Spatial and temporal activity patterns of the brood parasitic brown-headed cowbird at an urban/wildland interface

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Received 21 March 2002; received in revised form 22 October 2002; accepted 6 November 2002

Abstract

We examined the impact of the urban environment on the spatial and temporal activity of brood parasitic Brown-headed Cowbirds (Molothrus ater) in Boulder County, CO, USA. We found that cowbirds used the urban areas for foraging and roosting and traveled into the 3240 ha wildland preserve of ponderosa pine in the mornings to parasitize songbird hosts. Cowbird abundance decreased with distance from the urban/wildland boundary, and Plumbeous Vireo (Vireo plumbeus) nests closer to the urban/wildland boundary were more likely to be parasitized by cowbirds than those farther away. A linear regression accurately predicted the relative abundance of cowbirds based on parameters of distance from residential areas, and distance from roads and trails within the wildland preserve. For species of concern that are known cowbird hosts, creating larger preserves, reducing residential encroachment, and reducing preserve perforation by roads and trails might alleviate high frequencies of parasitism for a portion of the host population. However, even large preserves, such as found in Boulder, CO, USA cannot insulate all focal nesting species from the urban effect of increased brood parasitism. Efforts to reduce food resources and cover for cowbirds in the urban areas might prove to ameliorate host reproductive success close to the urban/wildland boundary through decreases in cowbird abundance.

Keywords: Birds; Brown-headed cowbird; Parasitism; Plumbeous vireo; Urban effects; Colorado (USA)

1. Introduction

Jurisdictions commonly establish open space or greenways with the intention that these lands will serve the public a variety of disparate functions, such as aesthetics, recreation, environmental education, alternative transportation, community development, growth management, reduction of habitat fragmenta-

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Brood parasitism is an additional factor known to impact many songbird populations, and a cause of endangerment for several species (Robinson et al., 1995). However, little is known about how brood parasitic Brown-headed Cowbirds (Molothrus ater) respond to the urban environment. Brown-headed Cowbirds are obligate avian brood parasites but they do not build nests of their own, instead they lay their eggs in the nests of other species, collectively called the “hosts.” Many hosts will raise cowbirds often to the detriment of their own reproductive success (Ortega et al., 2000). Cowbird parasitism is thought to be an important factor in the decline of many migratory songbird populations, and the cause of endangerment of a few species with small, localized populations (Robinson et al., 1995). Brown-headed Cowbirds are edge specialists, and the frequency of parasitism on forest dwelling host species is typically negatively correlated with distance from the forest edge (Brittingham and Temple, 1983; but see Robinson and Wilcove, 1994). Because of their parasitic nature, cowbirds are capable of spatially uncoupling breeding and foraging aspects of their home range. Whereas most nesting species need to locate nest sites, foraging substrates, and safe roosting locations all within a territory, typically all in one habitat type, cowbirds are capable of separating these important components by up to 12 km within a large home range (Rothstein et al., 1984; Goguen and Mathews, 1999; Curson et al., 2000). The home range often centers on foraging areas within short commuting distances to host nests. However, few studies of cowbird habitat selection have examined the role of urban areas as a source of foraging opportunities from which cowbirds enter native habitats to parasitize host populations. The urban/wildland boundary created by many open space programs creates a potential avenue for attracting cowbirds and increasing parasitism rates, the exact opposite of the conservation mission of many open space programs (Little, 1990; Smith and Hellmund, 1993). The city of Boulder, CO, USA, population 94,673 (US Census Bureau, 2000), is located at the transition from the forested ponderosa pine (Pinus ponderosa) foothills along the east slope of the Rocky Mountain Front Range and the eastern grassland plains. The urban/wildland boundary is most distinct along the city’s western edge where high-density residential land use (6.45 housing units/ha; US Census Bureau, 2000) is separated from more than 3000 ha of forest (Fig. 1). This striking urban/wildland boundary was established through a series of land acquisition and zoning ordinances beginning in 1898 and the creation of a City Open Space Department in 1973. Today, the Open Space Program of Boulder includes over 3000 ha of montane and lower foothill forests within a regulatory hierarchy that includes the City Charter, Long Range Management Plan, and, specific to our study, the 1999 City of Boulder Forest Ecosystem Management Plan (City of Boulder, 1999). A main goal of the Ecosystem Management Plan is to maintain or enhance native plant and animal species, their communities, and the ecological processes that sustain them (City of Boulder, 1999). We question if the urban area influences cowbird distribution and movement and consequently impacts breeding host populations on Open Space, ultimately compromising the goals to the Ecosystem Management Plan. A number of migratory songbird species that breed within the City of Boulder Open Space are considered sensitive in the southwestern US (Hall et al., 1997). Brown-headed Cowbirds coexist with and parasitize songbirds in the area, having a significant negative impact on the reproductive success of some species (Marvil and Cruz, 1989; Miller et al., 1998; Walsh et al., 1998; Chace et al., 2000). The adjacent urban areas may provide foraging opportunities for cowbirds from which they make daily movements across the urban/wildland boundary to parasitize nests. We examined the movements of cowbirds and the parasitism of Plumbeous Vireos (Vireo plumbeus) near the city of Boulder, CO, USA to determine if the spatial and temporal distribution of Brown-headed Cowbirds was consistent with this hypothesis. Additionally, we tested the prediction that parasitism frequency on a common cowbird host, the Plumbeous Vireo (Marvil and Cruz, 1989; Chace et al., 2000), would decline with distance from the urban center.
2. Methods

