flexible, ultimately allowing for the designation of codes to be responsive to the data. To minimize bias in our results, coding was performed by all the authors, and each author coded a unique portion of the transcript. Throughout the data analysis process, all the authors compared coding strategies for consistency.

We hypothesized that we would see some variation in the use of BAS in CAOs, and that one pattern of this variation would be along a gradient of jurisdictional population size. We used population size as a proxy for variables that might impact the use of science in policy, such as resource base, level of urban development, and distance to a metropolitan center. We therefore analyzed differences in the patterns of BAS use between jurisdictions of different population sizes. We grouped jurisdictions into size categories based on U.S. Census 2000 figures: small = 1–30,000 (n = 11 jurisdictions), medium = 30,001–100,000 (n = 8 jurisdictions), and large = >100,000 (n = 7 jurisdictions, including all five counties in the sample). It is worth noting that 67% of the large jurisdictions were counties, which may differ from cities in terms of their political structure, financial resources, staff resources, and other key characteristics that may influence the questions addressed in this research. However, for most of the results shown here, the responses from the two large cities did not vary consistently from those of the four counties. It is also important to note that, because not all individuals answered every question, sample size varies slightly throughout the results.

Results

Definition of Best Available Science

Jurisdictions of different population sizes varied with respect to the types of scientific information defined as best available science (BAS) and used in their critical areas ordinance (CAO). All the jurisdictions interviewed used a variety of types of scientific information in their BAS review process (Fig. 4.2). Of 25 jurisdictions, 17 considered peer-reviewed literature to be BAS. In addition, 15 of 25 jurisdictions deemed government agency publications, such as those produced by the Washington State Department of Fish and Wildlife, to be BAS. These two categories were the most commonly used types of scientific information by jurisdictions of all sizes (Fig. 4.2). Jurisdictions differed, however, when it came to classifying data that were not peer reviewed as BAS. Some small (10%) and medium-sized (25%) jurisdictions used information that was not peer reviewed, such as local monitoring or survey data, as a form of BAS, in contrast with large jurisdictions, which did not.

Consultants hired by jurisdictions used peer-reviewed literature more frequently than planners did in their science review process. Consequently, whether or not a jurisdiction hired a consultant influenced the type of scientific information it used in its CAO (4. 2). Additionally, jurisdictions that hired consultants relied on a broader range of types of BAS (Fig. 4.2a). Of 11 small jurisdictions in our sample, six hired consultants, and those that did were approximately twice as likely to use state agency literature as were small jurisdictions that did not hire consultants. Medium-sized jurisdictions that did not use consultants were much less likely to use peer-reviewed literature than were jurisdictions of the same size with consultants (33% vs. 100%). Large jurisdictions that hired consultants, including both cities in the category, frequently (50%) used agency literature and rarely (0%) relied on expert opinion (Fig. 4.2a). Large jurisdictions without consultants, in contrast, rarely (0%) used agency literature, but often (50%) relied on expert opinion (Fig. 4.2b).

Extent of Best Available Science Review

Our results show that different-sized jurisdictions varied in the extent to which they collected scientific information (Table 4.1). Small jurisdictions most often stated that they used an existing bibliography as a starting point for their literature review. These bibliographies were either compiled by another jurisdiction or by the Washington State Department of Community, Trade and Economic Development, the department responsible for assisting jurisdictions with their update process. For example, one respondent stated, " ... I think in this particular case the state was pretty involved in trying to identify those sources that were appropriate ... we didn't attempt to produce any of our own scientific info, with not having the resources to do that. So it wasn't really a question in most cases, because the state department was responsible to kind of identify what they considered to be BAS. So it didn't require a lot of analysis on our part."

Small jurisdictions did not conduct extensive inventories and did not have in place a program for regular, ongoing review of BAS. In contrast, medium-sized jurisdictions more often stated that they had extensive inventories of their critical areas and were conducting ongoing reviews of BAS. Large jurisdictions, which in this case comprise five counties and one city, did not use bibliographies from other sources, frequently had a BAS review process in place, and had some on-the-ground information about their critical areas (Table 4.1).

Small jurisdictions commonly (82%) solicited comments on their BAS reviews, draft ordinances, or other components of the update process from other jurisdictions, state agencies, or other stakeholders in the process (Table 4.1). Large jurisdictions also regularly (83%) communicated with others outside of their jurisdictions about the CAO update process. Medium-sized jurisdictions were the least likely (38%) to solicit comment from others about their CAOs.

Steps in the Critical Areas Ordinance Update Process

We found that jurisdictions varied with respect to how BAS was incorporated into the policy-making process. We developed a conceptual model for the CAO update process to describe two typical starting points subsequent to the requirement by Washington State that jurisdictions update their ordinances: BAS Review and Policy Directive. Policy Directive is the expression of the political goals of the jurisdiction, usually by city or county council (Fig. 4.3). In 45% of all jurisdictions, BAS Review is the first step in the policy formation process (Point A in Fig. 4.3). Typically, this is followed by a gap analysis in which the jurisdiction's existing ordinance is compared against scientific findings or the state's model ordinance and "gaps" or areas that require updating to bring the ordinance in line with scientific recommendations or the state's guidelines are identified. Following the gap analysis, recommendations for updates to the ordinance are drafted, typically by the person(s) who reviewed the science. These recommendations are given to the staff responsible for writing the ordinance, usually the jurisdiction's planning department, for inclusion in the revised ordinance. At this point (Policy Directive II), the planning department may consider the political climate of the jurisdiction or the political aims of the city or county council, which may in some cases result in a policy that diverges somewhat from the purely scientific recommendations. A draft policy is then produced and taken through a public review process, which is often iterative and results in more ordinance revisions. Once the public review process is complete, the draft is forwarded to either the city or county council for adoption. The council may request further revisions, after which the policy may be sent through the public process again.

