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Urban effects on native avifauna: a review

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Abstract

The effect of urbanization can be immense, yet our understanding is rudimentary. Here, we compile the most recent information on urban impacts on avian populations and communities. Compared to other vertebrates, birds are easily monitored by skilled observers and provide a mechanism to explore urban effects and responses to different urban designs. Taxonomically, bird communities in distinctly different habitats are most different in the least disturbed sites and the most similar in the most urbanized sites. Urbanization tends to select for omnivorous, granivorous, and cavity nesting species. Increased urbanization typically leads to an increase in avian biomass but a reduction in richness. Unlike most passerines, raptors may have home ranges that extend beyond the urban boundary and therefore do not need to meet all their ecological requirements within urban areas. Urban habitats are often of superior quality to raptors because there they are often free from persecution and have an adequate food supply. The processes that underlie the patterns of population and community level responses need more attention, but several areas of have been identified as being important. Birds respond to vegetation composition and structure, and urban areas that retain native vegetative characteristics retain more native species than those that do not. Avian fecundity in urban areas is a reflection of species-specific adaptability to urban resources, and to levels of nest predation and nest parasitism. Additionally, non-consumptive human activities that increase with urbanization are recognized as having negative impacts on avian populations and communities. Avian survivorship in urban areas is influenced by risk of collision with man-made objects, changes in the predator assemblage, food supply, and disease. Missing are thorough investigations in the regions of highest human population growth, e.g. Southeast Asia. Additionally, there is a paucity of information from regions of high avian diversity, e.g. tropical forests. Clearly, local knowledge and study is required before implementation of management policies to reduce urban impacts on bird communities. Hopefully, such policies will include long-term monitoring. Demographic parameters of fecundity and survivorship need to be examined in conjunction with measures of community diversity and density across the urban gradient to better understand the quality of different urban habitats, and the variation of quality among spatial patterns of urbanization within the native habitat matrix.

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1. Introduction

Urbanization can be defined as concentrated human presence in residential and industrial settings and their associated affects (Cringan and Horak, 1989; Marzluff, 1997), and for the purposes of ecological studies urban centers have been quantified as containing more than 2500 people (Dumouchel, 1975). The urban extent of most metropolitan areas is expanding into adjacent rural landscapes (Alig and Healy, 1987; World Resources Institute, 1994; UN, 1997). With the projected global increase of urbanization, land cover conversions for urban use will only increase altering ecosystem patterns and processes (Grimm et al., 2000).

The factors determining which species can coexist with human settlement include: (1) the presence and patch size of remnant (native) vegetation (Emlen, 1974; Gavareski, 1976; Rosenberg et al., 1987; Mills et al., 1989; Catterall et al., 1991); (2) competition with exotic species that have a longer history of human cohabitation (Major et al., 1996); (3) non-native predators (Churcher and Lawton, 1987; Paton, 1990); (4) the structure and floristic attributes of planted vegetation (Tweit and Tweit, 1986; Green et al., 1989); (5) supplementary feeding by humans (Recher, 1972; Brittingham, 1990; Major et al., 1996); and (6) residual pesticides (Major et al., 1996).

The number of studies that describe avian responses to urbanization is immense and growing (Marzluff et al., 2001). For the urban planner, we attempt to summarize into one paper the patterns of avian population and community response to the urban environment by major habitat types. Where possible we illustrate major points with specific species (scientific names in Appendix A) to assist the urban planner and others involved in the planning process to identify local species responses to landscape changes. Next, we review studies that have illuminated some of the major processes that have contributed to the observed patterns of population and community change with urbanization. Finally, we outline future avian research needs that will specifically aid urban planning decisions.

2. Patterns of urban impacts by matrix habitat type

Total breeding bird density is often higher in urban areas than in the surrounding native habitat (Walcott,

1974; Gavareski, 1976; Lancaster and Rees, 1979; Beissinger and Osborne, 1982). However, species richness is usually lower in urban areas, where the avian community is dominated by a few, often introduced, species (Gavareski, 1976; Lancaster and Rees, 1979; Beissinger and Osborne, 1982; Cam et al., 2000). Urbanization favors a few species but selects against most such that the avian community composition of urban environments differs dramatically from local natural environments (Beissinger and Osborne, 1982; Rosenberg et al., 1987; Mills et al., 1989; Jokimäki and Suhonen, 1993; O'Connell et al., 2000). Urbanization tends to favor granivores, aerial insectivores, and ground foraging insectivores (Emlen, 1974; Allen and O'Conner, 2000), and residents over migrants (Allen and O'Conner, 2000; Kluza et al., 2000; Poague et al., 2000). In studies where the urban gradient is more finely divided, the peak of avian diversity is found in areas of moderate levels of disturbance, often in suburban areas or at the urban/wildland interface (Jokimäki and Suhonen, 1993; Blair, 1999). Pre-development bird species drop out gradually from the community as sites become more urban (Blair, 2001).

2.1. Desert scrub

The avian community composition of the desert scrub surrounding Tucson, Arizona markedly changes within city limits (Emlen, 1974). Urbanization favors seed eaters, ground foraging insectivores, water dependent and crevice nesting species of desert scrub ecosystems (e.g. white-winged dove, Inca dove, and northern mockingbird), as well as exotics (e.g. house sparrow and European starling). Insectivores, cavity nesting species, and species with Type A territories (i.e. non-overlapping territories where the home range is approximately the same size and the defended territory space) disappeared from the urbanized desert scrub community. Urban and wild densities of the ash-throated flycatcher and curve-billed thrasher did not differ significantly, seemingly unaffected by urbanization (Emlen, 1974).

Mills et al. (1989) found a similar response among Tucson's avifauna. Density of exotic (house sparrow, rock dove, European starling) and urban-adapted native species (mallard, Inca dove, American robin, bronzed cowbird, and great-tailed grackle) increased significantly with urbanization. Other native species exhibited

no significant change in density across the urban gradient.

Both studies found a decrease in diversity with urbanization (Emlen, 1974; Mills et al., 1989); however, Mills et al.'s (1989) density and biomass estimates are most revealing of urban impacts. The urban community averaged 1230 individuals per 100 acres with an avifaunal biomass of 53,208 g, whereas the desert scrub community averaged a density of 47 individuals with 2052 g of biomass over the same area.

2.2. Closed canopy forests

Temperate: Beissinger and Osborne (1982) found the avian community response of biomass and density to urbanization in Oxford, Ohio similar to what Emlen (1974) reported in Arizona. Forests contained higher species richness but lower density (1020–1253 individuals per 40 ha; 4455–5736 g biomass) compared to residential areas (1320–1667 individuals per 40 ha; biomass 12,637–15,445 g). Urbanization favors seed eaters, omnivores, and ground foragers, while selecting against high canopy and foliage foragers, insectivores, bark gleaners and drillers. Specifically, rock doves, mourning doves, chimney swifts, American robins, European starlings, house sparrows, and common grackles responded positively to urbanization; flycatchers, red-eyed vireos, cerulean warblers, and most woodpeckers (except northern flickers and downy woodpeckers) responded negatively.

The effects of fragmentation of the eastern deciduous forest by agriculture and suburban development on bird populations has received considerable attention (e.g. Askins et al., 1990; Hagan and Johnston, 1992; Friesen et al., 1995; Kluza et al., 2000). Forests fragmented by urbanization into small forest tracts (4–25 ha) resulted in the decline of forest interior species such as the eastern wood-pewee, wood thrush, scarlet tanager, rose-breasted grosbeak, and Baltimore oriole, while great-crested flycatchers and red-eyed vireos were the least affected under those conditions (Friesen et al., 1995). Likewise, lightly treed parks often support suburban bird communities rather than species of forest interior or forest-dependent species (Hudson et al., 1997). Forests fragmented by rural residential development (0.01–6.7 house/ha) in western Massachusetts had fewer migratory and forest-interior species (e.g. veery, wood thrush and ovenbird; Kluza

et al., 2000). Along wooded rights-of-way in the grassland matrix of Nebraska, total relative abundance did not differ between rural and urban forests, while species richness was higher in the urban areas except during migration when migratory birds appeared to preferentially choose the rural woodland habitat over urban (Poague et al., 2000).

