CHAPTER 5

COWBIRD (MOLOTHRUS SPP.) ECOLOGY: A REVIEW OF FACTORS INFLUENCING DISTRIBUTION AND ABUNDANCE OF COWBIRDS ACROSS SPATIAL SCALES

Jameson F. Chace,1,8 Chris Farmer,2 Rachael Winfree,3 David R. Curson,4 William E. Jensen,5 Christopher B. Goguen,6 and Scott K. Robinson7

1Department of Biology, Villanova University, Villanova, Pennsylvania 19085, USA; 2Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, California 93106, USA; 3Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544, USA; 4Department of Wildlife Ecology, University of Wisconsin, 1630 Linden Drive, Madison, Wisconsin 53706, USA; 5Division of Biology, Kansas State University, 232 Ackert Hall, Manhattan, Kansas 66506, USA; 6School of Forest Resources, Penn State University, 2C Ferguson Building, University Park, Pennsylvania 16802, USA; and 7Florida Museum of Natural History, University of Florida, P.O. Box 117800, Gainesville, Florida 32611, USA

ABSTRACT.—Brown-headed Cowbirds (Molothrus ater; hereafter “cowbirds”) provide one of the best case studies for demonstrating the need to consider multiple spatial scales in managing a species and designing conservation strategies. An adaptive management program to reduce cowbird parasitism levels through reduction of cowbird abundance should mirror the multiple spatial scales to which cowbirds respond. At the continental scale (>50 km), cowbirds are widespread across most of North America, and their abundance declines with distance from the center of their distribution in the Great Plains and Midwest. Generally, cowbird parasitism frequency is highest in, and declines with distance from, the Midwest; however, abundance at that broad scale is by no means indicative of parasitism frequency at the local level, because regional, landscape, and local factors play a significant role in cowbird abundance, distribution, and parasitism levels. At the regional scale (10–50 km), cowbird abundance and cowbird:host ratio decline with increasing forest cover, resulting in lower parasitism levels in the Midwest, where most of the relevant research has been conducted. Studies from forested regions of the East and Far West and from nonforested systems are under-represented; nevertheless, it is clear that increasing the spatial extent of contiguous habitat for host species is a key priority in cowbird management. Within the landscape scale (<10 km), density and dispersion of feeding sites strongly influence cowbird distribution and abundance. Cowbirds are known to commute >10 km between feeding and breeding habitats; removal of feeding opportunities for cowbirds near targeted management areas is a key control measure. Removal of livestock-centered feeding sites has traditionally been a management focus. However, cowbirds use agricultural fields, residential backyards, and recreational areas, too, and those feeding opportunities need to be considered in land-use planning and zoning. Locally, cowbird breeding abundance and distribution are strongly influenced by habitat type, vegetation structure, and passerine species richness; however, variation in regional or local cowbird abundance may affect local cowbird distribution. Local management should strive to protect habitat for large host populations while reducing habitat edges and, in grasslands, known cowbird perching sites. Comparative studies of cowbird breeding-site use are needed in most regions, and future comparisons would benefit if field researchers used a consistent, standardized protocol for vegetation measurement.

RESUMEN.—Molothrus ater provee de uno de los mejores estudios de caso que demuestran la necesidad de tener en cuenta distintas escalas para el manejo de la especie y el diseño de estrategias de conservación. Un programa de manejo adaptativo que busque reducir los niveles de parasitismo del M. ater por medio de la reducción de su abundancia debería reflejar las

8E-mail: jameson.chace@villanova.edu
Understanding distribution and abundance of Brown-headed Cowbirds (*Molothrus ater*; hereafter “cowbirds”) is an important first step in developing management plans to reduce the effects of brood parasitism on host populations. The topic has generated considerable interest, because cowbirds present a conservation problem in many regions (e.g., Lowther 1993; Rothstein and Robinson 1994, 1998; Thompson 1994; Robinson et al. 1995a; Donovan et al. 2000; Smith et al. 2000). Cowbirds also demonstrate the need to consider multiple spatial scales in species management and design of conservation strategies (Robinson 1999). Cowbirds routinely commute ≤15 km between breeding, feeding, and roosting sites, which are often in very different habitats. Generally, cowbirds lay eggs in host nests in forests, forage in open areas among livestock, and roost communally in large trees.

Here, we summarize the most recent information on factors influencing cowbird distribution and abundance across continental (>50 km), regional (10–50 km), landscape (1–10 km), and local (within-site) scales. We finish our review specifically with the resource manager and land-use planner in mind, addressing practical aspects of cowbird management in the context of spatial ecology.

Factors Affecting Cowbird Distribution and Abundance at the Continental Scale

Cowbirds are widespread across North America and most abundant in the Great Plains (Fig. 1). Although it is generally presumed that the Great Plains was the historical center of cowbird distribution and that cowbirds were historically absent west of the Rocky Mountains (Friedmann 1929, Mayfield 1965), bison, and presumably cowbirds, were more widespread west of the Great Plains than previously believed (Chace and Cruz 1999), albeit at much lower densities than on the Great Plains. Cowbirds became widespread in the eastern United States by 1800 (Bendire 1895) and in the far West by the 1920s (Rothstein 1994, Ward and Smith 2000). During the 1900s, cowbirds invaded the Maritime Provinces of Canada and the southeastern United States (Cruz et al. 2000).
Since the beginning of the Breeding Bird Survey (BBS) in 1966, cowbirds have been declining across the BBS region (Sauer et al. 2003), primarily at the fringes of the distribution (Peterjohn et al. 2000, Wiedenfeld 2000, Sauer et al. 2003), including areas of southeastern Canada and the northeastern United States that have had significant levels of reforestation over the past 100 years (Askins 1993). However, cowbirds are increasing in several areas of the far West—for example, in the Central Valley of California (Wiedenfeld 2000), a recently invaded region (Rothstein 1994). Cowbirds are also increasing in Florida, an area where they were declining until the past decade and where cowbird populations are still very low. The BBS is designed to detect population change at large spatial scales and temporal patterns; it is not designed to measure change at the smaller spatial scales at which productivity and survivorship are most strongly influenced.