In nearly a quarter of jurisdictions examined, the policy formation process is initiated by the political directive of either the city or county council (Fig. 4.3). In these situations, policy directives drive the scientific review, either by directing the review of BAS toward certain findings to achieve a desired outcome, or by limiting the scope of the scientific review to certain sections of the ordinance update. As one interviewee noted, " ... [the city/county] council decided to ... write their own [critical areas ordinance] ... they figured this was their best shot at making their mark on a policy document. It actually says that in the contract—they want their policy direction to be incorporated. Now they would've had their shot at it anyway, once it got to them—it's a lot better if you can have your fingers in it from the very beginning and draft it and direct it all the way from the beginning to the very end."

From here, the process follows the review process described above, although the scientific review is typically abbreviated and less emphasis is placed on the gap analysis.

Two additional policy formation frameworks exist. In one, the model ordinance created by the state government is adopted largely without changes, including the biophysical standards for critical area protection, and no scientific review or policy directive is applied. This process is used by 14% of the jurisdictions. The last framework is one in which scientific information and political concerns are addressed simultaneously and throughout the policy formation process. In this framework, representing 18% of the jurisdictions, the basic steps are the same, but at each point the scientific information is considered in conjunction with the socio-political landscape of the jurisdiction. For example, in one jurisdiction, scientific information included in the state's model critical area code is considered alongside existing city code and planning commission recommendations. As one interview respondent explained, " ... what the consultant and the city staff have come up with is this matrix as a tool ... [The matrix describes] each different critical area and what the BAS ought to be, based on state statute requirements and ... the [state's] model code and GMA. [It summarizes] what the [state's] model code is saying, what our existing city code says, and then what the planning commission has been developing as recommendations to the city council."

Jurisdictions of different population sizes varied as to when BAS was incorporated into the policy process (Table 4.2). Approximately three-quarters of large jurisdictions, including both cities in this category, started by reviewing BAS at the beginning of their ordinance update process. Likewise, the number of small jurisdictions that considered science first was greater than the number that either started with a policy direction, or considered both policy and science concurrently. In contrast, none of the medium-sized jurisdictions stated that they began the policy update process by considering only scientific information. Further, in approximately two-thirds of these jurisdictions, policy directive drove the rest of the process. Approximately one-quarter of small jurisdictions relied on the state's model ordinance without using either the direction of science or policy to inform the update process.

Resolving Decisions About Conflicting Best Available Science

We found some variation in how jurisdictions make choices about conflicting scientific information. Because most cities and counties incorporate critical areas designations and protection measures into land use regulations, they typically include specific biophysical standards of protection, for example, wetland buffer widths. Therefore, jurisdictions often select single values even when they perceive that there is disagreement within the scientific community about appropriate protections. A majority of respondents (64%) said that they decide on these single values by evaluating the scientific information, whereas 31% considered political or legal influences. One example of how jurisdictions evaluated science was that they use the most reliable or rigorous science available, as described by another respondent, "So what we do is try to look at all of [the studies] and figure out which is most applicable and which is most reliable—which has been developed under the more controlled circumstances so that you can actually relate it, hopefully, to the situation that you're concerned with."

This pattern did not hold, however, for jurisdictions of all population sizes (Fig. 4.4). After evaluating science, the most common strategies for small jurisdictions were relying on state government sources (40%) and considering political or legal influences (50%). One respondent noted, "Scientists have the luxury of looking only at the science, whereas a city, a functioning multifaceted entity, a political entity has to think about and balance a wide range of considerations when applying the science."

Similarly, the second most common (38%) influence on choices for medium jurisdictions was politics or legality. Another respondent described this as, "Policy pull.

You look at what you're trying to do. When you have conflicting information like that you always have to look at what the goals of the city are. You have to look at where the council wants us to go in the future. We weigh towards policy."

In addition, medium-sized jurisdictions often (25%) said they applied a conservative or precautionary approach in the face of conflicting scientific information. A respondent from a medium jurisdiction stated, "I have a fairly conservative approach towards protecting resources where I think that in the absence of information, we should err on the side of protecting things. So that's probably the overarching philosophy that guides my decision making."

In contrast, the second most common (43%) strategy used by those reviewing science in large jurisdictions, both cities and counties, was to provide a range of scientific criteria to decision makers, rather than making a single recommendation.

Discussion

Environmental policies at all levels of government are increasingly expected to be developed through decision-making processes with a scientific basis. One of the goals of Washington State's Growth Management Act in requiring that policy makers use best available science (BAS) is to provide more specific policy direction to cities and counties that ensures protection of critical areas (Copsey 1999). However, the results of this study suggest that the use of scientific information by local governments in land-use policy is variable, and that requiring BAS may not serve the function intended for all jurisdictions.

Size Matters

We found that the size of a jurisdiction's population was important in determining how science was collected and used in developing their critical areas ordinance (CAO). Small jurisdictions with populations of less than 30,000 conducted less direct analysis of scientific information (Table 4.1). This could be because smaller jurisdictions may have more limited financial resources because of their small tax base; in addition, they may not have biologists on staff. No small jurisdiction interviewed had scientific experts on staff, as compared with 13% of medium jurisdictions and 71% of large jurisdictions. Small jurisdictions were more heavily reliant on outside resources in developing their ordinances, with little internal generation or analysis of BAS and little specific information about the distribution of critical areas on their landscape. This was evidenced by their preferential use of BAS bibliographies produced by state agencies or other jurisdictions (Table 4.1) as well as by the relatively high use of agency literature and communication with other jurisdictions and agencies (Figs. 4.2 and 4.4). This suggests that the choice of science used by small jurisdictions is at least in part influenced by their limited financial resources and related lack of scientific expertise in planning departments. One potential result of this is that state agencies may have more direct influence over critical areas protection policies in smaller jurisdictions, because the most commonly used BAS bibliography was the one prepared by the responsible state agency. The state of Washington was at least in part aware of the potential for this financial disadvantage, because they offered small grants (U.S. $16,000) to all jurisdictions to help defray the cost of the ordinance update process.

