Designing research to advance the management of birds in urbanizing areas

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Abstract

Managers charged with maintaining self-sustaining populations of native wildlife in urbanizing areas can protect habitat reserves and encourage development styles that minimize negative impacts on wildlife. Unfortunately, few data are available to guide these activities with respect to bird conservation. Studies are needed that determine principles of reserve design and development pattern that maximize reproduction and survivorship of native birds. Good experimental design is needed to insure such studies have strong inference. To optimize our ability to relate changes in urban areas to biodiversity we need to consider how to (1) select research sites, (2) describe the urban gradient, (3) quantify wildlife community parameters, (4) quantify wildlife population parameters, and finally (5) identify the mechanisms affected by human activity that link population level processes to community level patterns. We provide advice for these decisions from our ongoing studies of reserves and developments in the Seattle, Washington area. We encourage researchers to combine correlational and experimental studies to determine the mechanisms that link human activity to bird population viability. Especially useful studies will elucidate how the pattern of human settlement and the properties of reserves affect several important possible limiting factors (nest predation, food or nest site availability). Understanding of how local and landscape-level condition affect limiting factors allows managers to design ways to reduce effects on populations. Prescriptions for maintaining native bird communities should be built from such mechanistic understanding of how to protect several populations. Community prescriptions should not be built from simple measures of community composition because presence of a species may not indicate viability. It is important to measure reproduction and survivorship of individuals in urban landscapes. Direct measurement of reproduction should be supplemented with multiple indirect measures (e.g. ratio of juveniles to adults, rates of predation on artificial nests) to increase accuracy. Important limiting factors (e.g. nest predators, brood parasites, food sources) should be studied to determine how human activity directly affects them. Well designed studies provide managers with the information they need to accurately determine how a combination of reserves and developments of varying density and pattern combine to maintain native bird populations in an urbanizing environment.

INTRODUCTION

Although human population growth worldwide has slowed from its peak 30 years ago (2% annually), our population continues to grow (1.2% or 78 million annually; United Nations 1999). This growth and the recent migration to cities have, in part, fueled the formation of new urban centers and urban sprawl in the U.S. and abroad (Berry 1990). As the dominant land uses shift toward commerce, residence, and industry in urbanizing areas; native habitat is degraded and wildlife communities change.

Biologists charged with managing self-sustaining populations of native wildlife in urbanizing areas have 2 basic options: (1) set aside reserves of native habitat, or (2) minimize the impact of development on native species by adjusting features such as housing aggregation, housing density, and the

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relative composition of various land use types. The extensive literature on reserve design has lead to the adoption of a few rules that have not changed appreciably since their first mention and often blindly guide reserve selection: protect larger patches of native habitat, protect patches of native habitat that are farthest from development, and link patches of native habitat with undeveloped corridors (Wilson and Willis 1979; Adams and Dove 1989; Noss 1999). Unfortunately, little rigorous study is available to support these claims. Furthermore, few studies to date have investigated the relative impacts of various development styles despite growth management statutes that give managers substantial control over the spatial pattern of development.

Studies of birds in urban areas can help guide reserve design and suggest patterns of development that minimize negative effects on biodiversity. Birds provide a powerful signal of changes in landscape configuration, composition, and function. They are sensitive indicators of the cumulative effects of urbanization. A casual trip from any large city to the wild produces a transition from flocks of exotic Rock Doves (*Columba livia*), European Starlings (*Sturnus vulgaris*), House Sparrows (*Passer domesticus*), and corvids to less abundant, but more diverse native avifaunas. Despite the obvious impact of urbanization on birds, this phenomenon has attracted relatively little research interest (Marzluff et al. 1998).