In general, parasitism frequency on most host species reflects the current continental pattern of cowbird abundance, declining with distance from the center of cowbird abundance in the northern Great Plains (Hoover and Brittingham 1993, Smith and Myers-Smith 1998). Among grassland birds, for example, parasitism (which is often rare; Peer et al. 2000), is higher in the northern Great Plains than in the Midwest (i.e. Minnesota south to Missouri and east to Ohio; Davis and Sealy 2000, Koford et al. 2000). Likewise, Wood Thrush (Hylocichla mustelina) parasitism levels are higher in Illinois (80–100%; Robinson 1992, Hoover and Brittingham 1993, Robinson et al. 2000) than in Maryland (<25%; Dowell et al. 2000, Petit and Petit 2000). At the continental scale, cowbird abundance is a good predictor of parasitism levels; however, regional, landscape, and local factors can very strongly influence cowbird abundance and parasitism pressure on host species.

**Factors Affecting Cowbird Distribution and Abundance at the Regional Scale**

The regional (10–50 km radius) scale is relevant for studies of cowbird distribution, because it encompasses the species’ large home range. The cowbird’s maximum recorded daily travel distance is 15 km (Curson et al. 2000). That maximum distance presumably explains why cowbirds are absent in extensively forested habitats that lack feeding areas (e.g. Holmes et al. 1992, Coker and Capen 2000). To exclude cowbirds from forest habitat, forest tracts must

![Breeding distribution and mean abundance of Brown-headed Cowbirds per Breeding Bird Survey (24.5 mile) roadside route, 1966–1996.](image)
be >700 km², which is generally not feasible in terms of land management. However, cowbirds’ responses to landcover at the regional scale can be used to guide management aimed at reducing, though not eliminating, cowbird parasitism.

At the 10-km-radius scale, cowbird abundance and parasitism show a consistent negative relationship to the proportion of forest cover surrounding the study site (Robinson et al. 1995b, Donovan et al. 2000, Thompson et al. 2000). Cowbird abundance can be positively correlated with host density (Gates and Gysel 1978, Rothstein et al. 1986), forest perimeter:area ratio, and forest–nonforest edge density; and negatively correlated with forest-tract size and forest core area. However, those variables are often intercorrelated, making them hard to separate from the proportion of forest cover. Results of relevant studies are as follows. Parasitism-induced nest failure for three forest-breeding host species was higher in a fragmented landscape (mean 31% forest cover) than in a nonfragmented landscape (mean 93% forest cover), decreased with increased forest-patch size and forest core area, and increased with edge density (see tables 1 and 4 in Donovan et al. 1995). Parasitism decreased monotonically as forest cover at a 10-km radius increased from a low of 6% to a high of 95% (Robinson et al. 1995b). The trend was significant for five of nine host species and overall. Cowbird abundance and nest parasitism levels decreased with increased forest-patch size and forest core area, and increased with edge density (see tables 1 and 4 in Donovan et al. 1995). Parasitism decreased monotonically as forest cover at a 10-km radius increased from a low of 6% to a high of 95% (Robinson et al. 1995b). The trend was significant for five of nine host species and overall. Cowbird abundance and nest parasitism levels decreased with increased mean forest-patch size and with increasing proportion of forest cover and core area (Thompson et al. 2000). Cowbird abundance generally increased with edge density (meters per hectare). Cowbird abundance decreased significantly with increasing forest cover (20–92%), and increased significantly with increasing forest perimeter:area ratio (Donovan et al. 2000). When the relationship between scale of forest cover and cowbird abundance was explicitly examined across 1- to 10-km radii, the most significant relationships occurred for male and female cowbirds combined at the 10-km radius, and for female cowbirds only at 3- to 5-km radii (Donovan et al. 2000).

A limitation of the studies discussed above is that they were all conducted in the Midwest and shared some of the same data. To address the relationship between forest cover and cowbird parasitism in other geographic areas, Hochachka et al. (1999) used nest records from the BBIRD database (see Acknowledgments) for 26 sites across the United States to investigate the relationship between percentage of forest cover at a 10-km radius and the proportion of host nests parasitized. Across a range of forest cover (5–99%), they found a small but significant decrease in parasitism with increasing forest cover: a 10% increase in forest cover reduced parasitism by ~1%. It is not clear whether the weaker effect found by Hochachka et al. (1999) reflects regional differences in patterns of cowbird abundance or differences in methodology.

Only two studies have considered the relationship between cowbird abundance and forest cover at spatial scales larger than a 10-km radius. As suggested by Hochachka et al. (1999), scales exceeding the cowbirds’ daily travel distance could be relevant to explaining cowbird abundance if cowbirds show a numerical as well as a functional response to landcover. Results at the 50-km radius are ambiguous; however, cowbird parasitism was positively but nonsignificantly related to percentage of forest cover (Hochachka et al. 1999). At an intermediate scale (864-km² hexagons, or ~2.7× the 10-km radius), cowbird abundance decreased significantly as forest cover increased (Donovan et al. 1997). Given the limited number of studies, it is not possible to identify the scale most strongly related to cowbird abundance, but it is probably greater than the 3-km radius and less than the 50-km radius.