The patterns of collection and use of BAS by medium-sized jurisdictions demonstrates that these jurisdictions have greater resources as well as a higher degree of on-the-ground knowledge about their critical areas. Higher levels of financial resources, as would be expected because of the larger tax base, as well as larger staffs with more biologists allowed for ongoing review and collection of scientific information as well as extensive inventories (Table 4.1). Extensive inventories, which usually include detailed mapping and classification of all the critical areas in a jurisdiction, are a source of information about local conditions and are often costly and time-consuming to produce. The Growth Management Act (GMA) requires jurisdictions to designate their critical areas, and medium-sized jurisdictions are consistently able to do this.

The relatively high level of internal biogeographical knowledge in medium-sized jurisdictions that did not hire consultants was coupled with some reclusive tendencies, such as relatively low reliance on expert opinion as BAS (Fig. 4.2), little communication with other jurisdictions or agencies regarding their BAS reviews (Table 4.1), and low levels of expert consultation or government agency input to help resolve conflicts (Fig. 4.4). This infrequent consultation with agencies or other experts implies a more inward focus, with an emphasis on local conditions and locally generated information. In addition, some medium-sized jurisdictions were highly insular, indicating no use of peer-reviewed literature or government agency data but, rather, high dependence on locally generated information. As one respondent noted, "I intend to show people we're using local knowledge, local resources, local science, local common sense, and we are not flying in from Harvard with a 1500-page manual on how wetlands should be."

This locally focused approach by medium-sized jurisdictions was coupled with a greater influence of politics on the ordinance update process. After evaluating science, the most common influences on the choices made by medium-sized jurisdictions about conflicting scientific information were politics or legal issues (43%) and the use of a conservative or precautionary approach (29%; Fig. 4.4). Policy direction from city or county councils and stakeholders is not uncommon at this stage of the process, and, in the face of scientific uncertainty, a conservative approach is often the safest one, both legally and ecologically. Critical areas ordinances are subject to challenge by any party, and such disputes are resolved by the Growth Management Hearings Board (GMHB). If a jurisdiction's CAO is challenged and found to be out of compliance with the GMA by the GMHB, the jurisdiction may risk the loss of state funding.

Small jurisdictions were also influenced by politics, but this influence probably had less effect on the overall update process. Although nearly half (45%) of small jurisdictions also considered political influences when making choices about conflicting science, only 9% used this as their sole strategy when making choices. This is in contrast to medium-sized jurisdictions, 29% of which relied on political or legal considerations as their sole strategy in making decisions about conflicting science. Political influence ultimately is reflected in the policy update process. Medium-sized jurisdictions most frequently started their ordinance update process with policy directives or other political influences, rather than science. Thus our results suggest that medium-sized jurisdictions have enough resources to make them less reliant on outside sources, more inwardly focused, and more responsive to local political influences than to agency science.

Large jurisdictions, which included all the counties in our sample, have the greatest resource base, both financially and in terms of staff expertise. The patterns we observed in large jurisdictions are consistent with what might be expected of counties, given their elevated resource levels. However, we also found that the two cities in the large category shared these characteristics, suggesting that the patterns we see are not necessarily associated with a particular jurisdictional level, but rather with population size and resource base.

Not only did larger jurisdictions more often regularly review scientific information outside of the ordinance update process, but they also frequently conducted their own scientific research and generated their own BAS, which was often peer-reviewed and published (Table 4.1). The overwhelming majority of the BAS used by large jurisdictions is peer-reviewed literature, suggesting that large jurisdictions are familiar with the literature, probably because of their greater resources and expertise. Moreover, large jurisdictions, when faced with making choices about conflicting scientific information, evaluated the science itself and relied less on documents produced by government agencies. In several cases, the flow of information between large jurisdictions and agencies was reversed: counties and large cities often provided data and research findings to agencies. Thus, the larger jurisdictions generate their own BAS, are more familiar with the primary literature, and also provide BAS to government agencies.

The level of political influence in the ordinance update process was relatively low in large jurisdictions. These jurisdictions were less frequently guided by the political climate in their jurisdictions when confronted with conflicting results in BAS (Fig. 4.4), and instead preferentially relied on ranges of biophysical standards. In these cases, respondents frequently dealt with conflicting scientific information by giving a range of scientific values, also called scenarios (Bennett et al. 2003), to decision makers. This is a strategy common to consultants charged with scientific review, indicating their role in providing scientific information but refraining from making choices for the jurisdictions. As one consultant observed, "What we usually tell our clients and the cities and counties is that the science doesn't give you a one point, one answer. It gives you a range."

Additionally, the policy update process in large jurisdictions was most frequently informed by science, rather than by political direction (Fig. 4.3). It may be, therefore, that the high resource levels and high degree of connection to peer-reviewed literature in large jurisdictions supercede reliance on political motivations for decisions about critical area protection.

Role of Consultants

Consultants were commonly hired by the jurisdictions in our sample (62% of all jurisdictions hired consultants) to review BAS, make recommendations about protection standards, update ordinance language to meet state requirements, and, in some cases, write entire sections of the CAO. Another factor that influenced both the collection and use of scientific information was the involvement of consultants in the scientific review process, and this influence differed among jurisdictions of different sizes. Over half of the small jurisdictions in our sample hired consultants, many of them using grants from Washington State's Department of Community Trade and Economic Development (DCTED) to pay for consultant services. For these small jurisdictions, consultants increased the effective availability of scientific information for jurisdictions that might otherwise have been limited by their expertise and resources. Also, hiring consultants to review BAS more often was associated with using science to inform the rest of the update process in jurisdictions of all sizes. In some cases in which science was not the driver of the policy update process, and in which jurisdiction staff were responsible for the entire update process, jurisdictions simply adopted the model ordinance without any science review. Thus, it appears that one role of consultants in this process is to temper the isolation characteristic of small jurisdictions and broaden their access to science.