Marzluff's (1997) review of urbanization impacts on southwestern ponderosa pine forest communities suggests similar trends. Hummingbirds, corvids, swallows, blackbirds, European starlings, finches, American robins, and house sparrows respond positively to urbanization. Flycatchers, tanagers, vireos, warblers, thrushes, and bluebirds respond negatively to urbanization in ponderosa pine forests.

A few studies have measured temporal responses of bird populations and communities to urbanization (Walcott, 1974; Aldrich and Coffin, 1979; Nowakowski, 1996; Fitzgerald et al., 1999). Such studies provide direct inferences to changes associated with urban development. In Cambridge, Massachusetts Walcott (1974) compared birds censused on two plots between 1860 and 1964. Natural habitat declined from 95 to 30%, and from 50 to 15% on the two sites, respectively. Bird fauna changed from 26 species of mostly migratory breeders and a few transients, to 9 species, largely permanent residents. In Fairfax County, Virginia, the avifaunal community was examined between 1942 and 1979 (Aldrich and Coffin, 1979). The number of species increased as the deciduous forest landscape of 1942 became dominated by suburban residential in 1979 (23 species versus 29 species), and the density of birds increased by 140% (195 territories versus 277 territories). Most interesting was the dramatic shift in community composition among the ten most abundant species, especially those that were extirpated after 1942 and those that colonized by 1979 (Table 3). In the expanding urban center of Olsztyn, Poland, six rare species disappeared, five new species appeared (most significantly the rock dove), 11 species have increased significantly, and 15 species have decreased significantly between 1968 and 1993 (Nowakowski, 1996). Over the course of 5 years of urbanization in Missouri, Fitzgerald et al. (1999) found that the blue-gray gnatcatcher, indigo bunting, acadian flycatcher, black-and-white warbler, and the northern parula have declined significantly (the latter three species are forest interior specialists). Comparing bird populations in residential

communities of different ages (35, 20, and 10 years old) in Alberta, Canada, [Edgar and Kershaw \(1994\)](#) found that density, richness, and evenness increased with urban community age. The only species common to all three areas was the introduced house sparrow which was the most abundance species in all three urban communities.

Tropical: In Panama, 11 habitats were surveyed across an anthropogenic disturbance gradient, including residential areas ([Petit et al., 1999](#)). Nearctic–Neotropical migratory species were most numerous in residential, lowland forest fragments and shade-coffee plantations. Higher portions of frugivores and nectarivores characterize residential avian communities compared to native forest areas. In Jakarta, [Indrawan and Wirakusumah \(1995\)](#) found avian richness had decreased by over 50% in 40 years (199 species to <100 species).

A higher abundance of human commensal species (e.g. house swift and common myna) are associated with increases in built areas, while parkland and rainforest-associated bird species (e.g. greater green and short-tailed babbler) have increased abundance with native and managed vegetation in the tropical city of Singapore ([Sodhi et al., 1999](#)).

2.3. Grasslands

In Saskatoon, Saskatchewan species richness was not significantly different between rural and urban sites, however abundance was significantly higher in the urban sites ([Sodhi, 1992](#)). Most of the urban bird fauna was composed of non-grassland and introduced species, with the house sparrow being the most abundant urban species. The horned lark and western meadowlark dominated the rural sites, while the clay-colored sparrow was the only grassland species relatively common in urban sites.

Grassland birds in Colorado respond to edges and to the extent of urbanization ([Bock et al., 2001](#)). Bock and his colleagues found grassland nesting bird abundance twice as great on interior plots as on edge plots. Vesper sparrow, savannah sparrow, grasshopper sparrow, bobolink, and western meadowlark were most sensitive to urbanization. American robin, European starling, common grackle, house finch, and house sparrow were five times more abundant on grassland/suburban edges than on grassland interior plots. Reduced abun-

dance of grassland species (vesper sparrow, grasshopper sparrow, and horned lark) along the urban edge is due to the loss of preferred grassland cover-types at the urban-wildland interface ([Haire et al., 2000](#)).

[Engle et al. \(1999\)](#) examined the impact of low-density rural sprawl on bird communities of the Great Plains near Tulsa, Oklahoma. Human development favored the barn swallow, dickcissel and grasshopper sparrow at low human densities (<7 people km⁻²) and the American robin, common grackle, European starling, house sparrow, and purple martin at higher densities (>12 people km⁻²). Most notably, forest and edge species (e.g. tufted titmouse, Bewick's wren, Kentucky warbler, summer tanager, chipping sparrow), were replaced by species associated with human development, especially in the higher density rural areas.

2.4. Australian eucalyptus forest, bushlands, and subtropical rainforest

[Sewell and Catterall \(1998\)](#) surveyed bird communities across an urban gradient from large patches of bushland to urban sites without native vegetation in Brisbane, Queensland. They detected a decrease in diversity and an increase in abundance with increasing urbanization, pattern broadly consistent with other studies ([Emlen, 1974](#); [Rosenberg et al., 1987](#); [Mills et al., 1989](#)). However, suburban sites had the highest abundance and diversity, especially among low-density housing that retained eucalyptus canopy structure, and among the exotic-planted suburbs. However, these sites had a low abundance of eucalyptus forest birds, therefore suburban planting does not reverse the effects of deforestation of eucalyptus forest, but promotes a distinctive suburban bird community. Within urban environments, bird communities show little seasonal variation as compared to woodland or eucalyptus forest bird communities in Queensland, Australia ([Catterall et al., 1998](#)).

In wet sclerophyll and subtropical rainforest, [Wood \(1996\)](#) compared bird communities in a 5.4 ha degraded public reserve with an adjacent 55-year old residential area of Wollongong, New South Wales (population 200,000). In all seasons, the reserve had higher species richness but lower total abundance. There were 13 reserve specialists (e.g. white-browed scrubwren, eastern yellow robin, brown gerygone, and eastern whipbird, of which the latter two are the most vulnerable to local

extinction), 5 exotic, suburb specialists (e.g. common myna, red-whiskered bulbul, European starling, and house sparrow), and 17 generalists. Specialist species were similar in Wollongong and in a similar study in Brisbane (Catterall et al., 1989). Wood estimates that 15 species have been extirpated with suburban development.

2.5. Coastal sage-scrub

Large coastal sage-scrub reserves in urban areas may ameliorate urban impacts on the native community assemblage (Crooks and Soulé, 1999). Sauvajot and Buechner (1993) found no relationship of diversity and abundance associated with degrees of urban exposure in chaparral habitats of the Santa Monica Mountains; however, the study lacked an appropriate control site. The control site was a 5000 ha state park but was not independent of the urban area. Rather than an independent control, it served as a source population for some otherwise urban-sensitive species located on the urban treatment plots. Distance from urban areas is an important aspect (Munyenembe et al., 1989; Catterall et al., 1989, 1991; Bolger et al., 1997). Many coastal sage-scrub species occupied intact habitat even if immediately adjacent to urban areas. However, some of these coastal sage-scrub species respond to habitat patchiness: sage sparrow, California thrasher and California towhee were less common at edges, whereas the northern mockingbird and European starling were more common at edges (Kristan et al., 2003).

Steep undeveloped slopes in southern California coastal sage scrub serves as temporary habitat within urban matrix. Scrub-specialist disappearance in this landscape is related to fragment area and fragment age (i.e. time since isolation; Crooks and Soulé, 1999). Within this urbanized landscape Bolger et al. (1997) found that species distributions were likely influenced by landscape-scale vegetation patterns and by the aggregate amount of urbanized areas. The urban-edge affected species, that exhibited a significant reduction in abundance within 200–500 m of development edge, were sage, rufous-crowned, lark, and black-chinned sparrows. Edge enhanced species, with elevated abundance within 1000 m from an edge, included the house finch, northern mockingbird, lesser goldfinch, and Anna's hummingbird. Interestingly, within one of largest expanses of sage scrub within one of the largest

urbanizing landscapes, Los Angeles, Cooper (2002) found that several sensitive species, including California gnatcatcher, were confirmed or suspected of breeding in patches smaller than 100 ha during the study, and often at the urban interface.