The study was conducted in the city of Boulder, CO, USA (40°00′N 105°20′W, 1650 m elevation) and its western foothills. The city of Boulder is surrounded by open space, creating a sharp transition between residential communities and native habitats. Many greenway pedestrian and bicycle trails follow riparian corridors through the city and into the Mountain Parks. We established 165 fixed radius (50 m) point count stations in 1998 to census nesting songbirds and cowbirds across the foothills and valley of Boulder County. Points were censused three times once in each of three distinct time periods (1–15, 16–30 June; 1–15 July) in both 1998 and 1999. Census duration was 10 min, and they were conducted in the morning (sunrise ± 0.5 h until 3 h past sunrise), afternoon (1100–1400 MST), and evening (1500–1900 MST). These times correspond with known cowbird activities: nest searching and egg-laying (morning), feeding (afternoon), and feeding until going to roost at dusk (Rothstein et al., 1984; Goguen and Mathews, 1999).

Morning censuses continued through 2001 as part of a long-term study. Cowbird detections are reported as abundance per census effort (hereafter, “relative abundance”), such that the total number of cowbirds detected within 50 m of each point were divided by the number of times the point was censused. This fraction was then multiplied by 100 and reported as an index of relative abundance to allow for compar-
The 165 point count stations were distributed in ponderosa pine, *Pinus ponderosa*, forests (both far from town, i.e. >2500 m, *n* = 20, and close to town, *n* = 28), foothill riparian forests (*n* = 31), lowland riparian forests (*n* = 25), foothill residential along the edge of open space (*n* = 20), residential at the urban center (*n* = 10), and grassland habitat (*n* = 31). The ponderosa pine forest community was park-like in appearance with a semi-open canopy dominated by its namesake, but interspersed with Douglas’ fir (*Pseudotsuga menziesii*). The understory was dominated by chokecherry (*Prunus virginiana*), wax currant (*Ribes cereum*), skunkbrush (*Rhus aromatica*), small ninebark (*Physocarpus monogynus*), Oregon grape (*Mahonia repens*), kinnikinnick (*Arctostaphylos uva-ursi*), and various grasses (*Bromus, Achillia*, and *Stipa*).