What is uniformly clear in these results is the influence of the Washington State government on the CAO update process. Jurisdictions of all sizes, whether they hired consultants or not, relied heavily on the resources provided by DCTED. Nearly all jurisdictions had seen or used both the model ordinance and the Citations of Recommended Sources of Best Available Science prepared and circulated by DCTED when it was known as the Office of Community Development (OCD 2002). Because of this, there was a high degree of similarity among the bibliographies of all the jurisdictions included in this study, although we do not present the results of those analyses here. In addition, the appearance of a specific piece of scientific literature in a jurisdiction's bibliography was not necessarily associated with following the protection levels contained therein. State agencies often review draft CAOs for compliance with the GMA prior to adoption by the jurisdiction. This process provides an opportunity for BAS to carry more weight, but lower standards are allowed if they are explicitly justified by the jurisdiction in the context of the other goals of the GMA. Thus, despite an overarching similarity in the definition of BAS, the nature of the BAS used in critical areas ordinances by the jurisdictions in our sample varies widely.

Conclusion

Complex environmental policy decisions are often informed by scientific data, and calls for the inclusion of best available science (BAS) in environmental policies occur at local to global scales. As yet, scientists and policy makers have not determined how best to make this relationship work. It is expected that governments, which are required to represent all their constituents and their myriad needs, will consider many factors in decisions about resource use and protection. However, even in situations in which it has been determined that the protection of critical habitat should be the primary goal of the decision-making process, it is likely that this protection will vary.

Our results show that the incorporation of scientific information into local policies is not uniform, and that, in many cases, political rather than scientific forces have a greater influence on decisions about natural resources. This study reflects the common perception among those individuals responsible for protecting critical areas in western Washington State that they are straddling a science/policy divide. It is unclear to whom the responsibility belongs for this continued science/policy disconnect. Scientists often present conflicting information to policy makers without providing adequate tools for handling scientific uncertainty and disagreement. Further, there is room within the findings presented by scientists for policy makers to mask their political or social values with scientific data, confirming what others have suggested: that the different values and objectives inherent in science and policy prevent successful partnerships. It is also clear that financial resources and other pressures on local governments can influence the protection of natural resources, and that policy makers in different jurisdictions are not using the same science when making their decisions.

To fully understand the direct connection between the use of science and on-the-ground protection of natural resources, quantitative analyses of the variability in protection measures as a function of the policy process are necessary. As the world becomes more and more urban (Sadik 1999), the gap between scientific information, typically collected in "natural" settings, and the policy goals of growing cities may widen. The good news is that heavy involvement by state agencies, in this case in the form of suggested protection measures based on the review of scientific literature, can bridge the gap of limited financial and expertise resources. However, it is likely that, given the often divergent goals and values of scientists and policy makers, and until the pressing environmental questions are posed jointly, simply offering up the goods, i.e., BAS, and telling people to use them correctly will not work to uniformly protect natural resources.

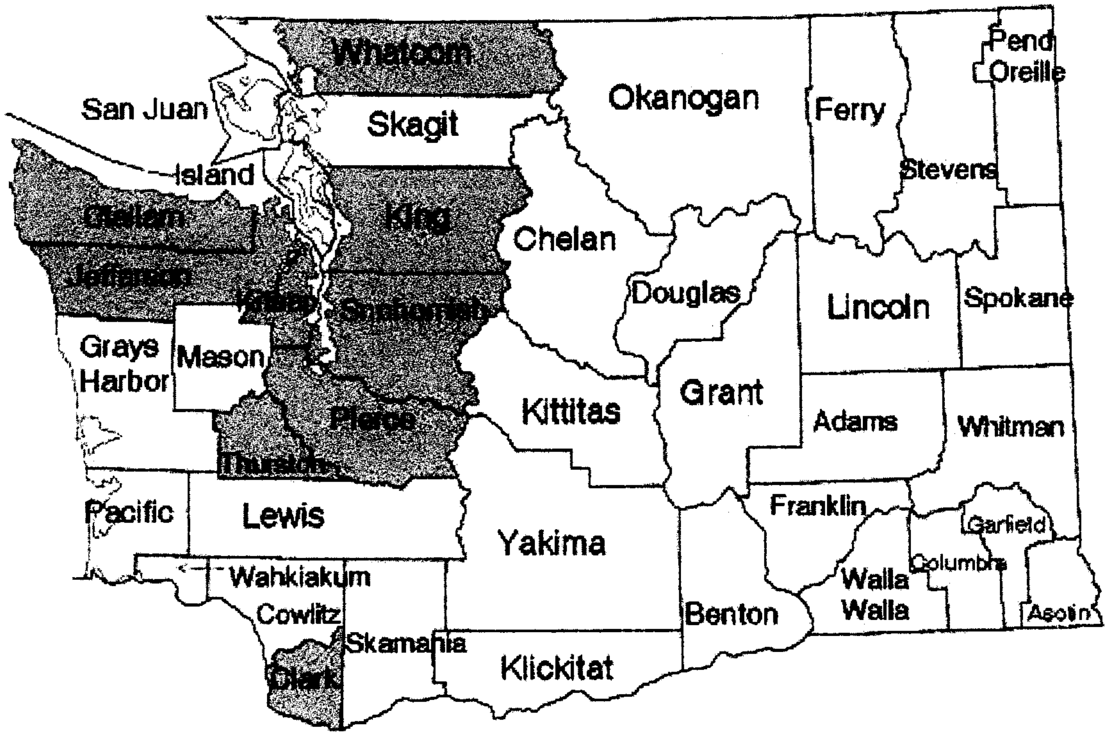
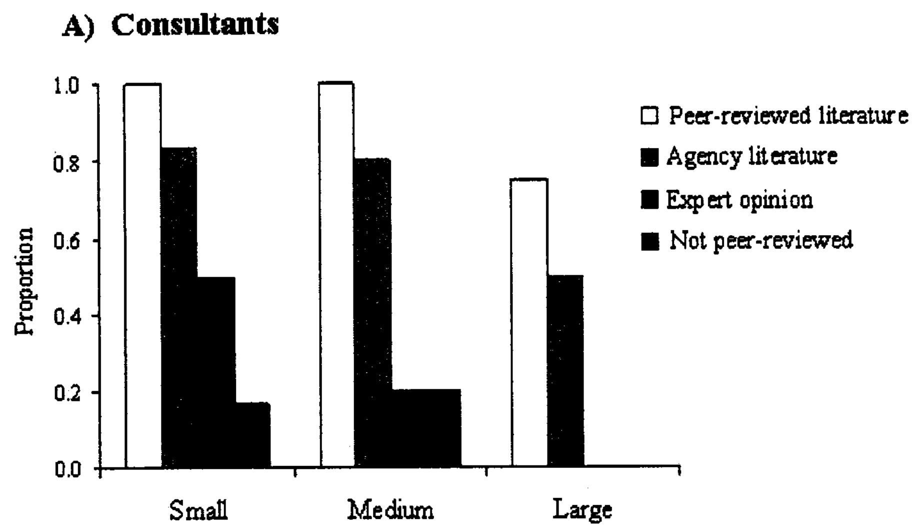