2.6. Oak woodlands

Along the pre-development to urban gradient, species richness and abundance were found to be highest in areas of intermediate disturbance (e.g. golf courses and low density residential), while the pre-development species dropped out of the community with increasing urbanization (Blair, 1996). The avian community was divided into three major classes based on their response to urbanization: urban avoiders, suburban adaptable, and urban exploiters (Blair, 1996). Of the pre-development community, the Western scrub-jay, Anna's hummingbird, and the mourning dove persisted across the urban gradient. Urban avoiders included the dark-eyed junco, blue-gray gnatcatcher, ash-throated flycatcher, Steller's jay, wren-tit, western wood-pewee, Hutton's vireo. Urban exploiters included the white-throated swift, rock dove and house sparrow; 30 other species were classified as urban adaptable (Blair, 1996).

Scott (1993) found that initial development (i.e. during the time of physical vegetation removal and construction) caused the loss of a number of species in southern California (including northern mockingbird, lazuli bunting, blue grosbeak, Costa's hummingbird, ash-throated flycatcher, California gnatcatcher, phainopepla, Hutton's vireo, orange-crowned warbler, and Bullock's oriole), but the increase in two species (black-chinned hummingbird and California thrasher).

Urbanization in the oak woodlands of California tends alter plant community composition and structure (Blair, 1996), as seen elsewhere (Beissinger and Osborne, 1982; Rudnicki and McDonnell, 1989). Increased urbanization in the suburbs may actually increase structural diversity (Emlen, 1974; Beissinger and Osborne, 1982) leading to the higher abundances and richness found by Blair (1996). However, in the most urban environments avian richness decreased to six species, including the three urban exploiters, species that are adaptable to the reduced floristic composition and structure (Blair, 1996). Most studies have examined avian community composition in urban and

non-urban areas, whereas Blair's (1996) work reveals changes that occur along the urban gradient. These results can be projected to predict trends in native communities as an area becomes urbanized over time. Blair's (1996) results from the oak woodlands of California are consistent with the intermediate disturbance hypothesis (Connell, 1978). They are also consistent with McDonnell et al.'s (1993) suggestion that biotic factors are more limiting to avian populations at the rural end, while physical factors are more limiting at the urban end of the urbanization gradient.

2.7. Generalizations

Taxonomically, the bird communities in distinctly different habitats such as California coastal sage-scrub and Ohio eastern deciduous forest are most different in the least disturbed sites and the most similar in the most urbanized sites (Blair, 2001). Urbanization selects for omnivorous, granivorous, and cavity nesting species (Emlen, 1974; Lancaster and Rees, 1979; Beissinger and Osborne, 1982; Rosenberg et al., 1987; Mills et al., 1989; Allen and O'Conner, 2000; Kluza et al., 2000). Increased urbanization leads to an increase in avian biomass but a reduction in richness, a pattern largely consistent across forests, desert scrub, and grassland habitats. Few studies have examined the response of species composition and abundance as development progresses.

The avian community changes with urban development (Scott, 1993). As time from development increases bird communities become at once more distinct from the native community (Wood, 1996; but also see Edgar and Kershaw, 1994) but more homogenous with other urban areas (Blair, 2001). This is one area needs to be explored in more detail. Studies with a greater coverage of time since development and over a greater range of plant communities are needed. Missing are more thorough investigations in the regions of highest human population growth, Southeast Asia, and there is a paucity of information from boreal forest and tropical forest biomes.

3. Urban impacts on raptors

Studies of passerine responses to urbanization are often devoid of important reproductive information that

Table 1

Ten most abundant species at Lake Barcroft, Fairfax County, Virginia 1942 and 1979 (data from Aldrich and Coffin, 1979)

1942	1979
Red-eyed Vireo ^a	Northern Cardinal
Ovenbird ^d	Northern Mockingbird ^b
Wood Thrush	Song Sparrow ^b
Scarlet Tanager ^a	Blue Jay
Hooded Warbler ^a	European Starling ^b
Acadian Flycatcher ^a	Gray Catbird ^b
Eastern Wood-pewee	American Robin ^b
Red-bellied Woodpecker	House Sparrow ^b
Blue Jay	Mourning Dove
Northern Cardinal	Carolina Chickadee ^b

^a Extirpated.

^b New to site.

is more descriptive of habitat quality than measures of abundance (Van Horne, 1983). Studies of raptors can be illuminating in this regard, as demographic parameters have often been measured on urban nesting owls, hawks, falcons, and eagles. However, an important caveat is that unlike most passerines raptors may have home ranges that extend beyond the urban boundary and therefore do not need to meet all their ecological requirements within urban areas.

Urban habitats are often of superior quality to raptors (Cringan and Horak, 1989) because there they are often free from persecution that is more typical of rural regions. Freedom from persecution and an adequate food supply may allow raptors to inhabit otherwise unsuitable nesting sites (Newton, 1986). Small raptors (e.g. eastern screech owl, tawny owl, Scops-owl, and collared Scops-owl, and sparrowhawks) often inhabit greenbelts and parks (Clark et al., 1984; Newton, 1986). Great horned owls are common in metropolitan areas, such as Seattle, Washington (Lambert, 1981). Raptors with large home range requirements are more likely to be negatively affected by habitat reduction or fragmentation that typifies the urban environment than are smaller raptors (Newton, 1979; Phillips et al., 1984; Scott, 1985) (Table 1).

Species that meet their food requirements within the urban setting can exhibit positive population responses. Many falcon species respond well to urban environments because of the large biomass of small birds (Dietrich and Ellenberg, 1981; Horak, 1986; Newton, 1986; James et al., 1987). The peregrine falcon, lesser kestrel, and American kestrel respond well,

Table 2
Summary of urban impacts on raptors

Species	Data type ^a			Notes	Region	Reference
	A	B	C			
Peregrine Falcon		X		34–58% of regional pop. nest in urban area. Three most common prey items: rock dove, northern flicker, blue jay Population size now > historical abundance	60 U.S. Cities	Cade et al. (1996)
Prairie Falcon	X			Scarce on urban plots	Boulder, CO	Berry et al. (1998)
Lesser Kestrel		X		Predation in urban < rural Lower prey delivery rates, and lower success, in urban < rural	Spain	Tella et al. (1996)
Japanese Lesser Sparrowhawk			X	Feeds primarily (90%) on small birds in suburban Tokyo	Japan	Ueta (1992)
American Kestrel	X			Not sensitive to urbanization	Boulder, CO	Berry et al. (1998)
Sparrowhawk		X		Success: village > rural > wild Village hawks breed earlier and lay more eggs	The Netherlands	Diermen (1996)
Mississippi Kite		X		Urban populations very successful	Midwest US	Parker (1996)
Red-shouldered Hawk	X	X		32% nest in urban areas (<i>N</i> = 170) Successfully nest in non-native trees	s. CA	Bloom and McCrary (1996)
		X		Avoid nesting near roads and buildings		Bednarz and Dinsmore (1981)
		X		>50% nests in exotic trees Success in exotic trees > native trees	CA	Rottenborn (2000)
	X			Significantly avoided suburban habitat	NJ	Bosakowski and Smith (1997)
Red-tailed Hawk	X			Not sensitive to urbanization	Boulder, CO	Berry et al. (1998)
	X			Significantly associated with suburban habitat	NJ	Bosakowski and Smith (1997)
Swainson's Hawk	X			Not sensitive to urbanization	Boulder, CO	Berry et al. (1998)
Ferruginous Hawk	X			Scarce on urban plots	Boulder, CO	Berry et al. (1998)
Rough-legged Hawk	X			Scarce on urban plots	Boulder, CO	Berry et al. (1998)
Cooper's Hawk		X		Highest known breeding density in suburbs Highest known reproductive success in suburbs (clutch size = 4.2, nestlings = 4)	WI WI	Rosenfield et al. (1996)
		X		Urban > wild: clutch size	AZ	Boal and Mannan (1999)
			X	Urban < wild: trichomoniasis Smaller home ranges in urban areas	Tucson, AZ	Mannan and Boal (2000)
Northern Goshawk	X			Avoids suburban habitat	NJ	Bosakowski and Smith (1997)

Table 2 (Continued)

