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A new bully on the block: Does urbanization promote Bewick's wren (*Thryomanes bewickii*) aggressive exclusion of Pacific wrens (*Troglodytes pacificus*)?

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ABSTRACT

Human conversion of land cover alters biotic communities and sets the stage for ongoing change as species interact within new environments. We studied the response of a native forest specialist, the Pacific wren (*Troglodytes pacificus*), to immediate and ongoing environmental changes facilitated by urbanization. We found evidence of a synergistic effect of native land cover loss followed by increased aggressive interactions with a native generalist, the Bewick's wren (*Thryomanes bewickii*), resulting in the decline of Pacific wrens in urbanizing environments. Pacific wren relative abundance decreased dramatically during and after development, while Bewick's wrens increased and persisted at greater abundance post-relative to pre-development. Breeding territories of the two species overlapped minimally, suggesting spatial segregation either by differential resource use or territorial aggression. A comparison of territory characteristics revealed the species generally used different resources, although territory composition was increasingly similar at urbanizing sites where the species co-occurred. Territorial playback experiments confirmed that the two species interact aggressively. Analyses of body size, body condition and reproductive success did not suggest Bewick's wrens negatively impact fitness of Pacific wrens at sites where they co-occurred. In established subdivisions (>10 years old) Bewick's wrens appear to limit the abundance of Pacific wrens, however this was not yet the case at sites we studied immediately after development. Although the results of this study are not conclusive, our findings are consistent with the hypothesis that new environmental gradients and communities created by urbanization increase competitive interactions among native species.

1. Introduction

Humans impact marine, freshwater, and terrestrial environments, fundamentally affecting how ecological systems function (Dudgeon et al., 2006; Halpern et al., 2008; Hoekstra et al., 2005; Vitousek et al., 1997). In terrestrial systems, widespread changes in land cover and land use are especially problematic (Foley et al., 2005; Houghton, 1994; Meyer and Turner, 1992). Urban sprawl and exurban development comprise the fastest growing source of land cover change in the United States, with serious implications for biodiversity (Brown et al., 2005; Miller and Hobbs, 2002). Loss of native land cover resulting from urban development is second only to invasive species as the leading cause of species endangerment in the US (Czech et al., 2000). Potential effects of urbanization on ecological communities include fragmentation, degradation and loss of natural habitats (Alberti, 2005; Matlack, 1993), biotic homogenization (McKinney, 2006; Olden et al., 2004), disruption of natural disturbance regimes and nutrient cycling (Goldman et al., 1995; Miller and Wade, 2003; Poff, 2002; Smith et al., 1999), diversion of water resources (Coleman et al., 2011; Wang et al., 2001), and increased temperatures (Taha, 1997). Nevertheless, there remains a need for increased ecological research in urban, suburban, and exurban landscapes regarding impacts on native species and surrounding ecosystems (Collins et al., 2000; Miller and Hobbs, 2002). Improving our understanding of the mechanisms driving organismal responses to urbanization is especially important for efforts to mitigate the impacts of urban sprawl on biodiversity (Agrawal et al., 2007; Hansen et al., 2005).

Humans affect the structure of ecological communities both directly and indirectly (Boren et al., 1999; Gido et al., 2010; Morrison et al., 2007; Ruhl and Smith, 2004). One well-documented pattern of community reassembly following urbanization is an increase in early successional species (both native and non-native), with a simultaneous decrease in native specialists (Ford et al., 2001; Marzluff, 2005; McKinney, 2006). The most obvious explanation is direct loss of indigenous vegetation upon which many native species rely, paired with an increase in edge environments that

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favor ‘weedy’ species (Nee and May, 1992). These new environments may challenge remaining native species with increased risks of predation, nest parasitism, and interactions with invasive species in isolated patches and along edges (Jokimaki and Huhta, 2000; Marzluff et al., 2007; Shochat et al., 2010).

A less well-studied potential threat to native specialists is increased aggression from newly expanding native generalists and synanthropes, following urbanization (Garrott et al., 1993). Native species that do not typically co-occur in natural environments may be brought into proximity and increasing contact as a result of rapid anthropogenic alteration of the landscape (Carrete et al., 2010; Montague-Drake et al., 2011; Sedlacek et al., 2004). In this context, native specialists may face the dual threat of direct habitat loss followed by altered biotic interactions with native generalists and opportunists that thrive in human-altered landscapes (Garrott et al., 1993; Montague-Drake et al., 2011).

Human-facilitated disturbances that occur in rapid succession may inhibit biological communities from recovering as they would to natural levels of disturbance (Paine et al., 1998; Brook et al., 2008). Unfortunately, there is a general lack of understanding of the compound, synergistic effects (Brook et al., 2008) of anthropogenic disturbance and ensuing shifts in biological dynamics (Alberti, 2005; Brook et al., 2008; Underwood et al., 2009). The potential deleterious effects of human development and subsequent altered interactions among native species deserve increased attention (Garrott et al., 1993).