The montane riparian forests were in the foothills and dominated at lower elevations by narrowleaf cottonwood (*Populus angustifolia*), box elder (*Acer negundo*) and Rocky Mountain maple (*Acer glabrum*), while at higher elevations the riparian habitats were dominated by quaking aspen (*Populus tremuloides*) and Douglas’ fir. Understory at all elevations was dominated by chokecherry and wild plum (*Prunus americana*). Lowland riparian sites along the floodplain were more diverse, especially with nonnative species, and dominated by plains cottonwood (*Populus deltoides*), narrowleaf cottonwood, peach-leaf willow (*Salix amygdaloides*), sandbar willow (*S. exigua*), crack willow (*S. fragilis*), snowberry (*Symphoricarpos occidentalis*), chokecherry, boxelder, and a number of introduced species, including Russian olive (*Elaeagnus angustifolia*), silver maple (*Acer saccharinum*), and Chinese elm (*Ulmus parvifolia*). The mid-grass prairie habitat (hereafter, “grassland”), were dominated by grasses (red three awn, *Aristida longiseta*), blue grama, *Bouteloua gracilis*, cheat grass, *Bromus tectorum*, buffalo grass, *Buchloe dactyloides*, needle and thread grass, *Stipa comata*, and, in a few locations, big bluestem, *Andropogon gerardii*, skunkbrush, salt brush (*Atriplex canescens*) and yucca (*Yucca glauca*). Residential areas were dominated by native and nonnative deciduous trees forming an overstory among lawns, parks, and greenways.

Plumbeous Vireos breed in the ponderosa pine forests west of the city and are known to be common hosts of the Brown-headed Cowbird (*Chace and Cruz, 1999*). Vireo nests were found in 1999–2001 during all stages of nesting cycle and subsequently visited once every 3 days. Care was taken to minimize disturbance and the attraction of cowbirds or nest predators to the nest site. Nests with complete host clutches with a cowbird egg were classified as nonparasitized, all other complete clutches that were incubated at least halfway through the 14 day incubation period without a cowbird egg were classified as parasitized. Nest locations were digitized with a global positioning system, Garmin 12XL (±10 m), and entered into a Geographic Information System (GIS) database (Arcview: ESRI, Redlands, CA) with additional layers provided by the City of Boulder Open Space and Mountain Parks.

A predictive model of the probability of detecting a cowbird was created using morning point count data from 1998 through 2001. The probability of detecting a cowbird at a point count location was determined by taking the total number of counts at that location between 1998 and 2001 (normally 6–12 total counts) and dividing by the number of those counts during which cowbirds were detected. Data on physiographic (slope, aspect, elevation, and distance from streams) and human impact (distance to residential areas and distance to roads and trails) variables were then extracted from existing GIS data layers maintained by the City of Boulder Open Space and Mountain Parks Department. Multiple linear regression was then used to determine how the probability of detecting a cowbird at a point was related to physiographic and human impact variables. Regression was deemed appropriate since probability of detecting a cowbird at a point ranged between 0 and 1 and was essentially continuous within that range. Distances to roads and trails, streams, and residential areas were measured in feet, because those were the units of the GIS data layers, and converted to meters. Spatial resolution of all data was 10 m (32.6 ft). Once a regression model had been created, the parameters of the model were used to create a new GIS data layer using the map calculator. This layer created the predictive model of probability of detecting a cowbird across the entire landscape. The probability of detecting a cowbird at Plumbeous Vireo nests could then be determined by...
overlaying the locations of those nests on the predictive model.

3. Results

Brown-headed Cowbirds were most abundant in foothill and lowland riparian habitats and ponderosa pine forests close to the urban edge of Boulder in the morning (Kruskal Wallis $H = 46.1010$, d.f. $= 6$, $P < 0.0001$; Fig. 2). In the afternoon, cowbird abundance was significantly greater in foothill riparian than in all other habitats ($H = 15.8106$, d.f. $= 6$, $P < 0.05$; Fig. 2). In the evening, cowbird abundance was significantly greater in foothill riparian habitats and urban habitats than all other habitats ($H = 30.2348$, d.f. $= 6$, $P < 0.05$; Fig. 2).

Within habitat analysis revealed some significant temporal shifts in cowbird abundance. In the lowland riparian habitat, cowbirds were more abundant in the morning ($36.0 \pm 9.7$) than in the afternoon ($10.9 \pm 5.5$; Wilcoxon $z = 2.5092$, $P < 0.05$) and evening ($12.8 \pm 7.3$, $z = 2.6390$, $P < 0.01$). Likewise, cowbirds were more abundant in the morning in ponderosa pine forests close to Boulder ($29.9 \pm 5.4$) than in the afternoon ($6.25 \pm 3.2$, $z = 4.3751$, $P < 0.0001$) and evening ($4.8 \pm 3.7$, $z = 5.0252$, $P < 0.0001$). Cowbirds were more abundant in the evening in urban residential habitats ($50.0 \pm 23.5$) than the morning when they were absent; however there was no significant shift in abundance during the evening and afternoon ($10.0 \pm 6.7$, $z = 1.2596$, $P > 0.2$). There were no other significant temporal shifts in cowbird abundance within habitat types.