Species	Data type ^a			Notes	Region	Reference
	A	B	C			
			X	Winter range concentrated near urban areas	Finland	Tornberg and Colpaert (2001)
Bald Eagle	X			Scarce on urban plots	Boulder, CO	Berry et al. (1998)
Osprey		X		Absence of suitable nest trees has lead to >75% use of man-made structures (power lines) Man-made nest success ($n = 366$) > natural ($n = 258$)	Germany	Meyburg et al. (1996)
Eastern Screech Owl		X		City population more dense, more productive, and more stable Avoids suburban habitat	TX NJ	Gehlbach (1996) Bosakowski and Smith (1997)
Barred Owl	X			Pref. mature forest over areas of human habitation	NJ	Bosakowski et al. (1987)
Burrowing Owl		X		Nestling and fledling success in urban > rural Lower predation and lower nest densities in urban Greater food availability in urban	NM FL	Botelho and Arrowood (1996) Millsap and Bear (2000)
Tawny Owl		X		Nesting success in urban = suburban	Rome	Ranazzi et al. (2000)
	X			Behavioral switch to small bird prey in suburban environment compared to small mammals in natural open areas		Tomialojc (1970)
Great-horned Owl	X			Associated with suburban habitat	NJ	Bosakowski and Smith (1997)

^a A: Abundance data; B: breeding data; C: other data type.

and have higher reproductive success in urban environments (Table 2), although the prairie falcon appears to respond negatively to urbanization (Berry et al., 1998). Sparrowhawks in The Netherlands have greater success in villages than in rural areas, which in turn have greater success than those nesting in forests (Diermen, 1996). Village sparrowhawks attract higher quality mates and have larger clutch sizes (Diermen, 1996). Village hawks also show the least variety of prey items selected, and the most ubiquitous nest structure selection (Diermen, 1996). Raptors that eat small prey, including insects, can successfully colonize urban environments, such as the Mississippi kite, burrowing owl, and screech owl. A number of small mammalian human-commensals respond positively to urban environments, and therefore raptors that prey on them also respond positively, including the red-tailed hawk and Swainson's hawk. Whereas, those that prey on larger

mammals often do not fare as well in the urban environment, e.g. ferruginous hawk and rough-legged hawk. Small accipiters respond positively to urban environments where small birds have clumped distributions by feeders; however, larger accipiters often do not exhibit a similar response. Osprey adapt to urban environments when fish populations are high and persecution is low (Spitzer et al., 1985). Vultures have increased worldwide in response to early stages of urbanization, but have decreased thereafter when waste supplies are reduced (Inigo, 1986; Piper et al., 1986; Table 3).

The establishment of raptors in urban environments is partially dependent on their ability to utilize new or artificial nesting substrates. Red-shouldered hawks show a varied response; they avoid suburban habitat in New Jersey, but nest successfully in non-native trees in southern California (Table 2). Blue (1996) reports that osprey, red-tailed hawk, great-horned owl, golden

Table 3

Raptor use of man-made nesting substrates and the impact on reproductive success and population dynamics

Species	Type of structure (<i>n</i>)	Use and reproductive success	Region	Reference
Red-tailed Hawk	Transmission towers (12) Billboard (3)	Artificial 100% (<i>n</i> = 15) vs. natural 77% (<i>n</i> = 84)	Wisconsin	Stout et al. (1996)
Osprey	Utility towers	Use of utility structures has increased with population growth along the Willamette River (OR) while use of natural structures has remained constant, 1976–1993 production equal	Oregon	Henny and Kaiser (1996)
	Hydro poles (118)	High use of towers in Canada and eastern US	New Brunswick	Stocek (1972)
	Transmission towers (14) Communication towers (52)	Increased use of artificial structures as population increased since 1945	Great lakes Basin	Ewins (1996)
	Buildings (12)	Reproductive output from artificial sites averaged 7.5% higher than natural sites		
	Platforms (126) Natural (579)			
	Power lines	Success: artificial sites > natural sites	Germany	Meyburg et al. (1996)
	Miscellaneous	Absence of suitable nest trees has lead to >75% use of man-made structures (power lines)	Germany	Meyburg et al. (1996)
	Utility poles	Success: man-made nest structure (<i>n</i> = 366) > natural structure (<i>n</i> = 258)		
		Utility pole nest success = natural site success	Oregon	Henny and Kaiser (1996)
Ferruginous Hawk	Artificial structures	Nest success: artificial > natural Young fledged: artificial > natural	Wyoming	Tigner et al. (1996)
	Transmission towers	Use of transmission towers	North Dakota	Gilmer and Stewart (1983)
Peregrine Falcon	Power plants Buildings, bridges, towers	High occupancy Population increases associated with artificial site use	Upper Midwest	Septon et al. (1996) Temple (1988)
	Bridges	Success lower on bridges than at natural nest sites	San Francisco, New York City	Bell et al. (1996)
American Kestrels	Nest boxes	Use in agricultural areas High use along highways	Idaho Iowa	Bechard and Bechard (1996) Varland and Loughin (1993)

eagle, bald eagle, American kestrel, Swainson's hawk, eastern screech owl, Harris' hawk, prairie falcon and zone-tailed hawk use power line structures in the US. Some species are more flexible in their use of structures than others (Table 2). The use of artificial structures has been an important aspect of raptor population restoration, and in some cases the populations today have exceeded historic numbers because of artificial structures, e.g. osprey (Table 2). Some species have even higher reproductive success on artificial nest sites than natural

sites, e.g. ferruginous hawks (Table 2). The impact of urbanization on migration routes is likely to be important, but this aspect has not been fully evaluated.

Behavioral response of raptors to humans is an important component of their ability to colonize urban environments. Ferruginous hawks home range was equal between suburban and wild sites in Denver, Colorado, while roosting time was lower for wild site hawks (Plumpton and Andersen, 1998). Red-tailed hawks habituate to human intrusion with call and dive rates at

nest sites lowest in areas of longest human contact (Knight et al., 1989). Habituation to humans as young may lead to higher mortality as adults. Cooper's hawk nestlings that had frequent exposure to human intrusion (research biologists banding and weighing young) were more likely to die from human-related causes, especially shooting (Snyder and Synder, 1974).

4. Processes that contribute to urban impacts on bird communities

4.1. Vegetation changes

There is often a strong positive correlation between the volume and structure of native vegetation and native bird diversity and species richness (Emlen, 1974; Mills et al., 1989). Likewise, non-native species diversity is correlated with exotic vegetation (Mills et al., 1989). Emlen (1974) found that certain native desert birds responded positively to urbanization in Tucson, Arizona, a city that maintains a high proportion of native vegetation. In support of Emlen's assertion, Mills et al. (1989) found that vegetation factors explained a greater proportion of species diversity variance than housing density. While Germaine et al. (1998) found a strong positive correlation between housing density and species richness for non-native species in Tucson, native bird species richness is positively correlated with the amount of native vegetation cover and negatively correlated with distance from desert washes (Germaine et al., 1998).

As the work in the Arizona desert attests, birds respond to vegetation composition and structure (Emlen, 1974; Mills et al., 1989; Germaine et al., 1998). Urban environments are often savannah in nature (Dorney et al., 1984), and usually have greater fragmented patches of native vegetation with more ground cover and less canopy cover (Beissinger and Osborne, 1982). In urban environments, vegetation is more fragmented, there is less coverage at mid- and upper-canopy levels, and there is more ground cover than in nearby wild sites. Native plants are replaced by exotics, and few dead standing trees remain. Therefore, it is not surprising that in urbanized forest ecosystems avian communities lack canopy foraging and bark drilling guilds, and have an increase in ground gleaners (Beissinger and Osborne, 1982; Rosenberg et al., 1987). The urban en-

vironment results in reduced diversity as total density of a few species increases, often in response to food provided by humans across the urban gradient. Such urban environments favor cavity-nesting and ground feeding granivorous or omnivorous species (Lancaster and Rees, 1979).