Figure 4.1. Map of counties of Washington State. Counties and cities therein required to update their critical areas ordinance by December 2004 are shaded. (Adapted from http://quickfacts.census.gov/qfd/maps/washington_map.html).



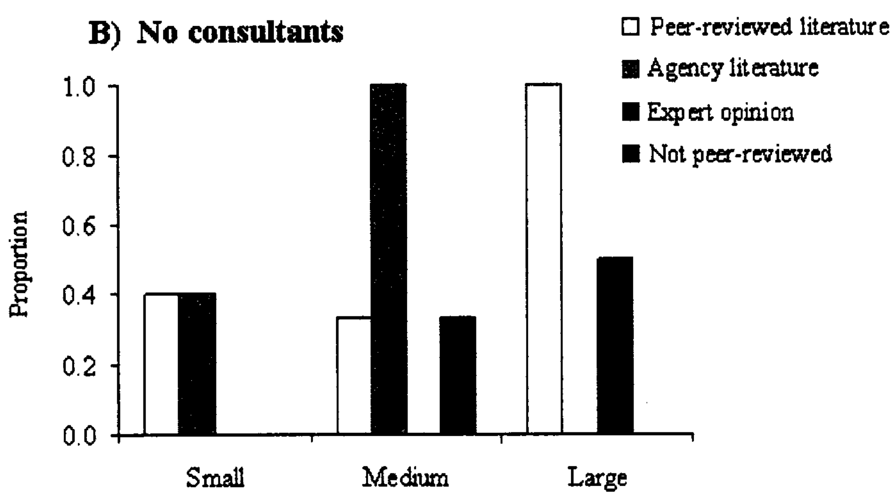


Figure 4.2. Types of scientific information considered best available science (BAS) by jurisdictions in Washington State. Of n = 25 jurisdictions, 15 hired consultants to review BAS (A), and 10 did not (B). Results for the large category include one city and three counties that hired consultants and two counties that did not. Because most jurisdictions consider more than one type of information to be BAS, total proportions shown for each population size category are greater than 1.0. Government agency publications include syntheses of peer-reviewed literature as well as internal research documents and reports that often are internally reviewed. Expert opinion includes the verbal opinions of jurisdiction biologists, agency biologists, consultants, and other individuals who were deemed to be "experts" on a given subject. Information that was not peer reviewed includes monitoring data, inventories, jurisdictional research, and other sources of data that have not gone through a peer-review process.