Urbanization affects birds both directly and indirectly (Marzluff 1997). It directly changes ecosystem processes, habitat, and food supply. Indirectly, it affects birds' predators, competitors, and diseases. These lead to quite significant changes in birds' population biology, and to resulting changes in bird communities. Urbanized habitats typically support larger (by biomass) and sometimes richer (more species), or less evenly distributed avian communities, dominated by a few very abundant species (Pitelka 1942; Emlen 1974; DeGraaf and Wentworth 1981; Rosenberg et al. 1987; Mills et al. 1989). Urbanization alters normal selective pressures so that the composition of urban avian communities differs from those found in native environments (Beissinger and Osborne 1982; Rosenberg et al. 1987; Mills et al. 1989; Blair 1996; Bock et al. 1997). Species able to exploit urban environments (especially introduced exotics) have dense and stable populations because ameliorated climate, abundant food and water, reduced predators, and increased nest sites allow for lengthened breeding seasons, increased survival, and increased productivity (Gehlbach 1994, 1996). Many native species do not attain dense and stable populations in urban areas because of the scarcity of natural habitat and intolerance of human activity.

HOW SHOULD WE STUDY THE INFLUENCE OF URBANIZATION ON BIRDS?

Studies of the effects of urbanization on birds are typical of ecological studies in general. They are usually correlational and limited in time and spatial extent (Marzluff and Sallabanks 1998). A recent review of 102 published studies of bird responses to urbanization characterizes the typical urban bird study as lasting 3 years (median duration), measuring community composition, and employing a correlational approach (Marzluff and Donnelly in press). Only 10 studies (9.8%) addressed important mechanisms (nest predation, food availability) that limit bird populations. Correlational studies are valuable first assessments and important as hypothesis generators. However, to fully understand how humans affect natural systems (and provide managers with ways to successfully reduce these effects) we need long-term, widespread, experimental studies (Kareiva and Anderson 1989; May 1994). Moreover, empirical and theoretical research suggests we need move beyond simple measures of community composition and measure population demographics across urbanization gradients (Van Horne 1983; Pulliam 1988).

We suggest that future studies build on past research by incorporating correlational and causal investigations of bird responses to urbanization. Studies should seek to describe community level patterns and explain them with mechanistic understanding of population- and community-level processes. When the population-level responses of many species are known we can begin to understand how urbanization affects the entire community. However, community-level patterns remain only superficially understood if they are not based on a detailed understanding of populations. To understand population responses requires us to understand how urbanization affects limiting factors. For bird populations, nest predation, brood parasitism, and food availability are important limiting factors (Robinson and Wilcove 1994; Newton 1998).

Studies should also acknowledge that planners and managers to provide for wildlife by (1) protecting patches of native habitat and (2) minimizing the negative effects of development. Although reserve design has received considerable attention from researchers and policy makers, it is unwise to rely on reserves alone to conserve biodiversity in urban areas because development quickly surrounds and impacts even well protected land. Some species may only be maintained in large reserves (notably habitat interior specialists), but many species can be maintained in developed areas if we identify required habitat elements and suggest how these can be provided within proposed developments. Designing reserves and managing development should proceed in tandem to preserve a substantial fraction of our native biodiversity. In this paper we suggest how researchers can design studies to guide reserve design and development pattern. We draw on our ongoing study of birds along a gradient of urbanization intensity in the Seattle, Washington area to discuss (1) a correlational approach to the study of reserve design, (2) a correlational approach to the study of urban pattern, and (3) an experimental approach to understanding how the pattern of development affects birds.

CONSIDERATIONS FOR THE DESIGN OF URBAN WILDLIFE STUDIES

Urban areas provide many opportunities for the researcher because modifications to the landscape are rapid, often replicated, and variable. This makes it possible to (1) determine how size, shape, and surrounding development affect the ability of reserves to conserve species, (2) correlate development pattern with diversity, and (3) observe changes in diversity through time as development proceeds. To optimize our ability to relate changes in urban areas to biodiversity we need to consider how to (1) select research sites, (2) describe the urban gradient, (3) quantify wildlife community parameters, (4) quantify wildlife population parameters, and finally (5) identify the mechanisms affected by human activity that link population level processes to community level patterns. We discuss all but quantifying the urban gradient below. Alberti (in press) discusses quantification of the urban gradient.