Linear regression indicated that cowbirds did not show any significant responses to slope ($P = 0.881$), aspect ($P = 0.557$), or elevation ($P = 0.761$). However cowbirds became less common with in-
creasing distance from residential areas (estimate
\(= -0.000093, P = 0.006\)), and increasing distance to
roads and trails within the wildland preserve (estimate
\(= -0.000015, P = 0.009\)). Probability of detecting
a cowbird was not affected by distance to streams
\((P = 0.766)\), but when cowbirds were detected in
riparian areas they were generally in larger groups.

In the morning when cowbirds typically lay eggs,
not only was cowbird abundance significantly greater
in the ponderosa pine forests close to the city of Boul-
der than those farther away, but the frequency of cow-
bird parasitism was significantly higher on Plumbeous
Vireos nesting closer to the urban boundary (68%,
\(n = 19\)) than farther (>3400 m, i.e. the median dis-
tance of vireo nests from the urban boundary, range
1170–8800 m) away (16%, \(n = 19\); Fisher’s exact,
one-tailed, \(P = 0.0025\)). Overall, parasitized nests
were closer to the urban boundary (3040 ± 380 m,
\(n = 16\)) than nonparasitized nests (4852 ± 449 m,
\(n = 22\); Wilcoxon two-sample test \(z = 2.7940, P =
0.005\). The predicted probability of detecting a cow-
bird was lower at nonparasitized nests (0.19 ± 0.01,
\(n = 22\)) than parasitized nests (0.23 ± 0.00, \(n = 16\);
\(z = 2.4717, P < 0.05\)).

4. Discussion

Diurnal movements of cowbirds are landscape
dependent, where feeding and breeding sites are in
close proximity the daily distances moved by breed-
ing females is shorter than observed in landscapes
where those elements are separated. In Colorado,
we used changes in relative abundance as an index
of diurnal movement. This assumption is based on
radio-telemetry studies that have clearly demonstrated
that the pattern of temporal and spatial separation of
cowbird breeding and feeding activities occurs across
different landscapes. In agriculture-dominated mid-
wester landscapes, females feed near breeding sites
when short grass habitat is available, and in distant
(1–3 km) pastures and row crops (Raim, 2000). Cow-
birds breed, feed, and roost in spatially distinct areas,
moving on average 3.6 km between evening roosts
and morning breeding areas, 1.2 km between morn-
ing breeding areas and afternoon feeding areas, and
2.6 km between afternoon feeding areas and roosting
areas (Thompson, 1994). In the low-density resi-
dential areas of the central Appalachians, Gates and
Evans (1998) found that females commuted 3.1 km
from roosting to breeding sites, 4.1 km from breeding
to feeding, and 3.0 km from feeding to roosting sites.
Cowbirds move up to 7 km between breeding and
feeding areas in the midwest and far west (Rothstein
et al., 1984; Thompson, 1994), and over 10 km in the
Intermountain West (Curson et al., 2000).

Habitat selection by cowbirds varies temporally. We
found that cowbirds were more abundant in ponderosa
pine and riparian habitats in the morning, and urban
habitats in the afternoon and evening. In the mid-
west, cowbirds prefer forest and shrubland habitats,
where host density is highest, in the morning, and
grass, feedlot, and developed habitats in the afternoon
(Robinson, 1999; Thompson and Dijk, 2000). In the
Sierra Nevada of California, cowbirds are found in
the forested habitats in the morning, and around liv-
ery stables in the afternoon (Rothstein et al., 1984). In
northeastern New Mexico, cowbirds forage with cattle
in the grasslands and savannah during the after-
noon following a morning period of egg-laying in the
pine-juniper uplands (Goguen and Mathews, 1999).