Two studies, both done at the 10-km radius, have examined how the ratio of cowbirds to hosts changes with increasing forest cover. The cowbird:host ratio is difficult to interpret, because species vary widely in their quality as cowbird hosts (Winfree 2004), making the binary classification of “host” and “nonhost” problematic. Nonetheless, the ratio is of interest, because it roughly assesses the degree of parasitism pressure per host individual. The cowbird:host ratio decreased with increased mean forest-patch size (Thompson et al. 2000) and with increasing proportion of forest cover (see fig. 5 in Donovan et al. 1997). Those results suggest that breeding cowbirds do not track their hosts perfectly in more-forested landscapes, presumably owing to the energetics of commuting long distances from feeding sites.

The single study examining survival of cowbird offspring as a function of forest cover found
a significant positive relationship, attributable to lower nest-predation in more-forested landscapes (Donovan et al. 2000). That result suggests that, although the total number of breeding cowbirds decreases with increasing forest cover, per-capita reproductive success may increase.

In conclusion, all studies done at the 10-km-radius scale have found that cowbird abundance, parasitism of forest-breeding hosts, and cowbird:host ratio all decrease with increasing forest cover. Those results should be robust, because they reflect virtually the entire forest-cover gradient, from <5% to >95%. There is no evidence at the 10-km scale for a nonlinear response to forest cover by cowbirds, as would be expected if cowbirds were limited by feeding-site availability at the high end of the forest-cover gradient and by host availability at the low end. Responses may be nonlinear, however, at smaller spatial scales (e.g. Gustafson et al. 2002). An important role of landscape at the 10-km scale is that it may determine the strength of edge effects at smaller scales. For example, in highly fragmented landscapes saturated with cowbirds, edge effects may not occur, but as forest cover at the landscape scale increases, cowbirds may be limited to forest edges.

Our understanding of cowbird responses to landcover at the regional scale would benefit from several lines of future research. First, some of the scatter in existing relationships may be attributable to use of low-resolution landcover data. Many studies used 1-km\(^2\) grid cells, which would miss many openings that could provide feeding or parasitism opportunities for cowbirds (e.g. Chace and Cruz 1999). Second, studies are needed in the eastern and western parts of the continent to find out whether patterns observed in the Midwest are found in other regions. Finally, all studies to date have focused on forest-breeding host communities. The effect of surrounding land use on parasitism of hosts in other habitats is an interesting and under-studied question.

Factors Affecting Cowbird Distribution and Abundance at the Landscape Scale

At the landscape scale, cowbird distribution and abundance are determined primarily by relative spatial distribution of preferred foraging habitat and breeding habitat. Cowbirds are unusual among passerines in using distinct habitat types for foraging and breeding and establishing spatially separate home ranges for those two activities. Cowbirds are ground-foragers and require open habitats for feeding, often exploiting a wide variety of feeding sites across anthropogenic landscapes: grazed grassland, agricultural fields, row crops, livestock corrals, lawns, and campgrounds (Friedmann 1929, Mayfield 1965, Otega 1998). Cowbirds are well known for their commensal relationship with livestock. Large ungulates provide foraging opportunities for cowbirds via mechanisms including creation of feeding microhabitats, increased insect abundance, and flushing of insects while grazing (Goguen and Mathews 1999).

For breeding, however, cowbirds prefer to use habitats with more complex structure, such as forest, savannah, shrublands, and old fields. Where direct comparisons have been made, parasitism frequencies are higher in such habitats than in adjacent grasslands (Hahn and Hatfield 1995, Strausberger and Ashley 1997, Robinson et al. 1999). That habitat preference is most likely attributable to higher densities of hosts in more-structured habitats and the presence of elevated perches from which cowbirds can search for host nests.

Commuting Behavior: The Link between Breeding and Feeding Sites

An important consequence of the spatial separation of cowbird breeding and feeding locations is that abundance of cowbirds at any location depends not only on quality of the habitat at that location but also on characteristics of the surrounding landscape. To predict cowbird abundance in breeding areas where hosts are most exposed to the effects of parasitism, we must consider the surrounding distribution of cowbird feeding sites. The most important factors for cowbird breeding distribution at the landscape scale are likely to be (1) distance to nearest feeding site, (2) density of feeding sites, and (3) cowbird feeding-site preference.

In landscapes where feeding and breeding habitats are spatially separated, cowbirds commute daily between the two, maintaining regular home ranges in each throughout the breeding season (Rothstein et al. 1984, Thompson 1994, Gates and Evans 1998, Goguen and Mathews 2001). Radiotelemetry studies of
Cowbirds at widely separated sites across North America have revealed a typical daily behavior pattern, consisting of morning breeding activity in forested habitats and afternoons spent foraging at livestock corrals and feeders (Rothstein et al. 1984), agricultural land and feedlots (Thompson 1994, Gates and Evans 1998), or grazed prairie (Goguen and Mathews 2001).

Distance to nearest feeding site.—Distance commuted between morning breeding sites and afternoon foraging sites appears to depend on the landscape context. Where breeding and feeding opportunities are tightly interspersed, many cowbirds have overlapping home ranges for those activities (Dufty 1982, Raim 2000) and thus do not commute daily. Where cowbirds commute, mean breeding-to-feeding distances tend to be 1–3 km: 1.2 km in Missouri and Illinois (Thompson 1994), 2.27 km in the Appalachians of western Maryland (Gates and Evans 1998), 4.1 km in the Sierra Nevada of California (Rothstein et al. 1984), and 1.47 km at a sharp forest–prairie interface in New Mexico (Goguen and Mathews 2001). In unfragmented forest in New Mexico, female cowbirds trapped at breeding areas in the forest interior commuted 9.3–13.2 km to foraging sites in the nearest available grazed prairie (Curson et al. 2000).