Selecting Research Sites

Specific research objectives determine many attributes of research sites, but some generalities exist. Any correlational study of response along a gradient requires study sites to be distributed along the gradient and replicated at several points. Replication at end-points and mid-points along the gradient provides the ability to test for lack of fit, a crucial design property for urban studies where one needs to determine if biological processes respond to urban development in a linear or nonlinear fashion (Marzluff 1986). Causal studies also require replication, but they are dependent on comparisons of treatments and control sites. In urban settings, spatial and temporal comparisons can be used to determine causation. Temporally, biological responses can be compared before and after development. Spatially, biological processes can be compared at matched pairs of developed and undeveloped sites. Both comparisons should be included in designs so that the generality of well controlled, before-after comparisons can be tested. Causal studies therefore require study sites that are (1) likely to be developed, (2) currently being developed, and (3) undeveloped but similar to developed sites.

In our study, we selected 3 sets of sites to determine how urbanization affects birds: (1) an extensive series that varies in reserve size and surrounding landscape, (2) an extensive series that varies in existing development pattern, and (3) a small number of sites slated for development to monitor biological responses before, during, and after development. Sites to be developed often function as reserves prior to development and reserves that are never developed often function as low development endpoints for the study of urban pattern.

Sites that we selected for our study of urban reserves varied in size and surrounding landscape. Size can be neatly quantified from digital orthophotos. Landscape variables such as land use intensity and land use heterogeneity are more difficult to measure, but a first approximation can be made using moderately sized buffers (~1-3 km) around the site. Measures of intensity have traditionally been limited to population density and housing density. However other measures of intensity such as job density and mean income level are acceptable and may be more sensitive indicators of ecological function (Alberti in press). Distance from the urban core is not recommended as a land use intensity metric. Measures of heterogeneity can include the juxtaposition and dominance of any of the intensity measures. The results of landscape analyses are likely to be dependent on the scale at which landscape variables are measured. Therefore, we also suggest measuring these variables at multiple scales (e.g. land use intensity within 0.5, 1, 3, and 5 km buffers around sites) that are based upon logical arguments, such as distance to nearest food source for brood parasites or nest predator territory size. Remember that species may respond at multiple scales and those scales may vary among species (Hostetler in press).

<u>Reserve Design</u>.—In our study of reserves, we selected 27 patches of native forest that represent the range of reserve sizes and land use intensities across the study area. Site selection was facilitated by grouping sites at three nodes along gradients of size and landscape composition (Table 1). Replicated points on the urban gradient should represent differences expected to affect animals. Average responses can later be cast into categories of land use intensity regularly used and defined by urban

planners. All sites will be monitored for 4 years to minimize the effect of annual variation on wildlife community parameters.

Correlative Study of Urban Pattern.—To begin to understand how the pattern of urban development affects birds we identified areas where human population density was constant and selected 30 sites which varied in urban form and land use heterogeneity. As with the study of reserves, our study sites include 3 points on a continuum of urban form (highly concentrated, moderately concentrated, dispersed) and 3 points on the land use heterogeneity spectrum (highly mixed, moderately mixed, and uniform). Since survey points at each site will be placed within the development and in abutting reserves, some sites may be used for study of both reserve characteristics and housing aggregation/heterogeneity.

Experimental Study of Urban Pattern.- Determining how urban patterns cause changes in avifaunas required us to consult with county or state wildlife and engineering review staff who are well acquainted with the development permit process. They helped us select tracts of native habitat in the areas that are likely to get developed (typically exurban) at a range of densities in the near future. Regional economic downturn or permit appeals may limit the number of sites actually developed, so we choose extra sites with the knowledge that some will not be developed. Sites that do not get developed during the study can be used as controls, essential elements of research design for landscape studies. Regardless of how well sites are chosen, measuring potentially confounding variables is important because no two experimental sites are identical. Important variables include age and composition of remaining habitat, disturbance history, wildlife feeding and yard maintenance, elevation, and proximity to large habitat reserves.

Quantifying Wildlife Community Parameters

Community parameters (diversity, species richness, equitability) are coarse measures of how development influences wildlife. They indicate what species are able to persist in urban environments and may suggest causation if particular guilds decline with urbanization. Community statistics are merely suggestive because "persistence" does not necessarily imply "viability". Long-lived, vagile organisms like birds may persist in or annually colonize an area with a net rate of reproduction (R_o) less than one. We need to distinguish between persisting populations that are at a minimum self-sustaining and "population sinks" (Pulliam 1988) by measuring individual survival and annual reproductive success.