Native species typically drop out of the community along the gradient from native to completely urban environments (Blair, 1996). Blair (1996) found that in the oak woodlands of California total avian richness peaked under moderately disturbed conditions (e.g. golf courses and low-density, detached, single-unit homes), which runs counter to the results of many other studies (Graber and Graber, 1963; Tomialojc, 1970; Batten, 1972; Emlen, 1974; Guthrie, 1974; Walcott, 1974; Vale and Vale, 1976; Hohtola, 1978; DeGraff and Wentworth, 1981; Jones, 1981; Beissinger and Osborne, 1982; Green, 1984; Bezzel, 1985; Rosenberg et al., 1987; Ruzsczyk et al., 1987). This is primarily due to Blair's (1996) explicit design to explore the avian response to the gradient of urbanization while the previous work primarily examined discrete urban and non-urban areas. This examination of the urban gradient is illuminating of the processes that take place during the urban transformation, and how avian communities respond. Low levels of urban development can increase the abundance and diversity of resources available to birds. While urbanization alters plant community composition, in some, especially arid, environments, it may increase structural diversity (Emlen, 1974; Rudnicky and McDonnell, 1989). Resources are extremely diminished at the highest levels of urbanization in the commercial and business districts resulting in the reduction in avian diversity reported in the studies previously mentioned. This results from the removal of substantial areas of primary productivity, diminishing vegetative cover, and compositional change to hardy ornamental/exotic plant species (Whitney and Adams, 1980); native birds respond positively with native vegetation density, while non-native species respond positively to exotic plant biomass (Mills et al., 1989).

4.2. Fragmentation

Forest area is key to predicting presence and abundance of Nearctic–Neotropical migrants (Ambuel and Temple, 1983; Askins et al., 1990). However, even if forest size does not change with urbanization—the

urban surroundings degrade the forest patch impacting the abundance and richness of the avian community. In an attempt to disentangle the effects of residential development from effects of forest size, Friesen et al. (1995) examined the abundance of breeding migratory passerines in forest patches of different sizes surrounded by different levels of urbanization. Nearctic–Neotropical migrants consistently increased in richness and abundance as forest size increased. The number of houses surrounding the forest patch undermined its suitability, such that a 4 ha patch with no houses had more species than a 25 ha urban patch (Friesen et al., 1995).

In urban parks of different sizes in Seattle, larger parks were positively associated with natural community composition, whereas smaller parks had fewer species, and typically a greater proportion of those were urban birds (Gavareski, 1976). Based on her results, Gavareski (1976) suggested that the diverse avifauna characteristic of Pacific Northwest lowland forests can be supported in urban areas provided large park areas with native vegetation are maintained. However, without demographic information a management strategy to maintain populations of forest birds may fail if parks are population sinks. This highlights a need for additional research that documents productivity and survivorship across the urban gradient.

4.3. Exotic plants

In the urban and surrounding suburban environment native plant communities are being replaced with managed systems of altered landscape structure, influencing ecological and environmental relationships (Burgess and Sharpe, 1981; Krummel et al., 1987; Engle et al., 1999). Managed urban areas tend to increase plant species richness due largely to exotic plantings (Pavlik and Pavlik, 2000). Bird community composition shifts in response to exotic plantings (Green, 1984; Mills et al., 1989; Lenz, 1990; Pavlik and Pavlik, 2000) or by an increase in total vegetation cover in gardens (Vale and Vale, 1976; Lancaster and Rees, 1979; Luniak, 1980; Munyenembe et al., 1989; Mills et al., 1989). In Tucson, Arizona, many residential areas maintain native vegetation, and consequently maintain native avifauna. Developments in Tucson that have removed native vegetation cause a dramatic change in the avian community that has eliminated or greatly re-

duced most native bird species, and increased numbers of northern mockingbirds, house finches, and Inca doves as well as house sparrows and other non-native species (Tweit and Tweit, 1986; Mills et al., 1989). Urban habitats may provide refuge for species whose native habitats have been greatly diminished, as suggested by Gavareski (1976), Rosenberg et al. (1987), and Mills et al. (1989), however demographic information obtained from urban and wild nesting populations of native birds is needed to ensure that the urban refugium is not a short-lived population sink. What is known about breeding site selection in the urban environment is that some species prefer to nest under the greater protective cover of exotic plants than native plants, and for the red-shouldered hawk, at least, there was no difference in nest success between nests in native and non-native vegetation (Rottenborn, 2000).

4.4. Urbanization impacts on fecundity

A few studies have explored the urban impacts on reproductive success. Schnack (1991) found that the song thrush and European blackbird exhibited lower fledgling success per eggs laid in urban sites in Vienna, Austria than in adjacent wooded forests. The blackbird is more flexible in using artificial nesting structures and food resources, and therefore had equal to higher nesting densities in urban versus wooded sites than the song thrush, which had similar to higher breeding densities in wooded sites. The variety of food fed to nestlings had a higher animal component in wooded sites, and the diet of blackbird nestlings had an overall higher animal component than the song thrush nestlings. The nearly complete lack of anthropogenic food resources in urban song thrush nestling diet is in stark contrast to the blackbird. Animal material in song thrush nestling diets was significantly lower in urban environments (10%) than forests (50%). It appears that the lower success in urban environments for these species is tied, in part, to their inability to obtain appropriate food resources.

4.4.1. Raptors

Many species of raptors have taken advantage of artificial nest sites, which often confer a greater reproductive advantage than wild sites (Table 3). Cooper's hawks in Tucson, Arizona nest earlier and have larger clutches than wild nesting pairs. Urban pairs have lower

nesting success because of the high nestling mortality rate due to Trichomoniasis (80%), leading to higher failure rate (53% versus 21%) of urban nests (Boal and Mannan, 1999). Reproductive success of American kestrels nesting along highways in Iowa is similar to kestrels in other areas (Varland and Loughin, 1993). Tawny owls in Rome exhibited similar reproductive success in both urban and suburban areas (Table 3; Ranazzi et al., 2000). Burrowing owls in Florida had greater nest densities and a greater number of fledged young in lower density residential sites than in higher density residential sites (Millsap and Bear, 2000).

4.4.2. Egg size

Vengerov (1992) found a decrease in egg size among urban nesting chaffinches, song thrushes, and black-billed magpies, but no effect among European starlings. Increased intraclutch variation would presumably result in a greater variation in nestling quality, and therefore survivorship. The degree of variability depends on the physiological condition of the female (Ricklefs, 1984), as anomalous eggs arise more often in females in lower physiological condition (Horsefall, 1984; Jarvinen and Ylimaunu, 1986). Therefore, the smaller egg sizes found by Vengerov (1992) in urban environments may be a manifestation of females in poor physiological condition; hatching success, offspring survival and measures other measures of reproductive success may be correlates of female condition. In this sense, the pattern of community change following urbanization that favors granivorous birds at the expense of bark gleaners may be the result of females of the former being able to find ample food resources (e.g. bird feeders), while females of the latter suffer as many dead and decaying trees are removed in urban areas.

4.4.3. Nest predation

Corvids often have positive associations with urban environments suggesting that their reproductive success is equal or higher in the urban than local wildlands (Soh et al., 2002). Florida scrub jay nests survive longer in urban areas than wild areas, even though nest success does not differ between to two environments (Bowman and Wolfenden, 2001). American crow reproductive success varies greatly across the urban gradient; success is consistently low on golf courses, universities, and woodlots in urban settings, and high in suburbs as

well as in wildlands adjacent to human activity centers (Marzluff et al., 2001). If corvids are more successful in urban environments, then it would logically follow that the success comes at the expense of small passerine populations via nest predation by corvids, among other predators. Nest predation is probably the most important limiting factor on passerine populations (Martin, 1993), especially migrants (Bohning-Gaese et al., 1993). Introduced predators are more abundant in urban areas. Avian predators may increase in urban areas, and concentrate efforts on prey congregation sites such as lawns and feeders (Kristan et al., 2003). In coastal sage-scrub of California, coyotes, domestic cats and domestic dogs are more common at edges (Kristan et al., 2003). Large predators are often absent in urban areas and some local bird species may benefit. Corvids increase with urbanization that may result in higher nest predation (Cringan and Horak, 1989; Soloviev, 1991), although this has not been directly examined for most urban avian communities (but see Groom, 1993; Miller and Hobbs, 2000). Most studies are correlative, and detect negative correlations between corvids densities and passerine nesting success in urban area (e.g. Engels and Sexton, 1994). Other studies have used artificial nests and have found higher predation on artificial nests in urban than suburban areas (Jokimäki and Huhta, 2000), or urban than rural (Wilcove, 1985), and higher in managed parks than unmanaged parks (Jokimäki and Huhta, 2000). Corvids prefer edge habitats that urbanization creates and nesting success often declines therein (Matthews et al., 1999). Interestingly, some have shown that nest predation decreases with increasing urbanization (Russo and Young, 1997; Gerling and Blair, 1999) and with distance from recreational trails (Miller and Hobbs, 2000). Corvid abundance increases with urbanization but their impact on passerine reproductive success clearly needs more attention.