Two factors account for the long commutes observed in New Mexico: the unfragmented forest contained large areas of suitable breeding habitat distant from the nearest available feeding habitat, and the cowbirds studied were trapped in that breeding habitat and did not represent a random sample of the local population (Curson et al. 2000). Cowbirds are restricted in their choice of breeding areas to those within commuting distance of suitable foraging habitats. In severely fragmented landscapes, such as the Midwest, where cowbirds are abundant and forest exists only as small remnants, cowbirds parasitize host nests throughout the patch (Robinson et al. 1995b). However, in landscapes containing larger forest blocks, the result of cowbird commuting behavior is an edge effect at the landscape scale, with greater cowbird abundance and parasitism frequency observed near agricultural edges where cowbirds forage (Thompson et al. 2000).

That large-scale edge effect has been demonstrated by studies that measured a decline in cowbird abundance with increasing distance from cowbird feeding habitat. Studies from the Intermountain West have measured such declines across distances of 4 km (Tewksbury et al. 1999), 5 km (Chace et al. 2003), 8–12 km (Goguen and Mathews 2000), and >20 km (Young and Hutto 1999). Chace et al. (2003) and Goguen and Mathews (2000) found corresponding gradients in parasitism of a major cowbird host, Plumbeous Vireo (Vireo plumbeus), and one study east of the Great Plains described a declining gradient in parasitism of a forest-dwelling host, Kentucky Warbler (Oporornis formosus), across a distance of 2 km from an agricultural edge (Morse and Robinson 1999).

Distance from feeding sites appears to be one of the most important determinants of cowbird breeding abundance, having greater influence than forest type or host density in multivariate models (Tewksbury et al. 1999, Young and Hutto 1999, Goguen and Mathews 2000). It is important to recognize that the landscape-scale edge effect discussed here is distinct from the more widely reported edge effects resulting from cowbirds’ preference for nest-searching near structural edges (e.g. Brittingham and Temple 1983, Hahn and Hatfield 1995, Donovan et al. 1997); this effect differs in both scale and cause.

Density of feeding sites.—Cowbird abundance depends not only on distance to the nearest feeding site, but also on number of feeding sites within a given radius corresponding to the local commuting distance. In the Green Mountains of Vermont, where cowbird densities are low, cowbird occurrence in forest openings was positively related to number of livestock areas within 7 km but not influenced by distance to the nearest livestock area (Coker and Capen 1995). That may be attributable to low cowbird densities in the area. Where individual sites support low numbers of foraging cowbirds, number of feeding sites may be more important than distance to the nearest feeding site. A number of studies have related cowbird abundance or parasitism to the proportion of potential cowbird feeding habitat in the landscape at scales of 1.3 km (Hejl and Young 1999), 3 km (Stibley and Haufler 1999), and 7 km (Coker and Capen 1995). Cowbird abundance or parasitism increased with the proportion of open land (grassland and agriculture; Hejl and Young 1999) and agriculture (Stibley and Haufler 1999) in the landscape, and was negatively correlated with forest area at spatial scales >3 km (Donovan et al. 2000).
**Feeding-site preference.** — Distribution of feeding cowbirds at the landscape scale is determined not only by the presence of potential feeding sites but by the quality of those sites. Knowledge of cowbirds’ feeding-site preferences is thus essential for understanding patterns of cowbird abundance. Cowbirds forage primarily with livestock, in agricultural fields, or in urban areas.

**Livestock.** — There is no doubt that cowbirds show a strong preference for foraging with livestock. The best quantitative data on foraging location are provided by the relatively unbiased sampling method of radiotelemetry. In a Midwestern landscape offering alternative feeding sites, such as row crops and ungrazed grassland, 57% of foraging observations were with cattle (Thompson 1994). In short-grass prairie in New Mexico, 98% of foraging observations of radiotagged cowbirds occurred with either pastured or corralled livestock (Goguen and Mathews 2001).

An understanding of the role of livestock in determining cowbird distribution and abundance is crucial to the success of management efforts to reduce parasitism in landscapes where cattle-grazing is a predominant land use, such as the western United States. For example, we do not know if presence of livestock increases cowbird populations at a landscape scale or merely redistributes cowbirds to the vicinity of grazing herds that act as foci for cowbird feeding activity. A more specific question is this: how do cowbirds respond to altered distribution of livestock?

Because cowbirds may not commute when food and breeding habitat are near each other (C. P. Ortega pers. comm.), removing the food source is the most prudent first management step. That strategy is used by federal agencies to protect the endangered southwestern Willow Flycatcher (*Empidonax traillii*) during the breeding season (Goguen and Mathews 1999). The idea behind the strategy is that removal of cowbirds’ preferred foraging opportunities will force them to abandon their breeding areas. Unfortunately, it is difficult to evaluate the success of such measures, because they are generally carried out in conjunction with cowbird trapping programs (Finch and Stoleson 2000). Exclusion of cowbirds from host breeding areas requires removing their food sources so they are outside the maximum cowbird commuting distance of 15 km (Curson et al. 2000).

Two lines of evidence suggest that once the breeding season has begun, cowbirds’ attachment to their breeding areas may be difficult to break by removing livestock. First, in New Mexico, cowbirds responded to livestock movements by adjusting the length of their commuting flights to reach livestock at locations farther from breeding areas, increasing mean commutes from 1.47 km to 3.14 km when cattle were moved in early July (Goguen and Mathews 2001); at another site, they responded by repeatedly altering commuting length through the breeding season, according to the location of free-ranging bison (Goguen et al. 2005). Second, when few bison were within 10 km of cowbird breeding areas, cowbirds responded by commuting similar distances but feeding without ungulates (Goguen et al. 2005).