Behavior and parasitic interactions of cowbirds in
an urban context has been largely unstudied. Most
earlier work has examined cowbirds at the interface
of forest patches in a grassland matrix (primarily
midwestern row-crops; Robinson, 1999; Robinson
and Smith, 2000). Hersek et al. (2002) examined
cowbird parasitism on an area-sensitive neotropical
migrant population in an eastern US hardwood forest
fragmented by suburban development. They found
that parasitism frequency was less extensive than that
found in small forest patches embedded in the agri-
cultural matrix of the midwestern US (Donovan et al.,
1995). Among developed lakes on the mixed Northern
Forest (USA), cowbirds were significantly associated
with forest/development edges (Lindsay et al., 2002).

The type of matrix plays an important role in
avian reproductive success in forest patches (Hersek
et al., 2002), however, fragmentation of many western
forests occurs through natural processes and patches
are less well defined (Buskirk et al., 2000). The foothill
ponderosa pine forests of Boulder County are natu-
really fragmented through factors of differential slope
aspect, elevation, insect outbreak frequency and fire
history (Knight and Reiners, 2000; Veblen, 2000). The
ponderosa pine forest savannah creates small forest
canopy openings where cowbird parasitism is higher (Chace and Cruz, 1999). In addition, an abrupt vegetative change occurs at the pine forest/montane riparian ecotone. This natural fragmentation creates a corridor of cowbird movement along streams that stretch from downtown Boulder up into the Open Space forests.

The region studied here is largely absent of grazing cattle where cowbirds are known to congregate (Goguen and Mathews, 1999), however, the urban landscape creates a similar, albeit more stationary, food source where cowbirds congregate in the afternoons and evenings. While cattle do graze in the Open Space grasslands on the eastern half of Boulder, this study focused on the interactions on the western half along the urban/forest boundary. Cowbirds do associate with cattle in Boulder County, however our censuses suggest that cowbirds exhibit a stronger temporal and numerical response to the urban environment than to the grasslands (Figs. 2–5). It appears that bird feeders, and short, moist grass lawns provide the food resources for cowbirds (see also Mayfield, 1965; Goguen and Mathews, 1999). Therefore, the impacts of cattle grazing on cowbird parasitism notwithstanding, the urban context also plays a significant role in cowbird distribution, abundance and parasitism.

Landscape designers and environmental managers in the western US need to take the extent of residential encroachment on wildlands into consideration. The distance to the surrounding residential zones plays an important role in the frequency by which some host species are parasitized by cowbirds. In addition, it is also known that the urban area can have a similar influence on avian nest predators (Miller and Hobbs, 2000). If there are songbird species of particular concern that are known cowbird hosts then the distribution of residential areas surrounding protected open space becomes an important factor to consider. Providing larger patches of contiguous habitat could re-
reduce the parasitism on birds nesting far from the urban boundary, but not for those nesting near the urban/wildland edge. A more difficult goal is to reduce potential cowbird impacts on the reproductive success of species of concern nesting along the boundary. If it is possible to reduce cowbird foraging opportunities in urban areas through increasing residential lawn grass length, restricted watering, and curtailing bird feeding during the breeding season, cowbird abundance and parasitism intensity might be reduced (see also Mayfield, 1965; Goguen and Mathews, 1999), at least in the arid intermountain west. However, the effects of these landscape alterations on cowbird distribution and behavior need to be experimentally tested.

The Citizens of Boulder, Colorado have placed great value and have allocated significant resources towards the acquisition and management of Open Space. The web of regulation directing the planning, design and management of these lands clearly illustrates that the public values these lands for reasons such as aesthetics, recreational potential, and intrinsic ecological worth. For instance, the City Charter does not prioritize disparate Open Space purposes such as preservation of flora and fauna and passive recreation, but weighs potential benefits and impacts of proposed management actions under the consideration of the long-term viability and health of natural ecosystems. Long range management policies expand on the City Charter with an ecosystem approach. A resource management plan specific to our study site, the Forest Ecosystem Management Plan (City of Boulder, 1999), contains the goal to enhance native plant and animal species, their communities, and the ecological processes that sustain them. Although Boulder has taken great strides to preserve the ecological integrity of their open space, our findings suggest that significant ecological impacts may occur upon forested foothill habitats because of their adjacency to the urban boundary.