Nest predation can drive coexistence of species and community organization by selection for diversified nest sites to reduce density-dependent predation in undisturbed forests (Martin, 1988). However, it is unlikely that birds have evolved such adaptations to disturbed habitats such as parks. Sasvari et al. (1995) found that compared to a wild mixed oak-beech forest in Budapest, Hungary, nest predation in urban parks is strongly correlated with nest density and not nest type as predicted by the Martin (1988) model.

4.4.4. Brood parasitism

Brood parasitism impacts the fecundity of hosts that accept parasitic eggs of cowbirds, cuckoos, and other obligate interspecific brood parasites (Davies, 2000). Brood parasitic cowbirds frequent forest/field edges and directly impact the reproductive success of forest-nesting hosts along those edges (Gates and Gysel, 1978). Cowbirds commute between feeding areas and areas where eggs are laid therefore distance to feeding areas (e.g. livestock) plays an important role in cowbird distribution and parasitism intensity on a hosts within a forest patch (Rothstein et al., 1984; Robinson, 1999; Curson et al., 2000). Few studies have examined the impact of brood parasitism within the context of urbanization. Chace (2001) and Chace et al. (2003) found that cowbirds use the urban environment for feeding and roosting, and move to undeveloped forests to parasitize hosts. In Boulder, Colorado the abundance of brown-headed cowbirds drops off dramatically with increasing distance from the urban/wildland boundary (Chace et al., 2003). In Sierra Vista, Arizona, bronzed and brown-headed cowbirds feed and roost among golf courses, cemeteries, and urban backyards and fly at pre-dawn up to 6 km to regions of high host abundance (Chace, 2001).

4.4.5. Visitation disturbance

A growing body of evidence points to non-consumptive human activities having negative impact on bird communities (e.g. Knight and Gutzwiller, 1995). In many landscapes urbanization is correlated with increased human visitation to recreational areas; increased visitation can result in lower reproductive success (Miller et al., 1998) through desertion (Burger, 1981a,b), decreased hatching success (Hunt, 1972; Schreiber, 1970), decreased ability to feed young (Leseburg et al., 2000), increased predation (Kury and Gochfeld, 1975; Desgranges and Reed, 1981), and decreased parental attendance (Safina and Burger, 1983).

4.5. Urbanization impacts on survivorship

The major factors affecting survivorship of birds in urban environments are collisions with man-made objects, food acquisition, predation and disease.

4.5.1. Collisions

Twenty-five percent of all US bird species (917) have been documented striking windows. Sex, age, or

residency status has little influence on strikes (Klem, 1989). In Connecticut, Codoner (1995) found the greatest number of strikes during fall and spring migration. Car-strikes peak in May-June during adult activity for care of young, and car-related strikes predominant in species adapted to high human densities such as the rock dove, northern flicker, European starling, and eastern screech owl (Codoner, 1995). Window-strikes most often involve migrants, usually in lower density housing areas (Codoner, 1995). Power lines present another urban hazard. Collision with power lines near a cooling pond in Michigan resulted in the injury or death of 87 birds of 11 species (Rusz et al., 1986). The rate of death per 1000 use days varied from gulls (0.03), mallards (0.16), Canada goose (0.23), to the great blue heron (56.07; Rusz et al., 1986).

4.5.2. Changes in food supply abundance

Urban centers provide food for birds directly at feeders, and indirectly at areas of waste treatment, collection, and transfer (Marzluff, 1997). 82.5 million people a year feed birds in the United States, spending over US\$ 1 billion (Geis and Pomeroy, 1993). Seed eaters, nectarivores, and omnivores benefit from this commensal relationship, even though seed eating species use feeders as only part of their foraging requirements, and therefore feeders are not essential to birds' survival (Geis and Pomeroy, 1993). Food resources are also affected by changes in vegetation. For instance, exotic plants tend to have fewer insects than natives, while urban lawns provide rich, consistent feeding grounds (Rosenberg et al., 1987). Urbanization increases the population of many human-commensal small mammals which can provide additional food supply for raptors (Millsap and Bear, 2000; Ranazzi et al., 2000; Mannan and Boal, 2000).

Winter feeding can affect mortality due to disease and predation. In one study, disease transmission was calculated at a rate of (1/21.5 feeder-years), and the probability of mortality is associated with type of feeder and species composition at the feeder site (Brittingham and Temple, 1986). Such effects would not occur if primary cause of death were starvation and hypothermia, thus disease is probably a main cause of death (Brittingham and Temple, 1986), although there are no studies of disease transmission in wild granivorous birds (Brittingham, 1990). Birds that use feeders are often in better physiological condition than those

that do not, and therefore may be less likely to contract diseases (Brittingham, 1990). Feeders attract birds and provide predators with foraging opportunities. Urban nesting Cooper's hawks had higher rates of Trichomoniasis than wild hawks, presumably the disease is contracted through predation of infected feeder birds (Boal and Mannan, 1999). Domestic cats, Cooper's hawks, and sharp-shinned hawks were responsible for 80% ($N=1138$) of predatory incidents at one urban feeder study (Dunn and Tessaglia, 1994). Prey most vulnerable were those most common at feeders (10 of 62 species accounted for 92% of victims) (Dunn and Tessaglia, 1994). However, bird feeding does not appear to expose birds to a higher risk of predation than is encountered in the absence of feeders (Jansson et al., 1981; Dunn and Tessaglia, 1994). Birds make up small a small percent of the diet of feral and domestic cats (Eberhard, 1954; Coman and Brunner, 1972; Liberg, 1984), however these studies did not account for injuries (Adamec, 1976).

Feeding birds can affect overwinter survival of some species, under some conditions. Horak and Lebreton (1998) found that urban great tits survive better than rural tits in Tartu, Estonia. Jansson et al. (1981) found that extra food improved winter survival of willow tits and crested tits. Improved winter survival led to doubled breeding populations in the following spring, thus winter food abundance limits breeding population size of these species. Brittingham and Temple (1986) found that winter feeding doubled the survivorship of black-capped chickadees in Wisconsin during harsh winters. However, the difference was not as strong during mild winters, and, predictably, in a replicate study in Pennsylvania, where winters are more mild than in Wisconsin, feeders had no effect on overwinter survival (Egan and Brittingham, 1994).

Feeders may affect the local distribution and abundance of bird species within a region (Wilson, 1994), and local dispersal patterns (Egan and Brittingham, 1994). Because of the higher overwinter survival of some species that use feeders, feeders may be an important factor in the recent range expansion of some species. The blue jay population has shown a 30% increase while migration has declined between 1962 and 1971 (Bock and Lephian, 1976). Blue jays exhibited a positive numerical response to moderate housing density (0.6–6.7 houses/ha) in western Massachusetts, while open cup nesting species showed

significant declines (Kluza et al., 2000). It is possible that jays respond to feeders and edges with increasing urbanization, while preying upon the nests of open cup passerines. Feeders may also be important in the distributional shifts of the American goldfinch (Middleton, 1977), northern cardinal (Beddall, 1963), and the mourning dove (Alison, 1976). Feeder use by some species may cause an ecological shift by favoring species that use feeders over those that do not (Winter and George, 1981). Feeders also support introduced species (Brittingham, 1990).

Feeding birds in urban areas can affect activity budgets. Time activity budgets and intraspecific aggressive interactions of wintering mute swans were found to be altered in urban areas where they are fed versus rural where they are not in Cracov, Poland (Józkowicz and Górska-Klęk, 1996). Rural swans spent significantly more time foraging (48% versus 13%) than urban swans, and less time swimming (10% versus 28%) and "loafing" (18% versus 36%) than urban swans. Frequency of aggressive encounters between urban swans was significantly higher than among rural swans (Józkowicz and Górska-Klęk, 1996).