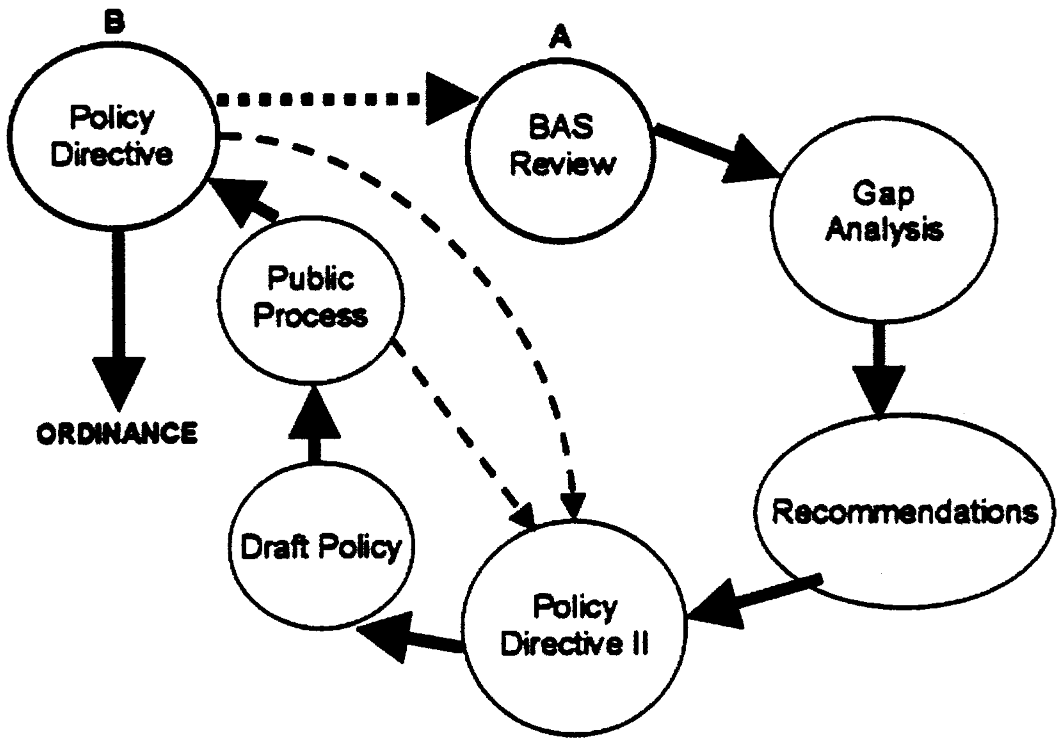


Figure 4.3. A generalized model of the critical areas ordinance update process. Point A represents one starting point, specifically, review of science; 45% of all jurisdictions review science as the first step in updating their ordinance. Point B represents an alternate starting point at which political considerations precede scientific information and often drive research; 23% of all jurisdictions consider politics before science in updating their ordinance. In gap analysis, a jurisdiction's ordinance is compared to scientific findings or the state's model ordinance to identify missing pieces. Policy directive is potentially applied by two stakeholders in the process: the City or County Council and the Planning Department, Planning Commission, or work groups that include political appointees and citizens.

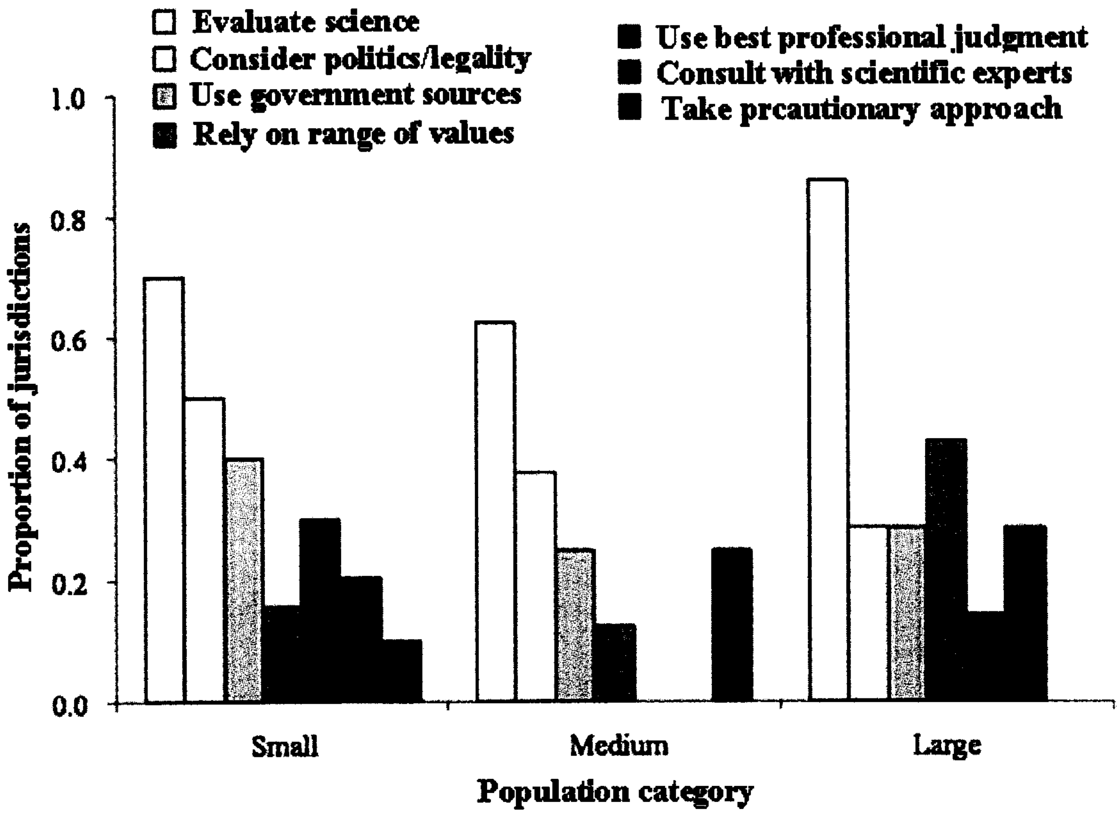


Figure 4.4. Strategies used by jurisdictions of different sizes to choose between conflicting scientific information (n = 11 small, 7 medium, and 7 large jurisdictions).

Table 4.1. Extent of the review of best available science (BAS) by jurisdictions of different population sizes. Numbers represent the percent of jurisdictions that followed one of four strategies for collecting scientific information used to update their critical areas ordinance (N = 25).

Population size	Used an existing bibliography (%)	Conducted ongoing BAS review (%)	Generated own BAS (%)	Extensive inventory of critical areas (%)	Solicited comments from others (%)
Small (n = 11)	91	9	0	0	82
Medium (n = 8)	38	25	0	50	38
Large (n = 6)	0	50	50	33	83

Table 4.2. Critical areas ordinance update process followed by jurisdictions in western Washington State. Numbers represent the percent of jurisdictions following one of four policy formation processes (N = 25). The first three processes are diagrammed in Fig. 4.2.