Standard survey techniques can be used to obtain community statistics. DeGraaf et al. (1991) found that transect counts performed better than point counts in the Midwest. For our reserve and causal studies, we use point counts because transects were not feasible in densely vegetated reserves and consistency among the reserve and pattern studies was desired. We conduct fixed radius (50m) point counts. The number of points per site varies from 1-8 depending on the size of the reserve or development. Small patches contain 1 point. Points were set within the medium and large reserves using 2 parallel transects with 150m between transects and between points on the transects. This systematic approach was modified in many instances in order to maintain a 100m distance from forest edges. For the pattern studies, points were set within native habitat to remain as green space and within the development that has or will occur; As a result, we can test for how the development affects the remaining green space and the site as a whole. After an initial settling period of 1 min at each point, all birds seen and heard during the following 10 minutes are identified to species and recorded. Surveys continue for an extra 10 minutes (total of 20 minutes) at each point in small patches and the 2 most distant points in larger stands. The additional survey time is required to get a realistic abundance estimate for animals with larger home ranges (e.g. corvids) or more secretive manners (e.g. mammals).

Once several surveys have been completed at each site, abundance data must be processed before calculation of community statistics. There are a variety of methods for summarizing these data. In order to minimize the effects of migrating individuals and wandering males of resident species in the spring and misclassified juveniles in late summer, we suggest reporting the mean number of non-corvid songbirds per point per survey. Calculate these values by averaging the number of individuals in each species observed per point during a survey, then divide the sum of those survey means by the number of surveys to obtain a grand mean. This method is more appropriate for these birds than a maximum count. Survey maximums are appropriate, however, for species such as corvids that are less likely to be detected as a result of their relatively large territory size. To estimate the abundance of such a species, average the number of individuals observed per 20 minute point, and identify the maximum of these average values. Measures of community diversity and equitability can be calculated using standard statistics (Magurran 1988).

Quantifying Wildlife Population Parameters

As stated above, we feel that the measurement of reproductive success and survivorship is essential to understanding how urbanization affects bird populations and, ultimately, bird communities. Ideally we would measure lifetime reproductive success for all species by monitoring nesting attempts and mortality. Since search time constrains the number the nests that can be found and indirect techniques for estimating productivity are fraught with biases (Major and Kendal 1997), it is best to supplement the monitoring of nesting attempts with multiple indirect measures of productivity. While their use may seem inefficient, redundant productivity measures can increase the accuracy of estimates by considering multiple lines of evidence. Supplemental measures include juvenile to adult ratios for individual species and artificial nest survivorship (especially if nest predation may be important). Netting to obtain a juvenile to adult ratio may facilitate estimation of individual survivorship through color banding, providing that the focal species exhibit high site fidelity and reasonably small territories.

In our ongoing studies, productivity and survivorship are estimated annually in 2 reserves representing the endpoints of both design variables (8 sites total; Table 1), in 2 reserves representing the median values for both design variables (2 sites total), and in all sites to be developed. Concentrating the productivity and survivorship effort at a subset of sites allows us to increase the sample of nests per site. Following the effort allocation scheme outlined above increases the probability that we will detect existing patterns and non-linear trends (Marzluff 1986).

Standard nest searching techniques are used to locate breeding attempts by birds nesting on the ground and in shrubs (Ralph et al. 1993, Martin and Geupel 1993). We focus on finding the nests of only a few species: American Crow (*Corvus brachyrhynchos*), American Robin (*Turdus migratorius*), Bewick's Wren (*Thryomanes bewickii*), Pacific-slope Flycatcher (*Empidonax difficilis*), Song Sparrow (*Melospiza melodia*), Spotted Towhee (*Pipilo erythrophthalmus*), Wilson's Warbler (*Wilsona Pusilla*), and Winter Wren (*Troglodytes troglodytes*). We selected this suite of species because it represents a range of nesting habits and guild associations, species in decline (Andelman and Stock 1993), common species offering a decent sample of nests, and potential nest predators. Constraining the total number of focal species also allows us to more easily develop and maintain nest search images.