4.5.3. *Changes in predator assemblage*

Predators can reach higher numbers in urban areas because of supplemental food. Urban ring-billed gulls consume greater amounts of earthworms and garbage than rural gulls (Brousseau et al., 1996). In a meta-analysis Marzluff et al. (2001) found that American crow pair breeding range is <15 ha in urban areas, 30–40 ha in rural/urban interface areas, and 1000–3500 ha in wild settings. However, American crow density does not correlate with the rate of nest predation on passerines because they are only one of many nest predators occupying urban areas (Marzluff et al., 2001). The pied currawong is a partially frugivorous bird native to Australia, and it benefits from the cultivation of exotic ornamental plants (Buchanan, 1989; Bass, 1995). In addition to fruit, currawongs are nest predators, and Major et al. (1996) found that 52% of 64% ($N=2000$) of artificial nest predation in Australian cities were attributable to the currawong. Thus, supplemental food resources that attract predators can have a significant effect on the persistence of small bird populations in urban environments.

Scavengers such as common ravens increase in number with the number of parallel rights-of-way in

the Mohave desert (Knight et al., 1995), and are more numerous along primary roads than secondary roads (Knight and Kawashima, 1993). Wintering golden eagles and resident black-billed magpies respond positively to roadways as road kill scavengers in Moffat County, Colorado (Beaver and Roth, 1997).

Urbanization can decrease large mammalian predator abundance, e.g. coyotes, which in turn “release” mesopredators, such as domestic cats (Crooks and Soulé, 1999). Cats are human commensals and are the most widespread terrestrial carnivore. Feral cats have greater home ranges than free-ranging domestics, with densities ranging from 2.2/km (in Galapagos) to 44/km (in Wisconsin). Feral cats hunt more often than domestic free-ranging cats. Churcher and Lawton (1987) studied prey remains of 70 cats and found that they averaged 14 prey per year. Cats primarily prey upon small mammals and birds. Rural cats take more mammals, suburban cats take more birds. In the suburbs, cat predation is density-dependent as the most abundant birds, which are typically non-natives, are taken most often.

4.5.4. *Introduced competitors*

Little information exists on the effects of introduced exotic species in urban habitats. In southern California at least 10 species of parrots appear to be naturalized in the greater Los Angeles area, with another 24 casually reported, non-established species. Of those 24, six are regularly imported species and are likely to establish naturalized populations in the near future (Garrett, 1997). Close association between urbanization and the establishment of exotic bird species in southern California is also found for groups of exotic doves, bishops, and manikins.

4.5.5. *Human activity*

Parks and reserves in urban areas receive a large number of visitors that partake in non-consumptive activities that may have negative impacts on bird communities (e.g. Boyle and Sampson, 1985; Knight and Gutzwiller, 1995). Bird communities have been shown to change in relation to human activity along trails through avoidance behavior (Miller et al., 1998). In high visitation areas, time spent foraging and capture rates are often compromised (Burger and Gochfeld, 1998; Leseberg et al., 2000), which may result in reduced survivorship especially if it occurs during criti-

cal periods such as migration stages (Burger, 1981b). Behavioral changes associated with human disturbance vary among species, in some situations birds habituate to disturbance (Burger and Gochfeld, 1998). Behavioral changes may not reflect population consequences, and establishing conservation priorities based on species-specific sensitivity may be misguided (Gill et al., 2001).

4.5.6. *Other factors*

Urban environments are warmer than nearby rural areas (Haggard, 1990) and urbanization may play a role in the range expansion and overwinter survival of some species along the east coast of the United States (e.g. Blue Jay—Bock and Lepthian, 1976), however this needs to be tested directly. Factors of disease and parasite transmission in wild and urban bird populations need to be examined more directly. Boal and Mannan's (1999) finding that trichomoniasis (80%) leads to a higher failure rate of urban nesting Cooper's Hawks, despite that urban hawks have larger clutch sizes, is cause for concern.

Corvids and raptors can minimize energy expenditures by habituation to human presence, and that recent colonization of cities may be, in part, a response to different levels of persecution in urban and rural areas (Houston, 1977; Knight et al., 1987). Human persecution plays an important role in determining flushing distances in bald eagles (Fraser et al., 1985). Common ravens are more cautious in nest defense in areas with frequent nest destruction by humans (Knight, 1984). American crows altered nest defense strategies in rural areas where they are persecuted versus urban areas where they are not (Knight et al., 1987). Red-tailed Hawks habituate to human intrusion with call and dive rates at nest sites lowest in areas of longest human contact (Knight et al., 1989).

Roads are synonymous with urbanization and road affects can result in fragmentation, isolating populations, increased noise, and automobile strikes. Direct mortality through collisions with automobiles may increase as habitat corridors are divided or if birds are attracted to the road corridor (Forman and Alexander, 1998; Mumme et al., 2000). Traffic noise may interfere with predator-avoidance communication during nesting and fledging phases (Forman and Alexander, 1998). Traffic noise has been found to be a key factor altering grassland and forest bird community composition for

hundreds of meters from roads through avoidance behavior (Reijnen et al., 1995; Green et al., 2000; Forman et al., 2002).

5. Conclusions

The effect of urbanization can be immense, yet our understanding is rudimentary. Taxonomically, bird communities in distinctly different habitats are most different in the least disturbed sites and the most similar in the most urbanized sites (Blair, 2001). Urbanization selects for omnivorous, granivorous, and cavity nesting species (Emlen, 1974; Lancaster and Rees, 1979; Beissinger and Osborne, 1982; Rosenberg et al., 1987; Mills et al., 1989; Allen and O'Conner, 2000; Kluza et al., 2000). Increased urbanization leads to an increase in avian biomass but a reduction in richness, a pattern largely, but not completely, consistent across forests, desert scrub, and grassland habitats.

Bird communities become distinct from the native community (Wood, 1996; but also see Edgar and Ker-shaw, 1994) and more homogenous with other urban areas (Blair, 2001) as time from urban development increases. This is one area needs to be explored in more detail. Studies with a greater coverage of time since development and over a greater range of plant communities are needed. Missing are thorough investigations in the regions of highest human population growth, e.g. Southeast Asia. Additionally, there is a paucity of information from regions of high avian diversity, e.g. tropical forests.

Studies of passerine responses to urbanization are often devoid of important reproductive information that is more descriptive of habitat quality than measures of abundance (Van Horne, 1983; but see Schnack, 1991). Studies of raptors can be illuminating in this regard, as demographic parameters have often been measured on urban nesting owls, hawks, falcons, and eagles. However, unlike most passerines, raptors may have home ranges that extend beyond the urban boundary and therefore do not need to meet all their ecological requirements within urban areas. Urban habitats are often of superior quality to raptors (Cringan and Horak, 1989; Table 3) because there they are often free from persecution and have an adequate food supply allowing use of otherwise unsuitable or unproductive nesting sites (Newton, 1986).

The processes that underlie the patterns of population and community level responses need more attention, but several areas of have been identified as being important. Birds respond to vegetation composition and structure, and urban areas that retain native vegetative characteristics retain more native species than those that do not (Mills et al., 1989). Typical urban vegetation in forest biomes results in the loss of canopy guilds and bark drilling guilds; however there is a general lack of similar information from other biomes. Even in urban areas fragmentation is important; in forested landscapes retaining large patches of native vegetation results in higher species richness and abundance of migratory passerines (Friesen et al., 1995). In some cases, the exotic plantings of urban areas may provide refuge for some species (Gavareski, 1976), but without demographic information it is not clear if such areas are population sinks or sources. Avian fecundity in urban areas is a reflection of their adaptability to urban resources (e.g. many raptors; Schnack, 1991), and levels of nest predation (Bohning-Gaese et al., 1993; Miller and Hobbs, 2000), and nest parasitism (Chace et al., 2003). Additionally, non-consumptive human activities are recognized as having negative impacts on avian populations and communities (Knight and Gutzwiller, 1995; Miller et al., 1998), factors that increase with urbanization. Avian survivorship in urban areas is influenced by risk of collision with man-made objects (Klem, 1989), changes in the predator assemblage (Major et al., 1996), food supply (Egan and Brittingham, 1994; Wilson, 1994), and disease (Boal and Mannan, 1999).

The obvious effects of urbanization: loss and degradation of habitat, introduction of exotic species, changes in predator community have received more attention, but all still need closer examination, especially among regions and major plant communities that have received little (tropical rainforests) or no (Indonesia) attention with respect to urbanization. In addition, some studies have found generalizations about predators and nest success to be false at the local, management level (Miller and Hobbs, 2000). Clearly, local knowledge and study is required before implementation of management policies to reduce urban impacts on bird communities. Hopefully, such policies will include long-term monitoring.