Management strategies that force cowbirds to extend commuting flights may reduce parasitism levels by lowering the fecundity of individual cowbirds. Curson and Mathews (2003) found that female cowbirds commuting ~12 km between breeding and feeding areas laid 50% fewer eggs in a five-day period than females with breeding–feeding commutes of ~2 km. Cowbirds meet the energetic need for egg production with their daily dietary intake (Ankney and Scott 1980), so egg production and commuting compete for physiological energy resources.

Removing livestock to outside the radius within which cowbirds are likely to commute might sever the commuting link between breeding areas and feeding sites. Recent research suggests that the distance can be ≥10 km and perhaps >15 km (Curson et al. 2000), requiring removal of all livestock within 300–700 km². That may be unrealistic in many cases, but it might be possible to deter cowbirds from establishing breeding territories at target locations if livestock are moved 10–15 km during the start of the breeding season. However, we know nothing about the extent to which cowbirds use distributions of livestock as cues to assess feeding-site quality when they are establishing breeding territories. There is a need for studies that evaluate the influence of such factors on efficacy of livestock removal programs within a sound scientific framework, using control sites and monitoring before and after removals occur. Ideally, the behavioral response of female cowbirds should be measured using
radiotelemetry in addition to parasitism levels on target hosts.

**Agriculture.**—Cowbirds do not feed exclusively with livestock. They regularly feed in agricultural habitats, including row crops, plowed fields, ungrazed grassy fields, and livestock corrals, as well as in lawns, at bird feeders, and on campgrounds (Mayfield 1965, Rothstein et al. 1980, Verner and Ritter 1983, Thompson 1994). Few studies have compared cowbird feeding preferences among open habitat types (Gates and Evans 1998, Morris and Thompson 1998, Thompson and Dijak 2000). In Missouri, Morris and Thompson (1998) found grazing, invertebrate density, and grass height to be important predictors of cowbird foraging abundance. Cowbirds preferred grazed over ungrazed grassland, and short grass over long grass. Cowbird numbers were positively related to invertebrate density (Morris and Thompson 1998), probably because female cowbirds require a high-protein diet to support their high levels of egg production (Ankney and Scott 1980). Short grass may be preferred because it may enhance cowbirds’ detection of food or detection of predators (Morris and Thompson 1998). Row crops appear to be of relatively low importance, yielding 2.4% of foraging observations in Maryland (Gates and Evans 1998) and 0–23% of observations in Missouri and Illinois (Thompson and Dijak 2000). Yet, in areas with little cattle, row crops may be relatively important feeding areas. Robinson (unpubl. data) has found that cowbirds make extensive use of late-planted, recently tilled soybean fields in Illinois, where beans are planted up to a month later than corn. Thus, long after the cornfields have grown to the point where they are rarely used by cowbirds, bean fields may continue to provide the bare-ground conditions favored by cowbirds. Therefore, subtle details of agricultural practices may strongly affect the distribution of cowbirds.

**Urbanization.**—Urban and suburban habitats and small areas of human development constitute important feeding habitat for cowbirds in many regions. Cowbird abundance is positively associated with new suburban development in rural regions of Vermont (Coker and Capen 2000), Wisconsin (Lindsay et al. 2002), and Maryland (Aldrich and Coffin 1979). Cowbirds are “suburban adaptable” (Blair 1996) and are known to exploit the resources of urban environments—in Arizona (Germaine et al. 1998), Ohio (Blair 2001), and California (Blair 1996)—from which, presumably, they commute to parasitize host nests.

It is fairly well established that urban and suburban areas provide foraging opportunities for cowbirds, yet few studies have examined the effects of brood parasitism within that context. In Boulder, Colorado, cowbirds use the urban environment for feeding and roosting, and move to undeveloped forests to parasitize hosts (Chace 2001, Chace et al. 2003). Abundance of cowbirds and parasitism frequency on Plumbeous Vireos drop off dramatically with increasing distance from the urban–wildland boundary (Chace et al. 2003). Likewise, parasitism of Warbling Vireos (*V. gilvus*) is higher in lower-elevation riparian drainages close to the city of Boulder than among Warbling Vireo nests far (>10 km) from the urban boundary (J. Walsh pers. comm.). In Sierra Vista, Arizona, Bronzed (M. aeneus) and Brown-headed cowbirds feed and roost on golf courses and in cemeteries and urban backyards and move ≤6 km to forested foothills and riparian drainages, regions of high host abundance (Chace 2001).

### Factors Affecting Cowbird Distribution and Abundance at the Local Scale

Understanding the factors that influence distribution and abundance of cowbirds at the local scale is challenging, because of factors operating at larger spatial scales. Locally, cowbird distribution and abundance is influenced by spatial and temporal variation and interaction among (1) habitat type, (2) vegetation structure, and (3) host abundance and diversity. Various studies have found that cowbird breeding habitat is characterized by different, and sometimes contradictory, combinations of those factors (Table 1). One reason for the apparent variation is that those studies were conducted across disparate habitats scattered widely throughout the continent. Additionally, habitat type, vegetation structure, and avian diversity are all inter-related, so it is difficult to determine whether cowbirds are using hosts or vegetation as cues for potential breeding sites. Temporal variation further obscures patterns, because habitat type, vegetation structure, host community composition, and local cowbird population change within and between breeding seasons;
therefore, the relative importance of those cues change over short intervals (Wolf 1987, Farmer 1999a).