Ecological design and management solutions addressing cowbird parasitism impacts on host populations are not difficult to conceive, but implementation of solutions is a more significant hurdle. Our work and other studies (e.g. Curson et al., 2000) have clearly shown that cowbirds are capable of traveling long distances to parasitize nests from established feeding locations. Establishment of large buffers and designated core areas far from the urban boundary would reduce parasitism pressure on host species. Zoning a management buffer with restricted activities specific for cowbirds (e.g. a no wildlife feeding ordinance) would also help. Buffers must be several kilometers wide to reduce cowbird parasitism rates in core areas far from the urban boundary for the most sensitive songbird populations. Where songbird populations are small, geographically localized, and highly impacted by cowbird parasitism, cowbird trapping and egg removal has occasionally proven to be an effective active management strategy (e.g. the Yellow-shouldered Blackbird, *Agelaius xanthomus*, Wiley et al., 1991; Lopez-Ortiz et al., 2002; the Black-whiskered Vireo, *Vireo atricapillus*, Eckrich et al., 1999; and the Least Bell’s Vireo, *Vireo bellii pusillus*, Griffith and Griffith, 2000). However, cowbird trapping and egg removal programs are expensive, require a long-term commitment due to the high dispersal ability of cowbirds, and address proximate rather ultimate causes of songbird decline, render many of these invasive strategies ineffective (Hall and Rothstein, 1999). For most sensitive songbird species that are common cowbird hosts, such as the Plumebeous Vireo, alternative landscape strategies are more likely to be successful.

One of the basic tenets of ecological planning and design is the built environment be in an "intrinsi-
Fig. 5. Spatial distribution of brown-headed cowbird detection probability during morning surveys (smoothed from data based on 38 census points) overlaid with distribution of parasitized and unparasitized Plumbeous Vireo nests in the ponderosa pine foothills west of the urban/wildland boundary in Boulder, CO, USA.
cally suitable location” based on environmental, social and political components of the landscape (McHarg, 1967). When these components are superimposed as layers they reveal a gradient of spatial suitability for the proposal (McHarg, 1967; McHarg and Steiner, 1998). While we recognize that landscapes vary in pattern and process, we can recommend a general environmental design component to insulate songbird hosts from cowbird parasitism near the urban/wildland interface. For proposed projects, buffers must be imposed at the scale to which cowbirds function, creating a core region (e.g. Noss and Cooperrider, 1994) where the likelihood of parasitism is low for a portion of the population. For existing urban/wildland environments where the option to create or add new open space does not exist, the creation of a spatially explicit management zone, operating as new proposal constraints or as zoning overlays with existing development, should be incorporated into the environmental design. For example, in Boulder, CO, USA a viable management strategy for a widespread, sensitive, host species such as the Plumbeous Vireo might include an Open Space buffer of 10 km to insulate a portion of the population from high parasitism levels in the ponderosa pine foothills, an area that might concomitantly have lower predation levels as well. The inability to create additional Open Space forces an examination of alternative management strategies (e.g. reduced cowbird feeding opportunities) within the urban context of the boundary region that would reduce cowbird abundance during the breeding season.

Acknowledgements

We thank the City of Boulder Open Space, Boulder Mountain Parks and Boulder County Parks and Open Space for providing us with access to properties under their respective jurisdictions; in particular we appreciate the assistance of Steve Armstead, Mark Brennan, and Cary Richardson. Joel Adamson, Mary Cloud Ammon, Cathy Bechtoldt, Lisa Cooper, Diane Cruz, Dan Evans, Andrea Kessler, Brie Larson, Patrick Lehman, Tug Levy, Shawn McKinney, Lisa Munger, Jonathan Parrot, Awilda Rodriguez, Meggan Stone, and Pablo Weaver provided field assistance. This project has been supported by the US Fish and Wildlife Service, City of Boulder Open Space, Boulder Mountain Parks, Boulder County Nature Association, Edna B. Sussman Environmental Internship, Undergraduate Research Opportunities Program at the University of Colorado, and the University of Colorado Graduate School. We thank Marina Alberti, Kern Ewing and two anonymous reviewers for helpful comments on an earlier draft of this manuscript.

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