Less obvious, indirect effects: climate change, human disturbance, ecosystem disruption, physiological

stress, food supplements, disease transmission, and competitive interactions require more study before these effects on birds can be generalized. The ultimate drivers of avian population and community change need to be identified and understood in order to establish the Best Management Practices for urban planning in areas of rapid urbanization. With this in mind, demographic parameters of fecundity and survivorship need to be examined in conjunction with measures of community diversity and density across the urban gradient to better understand the quality of different urban habitats, and the variation of quality among spatial patterns of urbanization within the native habitat matrix.

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Appendix A. Scientific names of bird species referred to in this paper

Acadian flycatcher	<i>Empidonax virescens</i>
American crow	<i>Corvus brachyrhynchos</i>
American goldfinch	<i>Carduelis tristis</i>
American kestrel	<i>Falco sparverius</i>
American robin	<i>Turdus migratorius</i>
Anna's hummingbird	<i>Calypte anna</i>
Ash-throated flycatcher	<i>Myiarchus cinerascens</i>
Bald eagle	<i>Haliaeetus leucocephalus</i>
Baltimore oriole	<i>Icterus galbula</i>
Barn swallow	<i>Hirundo rustica</i>
Barred owl	<i>Strix varia</i>
Bewick's wren	<i>Thryomanes bewickii</i>
Black-and-white warbler	<i>Mniotilta varia</i>
Black-billed magpie	<i>Pica pica</i>
Black-capped chickadee	<i>Poecile atricapillus</i>
Black-chinned hummingbird	<i>Archilochus alexandri</i>
Black-chinned sparrow	<i>Spizella atrogularis</i>
Blue grosbeak	<i>Guiraca caerulea</i>

Appendix A (Continued)

Blue jay	<i>Cyanocitta cristata</i>
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>
Bobolink	<i>Dulichonyx oryzivorus</i>
Bronzed cowbird	<i>Molothrus aeneus</i>
Brown gerygone	<i>Gerygone mouki</i>
Bullock's oriole	<i>Icterus bullockii</i>
Burrowing owl	<i>Athene cunicularia</i>
California gnatcatcher	<i>Poliophtila californica</i>
California thrasher	<i>Toxostoma redivivum</i>
California towhee	<i>Pipilo crissalis</i>
Canada goose	<i>Branta canadensis</i>
Carolina chickadee	<i>Poecile carolinensis</i>
Carrion crows	<i>Corvus corone</i>
Cerulean warbler	<i>Dendroica cerulea</i>
Chaffinch	<i>Fringilla coelebs</i>
Chimney swift	<i>Chaetura pelagica</i>
Clay-colored sparrow	<i>Spizella pallida</i>
Collared Scops-owl	<i>Otus bakkamoena</i>
Common myna	<i>Acridotheres javanicus</i>
Common raven	<i>Corvus corax</i>
Cooper's hawk	<i>Accipiter cooperii</i>
Costa's hummingbird	<i>Calypte costae</i>
Crested tit	<i>Parus cristatus</i>
Curve-billed thrasher	<i>Toxostoma curvirostre</i>
Dark-eyed junco	<i>Junco hyemalis</i>
Dickcissel	<i>Spiza Americana</i>
Downy woodpecker	<i>Picoides pubescens</i>
Eastern screech owl	<i>Otus asio</i>
Eastern whipbird	<i>Psophodes olivaceous</i>
Eastern wood-pewee	<i>Contopus virens</i>
Eastern yellow robin	<i>Eopsaltria australis</i>
European blackbird	<i>Turdus merula</i>
European starlings	<i>Sturnus vulgaris</i>
Ferruginous hawk	<i>Buteo regalis</i>
Florida scrub jays	<i>Aphelocoma coerulescens</i>
Golden eagle	<i>Aquila chrysaetus</i>
Grasshopper sparrow	<i>Ammodramus savannarum</i>

Appendix A (Continued)

Gray catbird	<i>Dumetella carolinensis</i>
Great blue heron	<i>Ardea herodias</i>
Great tit	<i>Parus major</i>
Great-crested flycatcher	<i>Myiarchus crinitus</i>
Greater green leafbird	<i>Chloropsis sonnerati</i>
Great-horned owl	<i>Bubo virginianus</i>
Great-tailed grackle	<i>Quiscalus mexicanus</i>
Harris' hawk	<i>Parabuteo unicinctus</i>
Hooded warbler	<i>Wilsonia citrina</i>
Horned lark	<i>Eremophila alpestris</i>
House finch	<i>Carpodacus mexicanus</i>
House sparrow	<i>Passer domesticus</i>
House swift	<i>Apus nipalensis</i>
Hutton's vireo	<i>Vireo huttoni</i>
Inca dove	<i>Columbina inca</i>
Kentucky warbler	<i>Oporonis formosus</i>
Kestrel	<i>Falco tinnunculus</i>
Lark sparrow	<i>Chondestes grammacus</i>
Lazuli bunting	<i>Passerina amoena</i>
Lesser goldfinch	<i>Carduelis psaltria</i>
Lesser kestrel	<i>Falco naumanni</i>
Mallard	<i>Anas platyrhynchos</i>
Mississippi kite	<i>Ictinia mississippiensis</i>
Mourning dove	<i>Zenaida macroura</i>
Mute swan	<i>Cygnus olor</i>
Northern goshawk	<i>Accipiter gentiles</i>
Northern cardinal	<i>Cardinalis cardinalis</i>
Northern flicker	<i>Colaptes auratus</i>
Northern mockingbird	<i>Mimus polyglottos</i>
Northern parula	<i>Parula Americana</i>
Orange-crowned warbler	<i>Vermivora celata</i>
Osprey	<i>Pandion haliaetus</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Peregrine falcon	<i>Falco peregrinus</i>
Phainopepla	<i>Phainopepla nitens</i>
Pied currawong	<i>Strepera graculina</i>
Prairie falcon	<i>Falco mexicanus</i>

Appendix A (Continued)

Purple martin	<i>Progne subis</i>
Red-bellied woodpecker	<i>Melanerpes carolinus</i>
Red-eyed vireo	<i>Vireo olivaceus</i>
Red-shouldered hawk	<i>Buteo lineatus</i>
Red-tailed hawk	<i>Buteo jamaicensis</i>
Red-whiskered bulbul	<i>Pycnonotus jocosus</i>
Ring billed gull	<i>Larus delawarensis</i>
Rock dove	<i>Columbia livia</i>
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>
Rough-legged hawk	<i>Buteo lagopus</i>
Rufous-crowned sparrow	<i>Aimophila ruficeps</i>
Sage sparrow	<i>Amphispiza belli</i>
Savannah sparrow	<i>Passerculus sandwichensis</i>
Scarlet tanager	<i>Piranga olivacea</i>
Scops-owl	<i>Otus scops</i>
Sharp-shinned hawk	<i>Accipiter striatus</i>
Short-tailed babbler	<i>Malacocincla malaccensis</i>
Song sparrow	<i>Melospiza melodia</i>
Song thrush	<i>Turdus philomelos</i>
Sparrowhawk	<i>Accipiter nisus</i>
Steller's jay	<i>Cyanocitta stelleri</i>
Summer tanager	<i>Piranga rubra</i>
Swainson's hawk	<i>Buteo swainsoni</i>
Tawny owl	<i>Strix aluco</i>
Tufted titmouse	<i>Baeolophus bicolor</i>
Veery	<i>Catharus fuscescens</i>
Vesper sparrow	<i>Poocetes gramineus</i>
Western meadowlark	<i>Sturnella neglecta</i>
Western scrub-jay	<i>Aphelocoma californica</i>
Western wood-pewee	<i>Contopus sordidulus</i>
White-browed scrubwren	<i>Sericornis frontalis</i>
White-throated swift	<i>Aeronautes sexatalis</i>
White-winged dove	<i>Zenaida asiatica</i>
Willow tit	<i>Parus montanus</i>
Wood thrush	<i>Hylocichla mustelina</i>
Wrentit	<i>Chamaea fasciata</i>
Zone-tailed hawk	<i>Buteo albonotatus</i>

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