Nest locations are described using landmarks and bearings so that the attempt can be monitored without threat of leaving cues for predators (Picozzi 1975). We visit each nest every 4-5 days and on the expected date of fledging in order to record the fate of the nest as successful, depredated, or parasitized (^{3} 1 host fledged), parasitized (only parasite fledged), or parasitized (abandoned). Care is taken to approach nests from a variety of directions to avoid making the nest conspicuous. Nests are not checked if corvids are in the area. We correct for the time at which the nesting attempts are discovered using the Mayfield method (Mayfield 1961, 1975) and appropriate modifications (Johnson 1979; Hensler and Nichols 1981). Every effort is made to follow banded breeders throughout the season so that we can calculate annual success rather than success per attempt. This may be a much more meaningful measure, since birds may compensate for nest predation or brood parasitism by renesting. Recent modeling indicates that birds in urban areas cannot compensate through such behavior (Schmidt and Whelan 1998), but field data addressing this question are lacking.

Ratios of juveniles to adults are obtained by capturing birds with mist nets from early May to early July. Ten mist nets are operated for 5 hours beginning at dawn; each site is sampled 3 times. This is a standardized technique used in the Monitoring Avian Productivity and Survivorship program (MAPS; Desante 1992). Each captured bird is aged according to Pyle's (1997) aging criteria and banded with a unique combination of colors in order to prevent double counting birds on a given trapping day. We consider juveniles greater than 1.5 weeks post-fledging to be potential immigrants and do not consider them when calculating daily ratio.

We also estimate productivity through artificial nest experiments. We place equal numbers of ground and shrub nests in productivity stands and check their status (depredated or active) every 3 days for a total of 27 days. This exposure time approximates the mean incubation and brooding time for many of the focal species. Rather than placing the same total number of nests in large and small stands, 24 and 16 nests are deployed respectively to avoid supersaturating smaller stands. One third of the nests within a height stratum are placed at 50 m, 100 m, and 200 m from the forest's edge. One experiment is performed in each stand, beginning within the second half of May.

Ground nests are made of grass wrapped around a minimal wire frame and placed in sword ferns (*Nephrolepsis obliterate*) or other natural ground vegetation providing 100% cover from 5 m in each of the 4 cardinal directions and overhead. Taken together, the construction and placement mimic nesting attempts by Song Sparrows. Shrub nests are constructed of grass and moss (more of the latter) wrapped around a minimal, but comparatively large, wire frame. These nests are placed around 2 meters off the ground in shrubs or small trees in order closely mimic the nests of American Robins. For each shrub nest, we record cover from 5 m in each of the 4 cardinal directions and overhead.

Into every nest we wired 2 blue, plastic eggs (18 by 12 mm) coated in paraffin. We score predation events by the presence or absence of marks on the eggs or, in some cases, in the nest lining. Nest predators are identified by matching marks in the paraffin to signatures defined at nests with motion sensitive cameras and tooth measurements from museum specimens. Two nests with camera sets run continuously from early May through mid-July in stands where we study productivity and survivorship. Once a predation event is recorded, we relocate the entire nest setup. These nests are not included in the formal nest predation experiment. The influence of stand-level design factors (reserve size, surrounding urbanization intensity, housing aggregation) and nest variables (distance from edge, height strata, and total cover) on the rate of nest failure are quantified using Cox's proportional hazard regression (Lee 1980).

Taken as a whole, the 3 measures of productivity described above provide a much more convincing argument than any single, obtainable measure. For example, American Robins showed consistently poor reproductive success in one of our large urban reserves: 33% of nests fledged young (n=9), 17% of artificial shrub nests were "successful" (n=24), and the juvenile to adult ratio was 0:2. Despite small sample sizes, these data strongly suggest that robins reproduce poorly in this reserve and may depend on immigration for maintenance. Averaging productivity metrics across replicates should provide a powerful test of the influence of design factors on reproductive success.