Further complicating any attempt to understand local factors affecting cowbird distribution and abundance is that most studies focus on influences on host parasitism frequency, which provides limited data on cowbird distribution patterns. Numerous studies have examined the relationship between host characteristics (e.g. abundance, defense, and nest location) and parasitism frequency (Smith and Arcese 1994, Uyehara and Narins 1995, Burhans 1997, Ortega 1998, Staab and Morrison 1999, Robinson and Smith 2000). However, local community composition and vegetation can dramatically alter individual species’ parasitism frequencies, without altering cowbird distribution or abundance (Clark and Robertson 1979, Freeman et al. 1990, Barber and Martin 1997, Burhans 1997, Dufty 2000, Strausberger 2001). It is difficult to generalize cowbird preferences using results from multiple study sites, because of differences in vegetation, habitat structure, and relative abundances of hosts and cowbirds (see below; Wolf 1987, Briskie et al. 1990, Barber and Martin 1997, Ortega 1998, Spautz 1999, Robinson et al. 2000, Robinson and Smith 2000). Even when community parasitism levels are obtained, projecting from parasitism frequencies to local cowbird distribution and abundance is not always straightforward (Robinson et al. 2000, Robinson and Smith 2000, Thompson et al. 2000, Winslow et al. 2000). Those studies refute the earlier assumption that cowbird parasitism is directly related to cowbird density (e.g. McGeen 1972, Mayfield 1977, Brittingham and Temple 1983). Furthermore, recent work suggests that female cowbirds may have (1) a much lower fecundity than previously reported and (2) variable commuting behavior that alters egg-laying patterns (Hahn et al. 1999, Curson and Mathews 2003, Woolfenden et al. 2003). Therefore, the validity of correlating cowbird abundance with parasitism frequency is questionable.

### Table 1. Avian influences on Brown-headed Cowbird distribution.

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Species richness (R)</th>
<th>Abundance (A)</th>
<th>Host species</th>
<th>Individual species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chace 2004</td>
<td>Southeastern Arizona</td>
<td>+</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Donovan et al. 1997</td>
<td>Illinois, Indiana, Missouri</td>
<td>+</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Donovan et al. 2000</td>
<td>Missouri</td>
<td>+</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evans and Gates 1997</td>
<td>Western Maryland</td>
<td>0</td>
<td>+</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Farmer 1999a</td>
<td>Coastal southern California</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>++</td>
</tr>
<tr>
<td>C. Farmer and J. C. Uyehara</td>
<td>Southern California</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>Goguen and Mathews 2000</td>
<td>Northeastern New Mexico</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hahn and Hatfield 1995</td>
<td>Eastern New York</td>
<td>+</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hahn and O’Connor 2002</td>
<td>United States</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lowther and Johnston 1977</td>
<td>Eastern Kansas</td>
<td>0</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Purcell and Vern 1999</td>
<td>Southern Sierra Nevada</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Robinson et al. 2000</td>
<td>Illinois</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tewksbury et al. 1999</td>
<td>Western Montana</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thompson et al. 2000</td>
<td>Illinois, Indiana, Missouri, Wisconsin</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Verner and Ri/erter 1983</td>
<td>Southern Sierra Nevada</td>
<td>–</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ward and Smith 2000</td>
<td>British Columbia</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young and Hut/ro 1999</td>
<td>Northern Rocky Mountains</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>+</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>R</th>
<th>A</th>
<th>R</th>
<th>A</th>
<th>R</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>++</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Different definitions of host species were used in each study.  
* Influence of hosts changed, depending on fragmentation and forest-tract size.
The effect of parasitism is frequently the ultimate factor of concern (e.g. Trine et al. 1998, Rothstein and Cook 2000, Morrison and Hahn 2002), and reducing cowbird numbers to reduce the parasite pressure is often a management objective (Kostecke et al. 2005). Below, we concentrate on explicit studies of distribution and abundance of cowbirds at the local scale, focusing on the primary local factors of (1) habitat type, (2) vegetation structure, and (3) host abundance and diversity.

Habitat Influences

Cowbirds breed in nearly every major habitat in North America (Rothstein 1994, Robinson et al. 1995a). Availability and proportion of habitat types and vegetation structure vary tremendously across the continent, so cowbirds’ local habitat preferences have to be interpreted in the context of habitat availability. Habitat preference, rather than habitat use, is demonstrated by explicit comparison of cowbird abundances or parasitism rates among the alternative habitats available at the landscape scale (e.g. Braden et al. 1997, Davis and Sealy 2000, Hejl et al. 2002). Habitat heterogeneity varies regionally; in the East and Midwest, small fragments of relatively unaltered habitat embedded in a matrix of heavily human-modified habitat limits breeding-habitat types available to cowbirds at the local scale (George and Dobkin 2002). The majority of the West has a much higher natural heterogeneity, such that numerous habitat types are often contained within the range of one cowbird (George and Dobkin 2002), allowing for more local-scale comparative studies. Differences in natural heterogeneity could lead to differences in cowbird responses to edge-effect (sensu Gates and Gysel 1978); therefore, we re-examine the conventional wisdom concerning cowbird responses to habitat edges. Given that patterns of natural and unnatural habitat heterogeneity have broad regional differences, we will discuss habitat preferences in three regional sections: the eastern, central, and western United States (Hochachka et al. 1999).

Edge effects.—We will focus on “hard” edges, where a sharp boundary exists between two very different habitats—a pattern known to increase nest predation and brood parasitism in some areas, with effects typically <300 m from the habitat discontinuity (Paton 1994). Results of parasitism studies within edge habitats are mixed. The preponderance of research suggests that cowbirds are an edge species, in that parasitism frequency decreases with increasing distance from edge habitats in forests (Gates and Gysel 1978, Chasko and Gates 1982, Brittingham and Temple 1983, Gates and Giffin 1991, Coker and Capen 1995, Evans and Gates 1997, Morse and Robinson 1999, Chace et al. 2000); however, some studies have found no effect of habitat edges on parasitism frequency (Robinson and Wilcove 1994, Hahn and Hatfield 1995, Thompson et al. 2000).