In Washington State, the greater Seattle metropolitan area and surrounding landscape has undergone and continues to experience rapid human population growth (Hepinstall et al., 2008). Avian communities in this region have shifted in response to urbanization, and it is likely that the effects of native land cover change are compounded by changes in the assemblages of species that now co-occur (Marzluff, 2005). While biomass typically peaks in urban bird communities, diversity peaks at intermediate levels of disturbance along an urban gradient, primarily as a result of invasions and colonizations by early-successional and synanthropic native species (Donnelly and Marzluff, 2004). Two confamilial, native wren species in this region have been brought into increasing contact in areas undergoing urbanization. Pacific wrens (*Troglodytes pacificus*) are a sensitive, native forest dependent species that decline with urbanization (Donnelly and Marzluff, 2006), whereas Bewick’s wrens (*Thryomanes bewickii*) are an early successional species that benefit from disturbance (Hejl et al., 2002; Kennedy and White, 1997). The two species generally do not co-occur; however, in urbanizing landscapes habitats suitable for both species are intermingled. Bewick’s wrens occur in various human-made environments, from urban and suburban neighborhoods to forest edges in parks, fields and clear-cut areas. They colonize forested areas in parks, greenspaces and reserves where Pacific wrens remain during development.

Our goal is to explore the synergistic effects of land cover change and increasing aggressive encounters among native species as potential mechanisms influencing the redistribution of Bewick’s and Pacific wrens following urbanization. There are several reasons to expect some level of aggression between these two species. First and foremost the extent of forest suitable for Pacific wrens is limited in developed areas; 54 developments we previously studied were imbedded in 1 km^2 landscapes comprised only of 35% native forest and most of this was distributed in small (<30 ha) patches (Donnelly and Marzluff, 2006). Second, although Bewick’s and Pacific wrens differ in foraging habits and overall diet composition, there is substantial overlap in prey items consumed (Beal, 1907; McLachlin, 1983). Both species are also opportunistic in selection of nest sites, and overlap in their use of existing cavities in trees and dead wood structures (Campbell et al., 1997). Lastly, there is precedence for aggression between wrens in the Troglodytidae family; sharp declines and extirpations of Bewick’s wren populations in the eastern U.S. have been attributed to interference competition from house wrens (*Troglodytes aedon*; Kennedy and White, 1996). To determine if aggression from Bewick’s wrens is potentially compounding the effects of habitat loss on Pacific wren abundance in urbanizing landscapes, we investigate their relative abundances, spatial dynamics, characteristics of breeding territories, levels of interspecific aggression, and relative fitness, both in areas where they occur separately and where they now co-occur.

2. Methods

2.1. Study region and site selection

The region from Seattle and the Puget Sound east to the Cascade Mountain foothills comprises a mosaic of urban, suburban, agricultural, and forested land cover. Using stratified random sampling, we selected 27 1-km^2 study sites representing a gradient of urban and forested land cover types, urban patch size, and forest aggregation (Fig. 1; see Donnelly and Marzluff (2004, 2006), Blewett and Marzluff (2005) for further details). We quantified land cover and patterns of settlement using a classified 1998 LANDSAT satellite image (Botsford, 2000). After visiting and assessing potential field sites, we selected sites in three main categories: (a) twelve sites were well-established settlements that had been constructed at least 10 years prior to the start of the study (hereafter ‘developed’); (b) four sites were heavily forested reserves composed of relatively mature mixed conifer and deciduous forest, similar to dominant land cover prior to European settlement (Booth, 1991; hereafter ‘reserves’); and (c) eleven sites were forested at the start of the study, but were converted to single family housing developments over a 1–5-year period during our study (hereafter ‘changing’; Fig. 2). The pattern and density of these developments varied; housing lots ranged from 0.1 to 10 ha, development was clustered and separated from small reserves or sprawled among mostly linear greenbelts of native vegetation, and 5–75% of the forest within a 1 km^2 area centered on the site was removed by 2001. Detailed temporal analysis of change is ongoing (DeLap and Marzluff, in prep.). We chose sites that were representative of immediately surrounding areas, and below 1000 m in elevation. Developed sites and reserve sites served as controls for changing sites undergoing development.

2.2. Relative abundance

From 1998 to 2010, we surveyed wren abundance at 166 points distributed throughout 27 main study sites. Each site contained 4–8 points that we surveyed four times during the breeding season (April–August), using 50-m fixed-radius point counts of 10 min duration (Ralph et al., 1993). We identified and clearly documented landmarks of known distance from each survey point, to aid with accuracy and consistency of observations during the 13-year study. In sites with both built and forested land cover we allocated more effort to built areas (6 of 8 points) because a previous study in this region showed higher variability in land cover and birds in built versus forested areas (Donnelly and Marzluff, 2006).

We counted birds seen and heard between the hours of 0500 and 1200, and did not survey when weather conditions interfered with audibility or visibility of birds. To induce normality (via the central limit theorem) and designate the site as the experimental unit we calculated average annual relative abundances for Pacific wrens and Bewick’s wrens at each site as the mean of the 16–32 counts conducted there each year.

We estimated relative abundance within areas of small and fixed radius because land cover within developments is not