Understanding Mechanisms

Once the urban researcher has an understanding of bird viability, they should investigate the mechanisms that cause bird communities to change in response to urbanization. Mechanistic studies improve the rigor of our science and provide managers with the information they need to successfully and accurately manage birds (Marzluff et al. in press). Important mechanisms to understand include: factors that limit avian populations, such as food and nest site availability, nest predation, and nest parasitism.

We study nest predation as a mechanism that links urban development to population productivity, and eventually community composition. This is arguably the most important limiting factor for open-nesting birds in many urban areas because nest predators have increased as a result of human introductions and diet supplementation (Martin 1995; Marzluff et al. in press). However, this is only a hypothesis and other limiting factors, such as food and nest site availability should be investigated. Ideal studies will investigate the interaction of important limiting factors. Understanding mechanisms that limit populations allows us to suggest how managers can improve conditions for urban nesting birds.

We encourage urban researchers to study mechanisms such as predation and move even further by studying the predators themselves. Few studies of avian nest predation actually study predators (Marzluff and Restani 1999). Nest predators are abundant and varied in urban settings. Among primary nest predators are corvids (jays, crows and ravens). Despite the importance of corvid predation, no study has focused on habitat use, productivity, and foraging behavior of these birds in urban landscapes. Small mammals (mice, rats, cats, squirrels) are abundant in urban settings, and are important nest predators (Churcher and Lawton 1987; Soule et al. 1988; DeGraaf and Maier 1996). Again, researchers have not linked small mammal population dynamics to bird viability in urban settings.

We suggest the following approach. Determine the suite of potential nest predators and their abundance by live trapping and observation at real and artificial nests. Determine their abilities as predators by observing their behavior at nests (video surveillance works best) or in a controlled lab setting. It is especially important to determine what, if any, nest contents can be eaten. Conduct detailed studies on important predators. For example, we monitor radio-tagged American Crows at least once per week to quantify survivorship and reproductive success. We also observe their foraging behavior and patterns of space-use for 1-2 hours weekly. Locations of radio-tagged corvids are plotted on maps/photos of the study site and used to calculate home range statistics. From this, we can determine land cover, land use patterns, and urban features that are important to crows.

CONCLUSIONS

Over the past 20-25 years, the rules of planning for wildlife on the landscape scale have been promoted to law through repetition rather than testing. Romesburg (1983) states that this lack of scientific rigor is the fundamental weakness of wildlife science that must be addressed if the field is to advance. As urbanization continues to encroach on wildlife, the need to advance is especially dire and can only be achieved by applying the hypothetico-deductive method. We should use this method to understand how birds respond to varying urban patterns (e.g. land use intensity, housing aggregation, and land use heterogeneity) at the suburban/exurban or suburban/wildlands interface. Here, native bird communities are relatively intact and managing development patterns to maintain, rather than replace, native communities is meaningful. This work should be completed in both habitat reserves and developments so that we can use the entire landscape, reserves and development, to our advantage.

To advance our knowledge of how urbanization affects birds we need to combine observational and experimental studies at several spatial and biological scales. Correlational studies that determine how the intensity and pattern of human development near and far from the study area affect avian community composition and population viability are critical first steps. However, full understanding of the effects of development requires causal investigations that compare sites before and after development or with and without development. Descriptions of community diversity provide only superficial understanding of how urbanization structures bird communities. This is an important start, but it should be based on a thorough understanding of how a representative sample of bird populations responds to urbanization. Understanding populations is enhanced by knowledge of how urbanization affects limiting factors such as nest predation, food abundance, and nest site availability.

In our study, nest predation is important to the urban planner interested in maintaining viable bird populations, because urban planning can directly affect the probability of nest predation. It can do so by affecting the abundance and distribution of predators and the ease with which they can find nests (e.g. by reducing nesting cover and fragmenting natural habitat). If attributes of habitat reserves and urban development can be linked to nest predation (or another mechanism), then we can arm urban planners and policy makers with prescriptions for conservation-minded development.

REFERENCES

Adams, L. W., and L. E. Dove. 1989. Wildlife reserves and corridors in the urban environment: a guide to ecological landscape planning and resource conservation. National Institute for Urban Wildlife, Columbia. 91 pp.