Population size	Consider best available science first (%)	Consider political influences first (%)	Science and policy are considered concurrently (%)	Used state's model ordinance only (%)
Small (n = 11)	36	18	18	28
Medium (n = 3)	0	67	33	0
Large (n = 7)	72	14	14	0

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APPENDIX. INTERVIEW TRANSCRIPT

The following is the full interview conducted with planners in western Washington State, as well as the consultants they hired, concerning the update of critical areas ordinances (CAOs) in their jurisdictions. The interviews were conducted primarily face-to-face, and the questions are a mix of three types: open-ended, fixed response, i.e., yes/no, and scale questions. The interviews were taped and later transcribed, and the text was used in the analyses presented in the main article. We do not present results from all of the data collected below in the present article.

Introduction Spoken to Interviewee Prior to Beginning Interview

We are interested in the science-policy relationship, and our goal is to understand how the critical areas ordinance update process varies across jurisdictions and what factors can explain this variation. Specifically, we are focusing on wetlands, fish and wildlife habitat conservation areas, and anadromous fish.

Questions to Planners

1. Within your department, please explain the main steps in the update process, and identify the main people involved and their roles.
2. What other groups are part of the update process, and how are they related to your department and each other?
3. What stage in the update is your jurisdiction currently in?

Questions to Consultants

1. Please explain what you were specifically hired to do for the city or county's CAO update.
2. How extensive of a review were you tasked with?
3. How far into this process are you?

Questions to All

4. Has your jurisdiction completed a critical areas inventory?
    a. How detailed is it?
5. Has your current CAO changed since the last CAO?
6. In a general sense, how much has it changed?
7. More specifically, what types of changes occurred?
8. Do you expect that this update process will lead to additional variances or exemptions in your new ordinance?
9. Considering all the changes you've just described, what are the main factors you think are responsible for these changes?
10. Are any of the changes being made to the current CAO a direct result of your best available science review?
    a. If yes, which ones? Please describe why.
    b. If no, please describe why not.

(If update not fully completed)

11. Do you anticipate that the final draft of your CAO will be different from your current draft?

a. On a scale of 1 to 5, how much do you expect it to change?

1 - no change 2 - minor change 3 - moderate change 4 - significant change 5 - very significant change ? - don't know (too early)

12. In addition to your critical areas ordinance, does your jurisdiction have other measures or regulations to protect or conserve specific critical area types?
13. What is your working definition of best available science (BAS)?
14. What types of scientific information constitute BAS?
15. How did you compile your BAS list? For example, did you start with an existing list?
16. Are you familiar with the BAS list prepared by the state Office of Community Development?
17. Does your bibliography vary from it? How? Why?
18. What qualities or characteristics of BAS make it useful to you?
19. When there is conflict in BAS, how do you decide what BAS to include in making recommendations for the CAO?
20. What types of information do you pull from BAS?
21. Using an example, could you describe how you synthesize multiple ideas, numbers, or information found in BAS?
22. If BAS suggests a range of biophysical criteria to protect a critical area type, how do you decide what criteria to recommend for the CAO?
23. How well does BAS apply to the critical areas in your jurisdiction?
24. Can you describe why/why not, using an example?
25. Are there any constraints on your review of BAS?

(Only for those who have completed their update process)

26. Did your BAS review lead to any specific biophysical changes?
    a. (If YES) Was one of those changes in your buffer widths?
    b. (If YES) Can you identify any specific BAS that led to the buffer width change?
27. If the BAS didn't lead to that change, how did you arrive at the specific change?
    a. (If NO) Why not?
28. Were there any other specific changes to the biophysical criteria?
29. We're interested in three main types of critical areas. I'd like to know which of them this jurisdiction has.
    a. Wetlands?
    b. Fish and Wildlife Habitat Conservation Areas?
    c. Anadromous Fish?

I'm going to read you a direct quote from the RCW (36.70A.172) related to critical areas ordinances and then ask you to interpret three parts of it.

"In designating and protecting critical areas under this chapter, counties and cities shall include the best available science in developing policies and development regulations to protect the functions and values of critical areas."

30. For each critical area type you just listed, how do you interpret "designating and protecting?"
31. For these same critical areas, how do you interpret "functions and values?"
32. How do you interpret "shall include the best available science?"
33. Are you working with scientific experts on this update? (If yes) What kind?
34. On a scale of 1 to 5, what is the priority of the update process for your jurisdiction?

1 - no priority 2 - minimum priority 3 - moderate priority 4 - high priority 5 - very high priority

35. Is there a specific person or group who is making the update a priority?
    a. (If yes) Who and why?
36. Does this priority impact the way the science is reviewed or how the ordinance is updated?
    a. (If yes) How?
37. What proportion of your time is devoted to the update process?
38. Are there any competing environmental regulatory issues you are dealing with?

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Honors: cum laude

Professional Experience

Co-Owner and Vice President, Alki Kayak Tours, Seattle, Washington, 2005-present.
Wildlife Technician, USDA Forest Service, Quilcene, Washington, 2001.
Wildlife Biologist, Duke Engineering and Services, Inc., Bellingham, Washington, 2000-2001.
Teaching Assistant, (Foundations of Biological Sciences I & II), University of Wisconsin-Milwaukee, Department of Biological Sciences, Milwaukee, Wisconsin, 1997-1999.
Field Research Assistant, University of Wisconsin-Milwaukee Field Station, Saukville, Wisconsin, 1998-1999.
Volunteer Bird Banding Assistant, Aves Sin Fronteras, Pewaukee, Wisconsin, 1999, and UW-Milwaukee Field Station, Saukville, Wisconsin, 1997-1998.
Field Research Assistant, Hastings Natural History Reservation, Carmel Valley, California, 1997.
Songbird Intern, Whitefish Point Bird Observatory, Paradise, Michigan, 1996.