Habitat edges can elevate parasitism frequencies without significant increases in cowbird abundance (Donovan et al. 1997, 2000; Winslow et al. 2000). At the continental scale, fragmentation resulted in increased parasitism frequency east of the Rocky Mountains but had no effect in the West (Cavitt and Martin (2002). Cowbird habitat preference is a function of greater habitat heterogeneity and concurrent frequency of edge habitat (e.g. in riparian habitat of the Southwest; George and Dobkin 2002, C. Farmer and J. F. Chace pers. obs.). The cowbird’s edge “preference” appears to be a function of larger-scale (>10 km) factors.

Eastern habitat preferences.—The eastern U.S. cowbird population has declined simultaneously with an increase in forest cover (Askins 1993, Robinson et al. 1995a, Peterjohn et al. 2000, Wiedenfeld 2000). Most research has focused on within-habitat studies of fragmentation and edge issues; among-habitat patterns have received less attention. In three eastern locations, three different, mutually exclusive results emerge. In Maryland (Gates and Giffin 1991, Evans and Gates 1997, Gates and Evans 1998), cowbirds were detected most often in stream bottomlands with home ranges that include brush and deciduous forest habitats. In southern New York, cowbirds preferred forest interior adjacent to old-field edges between the habitat types (Hahn and Hatfield 1995, 2000). Research in northern New England (Coker and Capen 2000, Yamasaki et al. 2000) suggests that cowbirds prefer breeding sites with higher proportions of residential or agricultural fields within 1,000 m.

Midwestern and Great Plains habitat preferences.—Cowbirds are most abundant in the tallgrass prairies of the Great Plains and Midwest, where they appear to saturate all potential breeding
sites, making identification of important local factors difficult (Robinson and Wilcove 1994, Robinson et al. 2000, Thompson et al. 2000). Parasitism frequencies in forested habitats were higher than in shrubland or grassland throughout Illinois (Strausberger and Ashley 1997; Robinson et al. 1999, 2000), though parasitism frequency can be high within some grassland communities (Elliott 1978, Robinson et al. 1995a, Davis and Sealy 2000, Herkert et al. 2003). Abundance of cowbirds and female cowbird morning activity were highest in forests and lowest in grasslands (Thompson 1994, Robinson et al. 1999). Cowbird abundance in Midwestern forest tracts was independent of tract size, but parasitism frequencies were lower in larger forest tracts (200–3,000 ha; Robinson et al. 2000). Perhaps at very large scales (>30,000 ha), interior forest habitats are too remote for cowbirds, thereby protecting hosts from parasitism (see below; Robinson et al. 1995b).

Western habitat preferences.—The West has much greater habitat heterogeneity than the East or Midwest, because of variable rainfall, aridity, influence of fire, and topographic diversity (George and Dobkin 2002). Willow–cottonwood riparian corridors are often bordered by oak woodland, manzanita, sagebrush, juniper, grasslands, or a combination of those vegetation types on the slopes or uplands. Natural fragmentation makes testing for local habitat factors easier than in other parts of the continent. Comparative studies among habitats suggest that cowbirds favor riparian vegetation in southern California (Farmer 1999b), Arizona (Chace 2004), and Idaho (Tewksbury et al. 1999), but use a wide range of habitat types (Lynn et al. 1998), including upland pine and fir forest (Ward and Smith 2000, Chace 2004). In the Sierra Nevada and Rocky Mountains, cowbirds use grasslands, coniferous forest, and riparian habitat (Verner and Ritter 1983, Rothstein et al. 1984, Hejl and Young 1999, Young and Hutto 1999). Comparison within western regions shows that cowbird abundance in some riparian habitat is lower than in fir forest, pinyon–juniper, shrubsteppe, or coastal sage-scrub habitats (Braden et al. 1997, Ellison 1999, Farmer 1999a, Goguen and Mathews 1999, Vander Haegen and Walker 1999).

Topography and elevation are additional, related factors that affect cowbird distribution in the West. Vegetation, avian community, and landscape context change in association with topography and elevation, so it is difficult to discriminate among those factors. Cowbirds were detected significantly less often in the canyons of western Montana (Tewksbury et al. 1999) and narrow riparian canyons of coastal southern California (Farmer 1999a). Cowbird abundance is lower at high elevations in the northern Rocky Mountains (Hejl and Young 1999, Young and Hutto 1999) and Sierra Nevada (Rothstein et al. 1980, Verner and Ritter 1983, Lynn et al. 1998, Purcell and Verner 1999); however, Finch (1989) found that cowbird habitat use was independent of elevation in Wyoming.

Current knowledge suggests that cowbirds prefer breeding in riparian habitat of the arid Southwest, but that preference is not as strong in the Mountain West and Northwest. Cowbirds avoid deep, narrow, and arid canyons and have a weak preference to breed at lower elevations in the Intermountain West. Future studies should explicitly evaluate the influence of topography and elevation on cowbird habitat use, abundance, and parasitism frequency to resolve potentially confounding influences in cowbird habitat-selection models.

Vegetation Structure

Vegetation structure can both influence a cowbird’s ability to find a host nest and serve as an indicator of future host breeding. Research has focused on discriminating vegetation structure (1) used by cowbirds (e.g. Evans and Gates 1997, Farmer 1999a), (2) between parasitized and unparasitized nests (e.g. Brittingham and Temple 1996, Burhans 1997, Chace and Cruz 1999), and (3) among members of the avian community (e.g. James 1971, Staab and Morrison 1999). A problem is that each researcher tends to collect different microhabitat data, making it difficult to determine how cowbirds use vegetation structure as settlement cues. Therefore, we urge researchers in the future to use established protocols (e.g. BBIRD; see Acknowledgments) to facilitate comparative studies.