Alberti, M. In press. Quantifying the urban gradient: linking urban planning and ecology. *in* J. M. Marzluff, R. Bowman, K. J. McGowan, and R. E. Donnelly, eds. Avian conservation in an urbanizing world. Kluwer Academic Publishers, Norwell.

Andelman, S. J., and A. Stock. 1993. Management, research and monitoring priorities for the conservation of neotropical migratory birds that breed in Washington. Washington Natural Heritage Program, Washington Department of Natural Resources, Olympia, WA.

Beissinger, S. R., and D. R. Osborne. 1982. Effects of urbanization on avian community organization. Condor 84:75-83.

Berry, B. J. L. 1990. Urbanization. Pages 103-119 *in* B. L. Turner, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and W. B. Meyer, eds. Earth as transformed by human action. Cambridge Univ. Press, New York.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506-519.

Bock, C. E., J. H. Bock, and B. C. Bennett. 1997. Songbird abundance in grasslands at a suburban interface on the Colorado High Plains. *In* P. D. Vickery, and J. Herkert, eds. Ecology and conservation of grassland birds in the Western Hemisphere. Cooper Ornithological Society, Berkeley.

Churcher, P. B., and J. H. Lawton. 1987. Predation by domestic cats in an English village. Journal of Zoology 212:439-455.

DeGraaf, R. M., A. D. Geis, and P. A. Healy. 1991. Bird population and habitat surveys in urban areas. Landscape and Urban Planning 21:181-188.

DeGraaf, R. M, and T. J. Maier. 1996. Effect of egg size on predation by White-footed Mice. Wilson Bulletin 108:535-539.

DeGraaf, R. M., and J. M. Wentworth. 1981. Urban bird communities and habitats in New England. Transactions of the North American wildlife and natural resources conference 46:396-413.

Desante, D. F. 1992. Monitoring avian productivity and survivorship (MAPS): a sharp, rather than blunt, tool for monitoring and assessing landbird populations. Pages 511-521 *in* D. R. McCullough and R. H. Barrett, eds. Wildlife 2000: populations. Elsevier Applied Science, London.

Emlen, J. T. 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. Condor 76:184-197.

Gehlbach, F. R. 1994. How urbanization influences raptor ecology. Journal of Raptor Research 28:46.

Gehlbach, F. R. 1996. Eastern Screech Owls in suburbia: a model of raptor urbanization. Pages 69-74 *in* D. M. Bird, D. E. Varland, and J. J. Negro, eds. Raptors in human landscapes: adaptations to built and cultivated environments. Academic Press, London.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42-53.

Hostetler, M. In press. The importance of multi-scale analyses in avian habitat selection studies in urban environments. *in* J. M. Marzluff, R. Bowman, K. J. McGowan, and R. E. Donnelly, eds. Avian conservation in an urbanizing world. Kluwer Academic Publishers, Norwell.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651-661.

Karieva, P., and M. Anderson. 1989. Spatial aspects of species interactions: the wedding of models and experiments. Pages 35-50 *in* A. Hastings, ed. Community ecology. Springer-Verlag, New York.

Lee, E. T. 1980. Statistical methods for survival data analysis. Lifetime Learning, Belmont. 482 pp.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton Univ. Press, Princeton. 179 pp.