Awards

EPA STAR Fellowship, 2004-2007
UW College of Forest Resources Lockwood Fund Travel Award, 2006
UW Graduate School Fund for Excellence and Innovation Travel Award, 2004, 2006
UW College of Forest Resources Dean's Travel award, 2004
NSF IGERT Fellowship, 2001-2004
North American Ornithological Conference, Marcia Brady-Tucker Award, 2002

Olympic National Forest, Outstanding Performance Award, 2001
Sigma Xi, Grant in Aid of Research, 1999
UW-Milwaukee Graduate Fellowship, 1998-1999
Wisconsin Society of Ornithology Nelson Award, 1998-1999
Ivy Balsam-Milwaukee Audubon Society Scholarship, 1998
Whitefish Point Bird Observatory Intern of the Year, 1996

Scientific Publications

Peterson, K. A., K. J. Thusius, L. A. Whittingham and P. O. Dunn. 2001. Allocation of male parental care in relation to paternity within and among broods of the common yellowthroat (*Geothlypis trichas*). Ethology 107(7): 573-586.

Thusius, K. J., K. A. Peterson, L. A. Whittingham and P. O. Dunn. 2001. Male mask size is correlated with mating success in the common yellowthroat. Animal Behaviour 62(3): 435-446.

Thusius, K. J., P. O. Dunn, K. A. Peterson, and L. A. Whittingham. 2001. Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. Behavioral Ecology 12(5): 633-639.

Francis, T., K. Whittaker, V. Shandas, A. Mills and J. Graybill. 2005. Incorporating Science into the Environmental Policy Process: a Case Study from Washington State. Ecology and Society 10 (1): 35. [online] URL: http://www.ecologyandsociety.org/vol10/iss1/art35/

Publications Pending

Marzluff, J. M., J. C. Withey, K. A. Whittaker, D. Oleyar, J. DeLap, T. Unfried, and S. Rullman. In Press. Consequences of Habitat Utilization by Nest Predators and Breeding Songbirds across Multiple Scales in an Urbanizing Landscape. Condor.

Whittaker, K. A. and J. M. Marzluff. In Review. Post-fledging mobility in an urban landscape. Studies in Avian Biology.

Whittaker, K. A. and J. M. Marzluff. In Preparation. Species-specific survival and habitat use in an urban landscape during the post-fledging period. Auk.

Mills, A., T. Francis, V. Shandas, K. A. Whittaker, and J. K. Graybill. In Preparation. Using Best Available Science to Protect Critical Areas in Washington State: Challenges and Barriers. Urban Ecosystems.

Presentations

Peterson, K. A., K. J. Thusius, L. A. Whittingham and P. O. Dunn. Male parental care and paternity in the common yellowthroat (*Geothlypis trichas*)(poster). American Ornithologists' Union Conference, Cornell University, Ithaca, NY, 1999.

Peterson, K. A., K. J. Thusius, L. A. Whittingham and P. O. Dunn. Male Parental Care and Paternity in a Double-brooded Species with Brood Division (poster). American Ornithologists' Union Conference, University of Washington, Seattle, WA, 2001.

Peterson, K. A., K. J. Thusius, L. A. Whittingham and P. O. Dunn. Male Parental Care and Paternity in a Double-brooded Species with Brood Division (presentation). North American Ornithological Conference, New Orleans, LA, 2002.

Francis, T., K. Whittaker, V. Shandas, A. Mills, and J. Graybill. Using science in the environmental policy process: A case study from Washington State (poster). Campaign UW: Creating Futures, Visiting Committee Luncheon. University of Washington, Seattle, WA, 2004.

Whittaker, K. A. and J. M. Marzluff. The Effects of Urbanization on the Dispersal of Native Forest Songbirds (presentation and panel discussion). EPA STAR Fellowship Conference: Ecosystem management in terrestrial habitats (breakout session). Hyatt Regency on Capital Hill, Washington, DC, 2004.

Whittaker, K. A. and J. M. Marzluff. The effects of urbanization on the dispersal of native forest songbirds (presentation). East Lake Washington Audubon Society meeting. Kirkland, WA, 2004.

Whittaker, K. A. and J. M. Marzluff. Differences between species in dispersal probabilities, movement patterns, and characteristics of urban landscapes used during the post-fledging period (presentation). University of Washington College of Forest Resources Graduate Student Symposium. Seattle, WA, 2006.

Whittaker, K. A. and J. M. Marzluff. Species-specific probabilities of dispersal and movement patterns through an urban landscape during the post-fledging period (poster). Conserving Birds in Human-Dominated Landscapes: The Center for Biodiversity and Conservation's Eleventh Annual Spring Symposium. American Museum of Natural History, New York, New York, 2006.

Whittaker, K. A. Urban Ecology & Urban Bird Communities of the Seattle area. Elderhostel Meeting, Red Lion Hotel, Seattle, WA, 2006.

Whittaker, K. A. and J. M. Marzluff. Species-specific movement patterns and mortality rates in an urban landscape during the post-fledging period (poster). EPA STAR Fellowship Conference: Hyatt Regency on Capital Hill, Washington, DC, 2006.

Whittaker, K. A. and J. M. Marzluff. Species-specific movement patterns and mortality rates in an urban landscape during the post-fledging period. North American Ornithological Council Meeting, Veracruz, Mexico, 2006.

Whittaker, K. A. and J. M. Marzluff. Species-specific movement patterns and mortality rates in an urban landscape during the post-fledging period. Partners in Flight Meeting, Corvallis, OR, 2006.

Professional Memberships

American Ornithologists' Union, 1997-present
Wildlife Society, 2003-present
Alpha Chapter, Xi Sigma Pi (Forestry Honor Society), 2005-present