Major, R. E., and C. E. Kendal. 1997. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. Ibis 138:298-307.
Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101-127.
Martin, T. E. and G. R. Geupel. 1993. Nest monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-519.
Marzluff, J. M. 1986. Assumptions and design of regression experiments: the importance of lack-of-fit testing. Pages 165-170 *in* J. Verner, M. L. Morrison, and C. J. Ralph, eds. Habitat relationships of terrestrial vertebrates. Univ. of Wisconsin Press, Madison.
Marzluff, J. M. 1997. Effects of urbanization and recreation on songbirds. Pages 89-103 *in* W. M. Block and D. M. Block, eds. Songbird ecology in southwestern Ponderosa Pine forests: a literature review. General Technical Report RM-GTR-292. Fort Collins, CO.
Marzluff, J. M., and R. E. Donnelly. In press. The study of urbanization effects on birds. *In* J. M. Marzluff, R. Bowman, K. J. McGowan, and R. E. Donnelly, eds. Avian conservation in an urbanizing world. Kluwer Academic Publishers, Norwell.
Marzluff, J. M., F. R. Gehlbach, and D. A. Manuwal. 1998. Urban environments: influences on avifauna and challenges for the avian conservationist. Pages 283-299 in J. M. Marzluff and R. Sallabanks, eds. Avian conservation: research and management. Island Press, Washington, D. C.
Marzluff, J. M., M. G. Raphael, and R. Sallabanks. In press. Understanding why forest management may affect avian populations: mechanisms, experiment approaches, prioritization and funding strategies. Wildlife Society Bulletin.
Marzluff, J. M., and M. Restani. 1999. *In* J. A. Rochelle, L. A. Lehmann, and J. Wisniewski, eds. Forest fragmentation: wildlife and management implications. Brill Academic Publishing, Leiden.
Marzluff, J. M. and R. Sallabanks. 1998. Past approaches and future directions for avian conservation biology. Pages 5-11 *in* J.M. Marzluff and R. Sallabanks, eds. Avian conservation: research and management. Island Press, Washington, D. C.
May, R. M. 1994. The effects of spatial scale on ecological questions and answers. Pages 1-17 *in* P. J. Edwards, R. M. May, and N. R. Webb, eds. Large-scale ecology and conservation biology. Blackwell Scientific, Oxford.
Mayfield. H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73: 255-261.
Mayfield. H. F. 1975. Suggestions for calculating nesting success. Wilson Bulletin 87:456-466.
Mills, G. S., J. B. Dunning, Jr., and J. M. Bates. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. Condor 91:416-428.
Newton, I. 1998. Population limitation in birds. Academic Press, San Diego. 597 pp.
Noss, R. 1999. Plenary lecture: the conservation significance of biological linkages or corridors in urban environments. International Symposium on Urban Wildlife Conservation. Tucson, AZ.
Picozzi, N. 1975. Crow predation on marked nests. Journal of Wildlife Management 39:151-155.
Pitelka, F. A. 1942. High population of breeding birds within an artificial habitat. Condor 44:172-174.
Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-661.
Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas. 732 pp.
Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. Desante. 1993. Handbook of field methods for monitoring landbirds. General Technical Report PSW-GTR-144. Albany, CA.
Robinson, S. K., and D. S. Wilcove. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. Bird Conservation International 4:233-249.
Romesburg, H. C. 1981. Wildlife science: gaining reliable knowledge. Journal of Wildlife Management 45:293-313.
Rosenberg, K. V., S. B. Terrill, and G. H. Rosenberg. 1987. Value of suburban habitat to desert riparian birds. Wilson Bulletin 99:642-654.
Schmidt, K. A., and C. J. Whelan. 1998. The relative impacts of nest predation and brood parasitism on seasonal fecundity in songbirds. Conservation Biology 13:46-57.
Soule, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75-92.
United Nations. 1999. Press briefing on population [Online]. Available: http://www.un.org/plweb-cgi/idoc.pl?421+unix+_free_user_+www.un.org..80+un+un+br1998+br19 98++population%26and%26growth [1999, March 3].
Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.
Wilson, E. O., and E. O. Willis. 1979. Applied biogeography. Pages 522-536 *in* M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Belknap Press, Cambridge.

Table 1. Experimental design matrix for our study of urban reserves. Each combination of size and land use intensity has been replicated three times for a total of twenty-seven sites. Exurban sites should be classed as rural where agriculture dominates the landscape, rather than forest.

Size	Land Use Intensity (housing density)
Small (0.5 – 2.5 ha)	Exurban / Wildland (< 0.5 housing units per ha)
	Suburban (0.5 - 2 housing units per ha)
	Urban (> 2 housing units per ha)
Medium (16 – 24 ha)	Exurban / Wildland
	Suburban
	Urban
Large (81 – 121 ha)	Exurban / Wildland
	Suburban
	Urban