Two aspects of vegetation structure have been examined in multiple studies of cowbird use: perch availability and nest-concealment vegetation volume. Cowbirds use high perches in trees to detect host nests (Friedmann 1963, Payne 1973, Norman and Robertson 1975, Gates and Gysel 1978), and nests near elevated perches have higher parasitism frequencies.
(Anderson and Storer 1976, Freeman et al. 1990, Uyehara 1996, Clotfelter 1998, Averill-Murray et al. 1999, Hauber and Russo 2000; but see Staab and Morrison 1999). It seems unlikely that trees and perches would be a limiting factor or an important cue underlying cowbird distribution, except perhaps in open Midwestern grasslands. Jensen (2003) experimentally tested that hypothesis by increasing perch sites in a Kansas tallgrass prairie and found no increase in cowbird abundance or parasitism frequency. Furthermore, cowbirds can use alternative methods of nest detection, such as walking, host flushing, and host defenses (Norman and Robertson 1975, Smith et al. 1984, Smith and Arcese 1994, Uyehara and Narins 1995, Clotfelter 1998, Hahn and Hatfield 2000).

Several studies that have used multivariate techniques to partition habitat use of an entire avian community suggest that cowbirds are habitat generalists whose distribution is influenced by plant species diversity, tree density, and vegetation volume or cover at various height classes (James 1971, Johnston 1977, Whitmore 1977, Rice et al. 1983, Finch 1989, Saab 1999). In western Maryland, cowbirds prefer breeding sites with high numbers of saplings (<7.5 cm diameter at breast height [DBH]), large snags (>22.5 cm DBH; Gates and Evans 1997), higher vegetation volume (0–3 m), and snag basal area (Evans and Gates 1997). In southern California, cowbirds were more frequent at sites with an open upper and lower canopy, few tree species, and high grass–forb cover (Farmer 1999a).

Many studies have examined how vegetative concealment of host nests affects parasitism frequency. Some studies have found no difference in vegetative concealment between parasitized and unparasitized nests (Anderson and Storer 1976, Best 1978, Best and Stauffer 1980, Smith 1981, Robinson et al. 1995a, Barber and Martin 1997). However, most of those studies were in the Midwest; some recent studies in the West have found that parasitized nests had less vegetative concealment (Averill-Murray et al. 1999, Spautz 1999, Staab and Morrison 1999, Ortega and Ortega 2001) and lower-density understory (Whitfield 1990, Uyehara and Whitfield 2000) than unparasitized nests. Habitat context further complicates the effect of nest concealment. Burhans (1997), for example, found that high levels of nest concealment among Indigo Buntings (Passerina cyanea) reduced parasitism in old fields, but not in forests; whereas concealment had no effect on parasitism frequency in Field Sparrows (Spizella pusilla) in old fields. For some host species, risk of parasitism depends more on nesting location in the vegetation layers than on nest concealment (Briskie et al. 1990). Conflicting results from nest concealment studies suggest that cowbirds use the environment at scales larger than the microhabitat. Research into the effects of mesoscale habitat and host factors will be more productive in understanding cowbird distribution patterns (Duffy 1982, Rothstein et al. 1984, Teather and Robertson 1984, Gates and Evans 1998, Thompson and Dijak 2000). Conflicting conclusions from nest concealment studies may result from different methods (Ortega et al. 2002) but may also suggest that cowbirds use the environment at scales larger than the microhabitat or that they rely more on host behavior to find nests.

**Avian Influences**

Many studies suggest that distribution of cowbirds at the local level is determined by distribution of their hosts (McGeen 1972; Elliott 1980; Chasko and Gates 1982; Rothstein et al. 1984, 1986; Gates and Giffin 1991; Thompson 1994; Robinson et al. 1995a; Evans and Gates 1997). Cowbirds could use four levels of the avian community as cues for settlement: (1) all bird species, to (2) all passerine species, to (3) all host species, to (4) an individual host species; researchers generally analyze relative abundance or richness within each level (Table 1).

**All avian and all passerine species.**—Avian abundance (Evans and Gates 1997) and richness (Farmer 1999a) have been found to be significantly higher at sites where cowbirds were detected. Passerine species richness was a better predictor of cowbird occurrence than passerine or host abundance in the southern Sierra Nevada (Purcell and Verner 1999), southeastern Arizona (Chace 2004), and southern California (C. Farmer and J. C. Uyehara unpubl. data). Farmer (1999a) found that passerine abundance was the best predictor of cowbird distribution in coastal southern California. Young and Hutto (1999) determined that both passerine richness and abundance had a positive significant relationship with cowbirds in Montana, but host species richness was the strongest predictor of cowbird distribution.
Host species.—Cowbirds have parasitized 228 species, but only 132 successfully raise cowbirds (DeGeus and Best 1991, Ortega 1998). Continental and regional variation occurs in both abundance and parasitism frequency of some host species, with suitable hosts (e.g., Red-winged Blackbirds; *Agelaius phoeniceus*) not parasitized in some locations (e.g., Hoover and Brittingham 1993, Winslow et al. 2000). Cowbirds sometimes even lay eggs in nests of rejecter hosts (Rothstein 1976, Friedmann et al. 1977, Scott 1977, Strausberger and Ashley 1997, Haas and Haas 1998). Although parasitism of rejecters will not contribute to cowbird population growth, cowbirds could perceive such species as part of the overall avian community when determining where to breed. Although numerous grassland and shrubland hosts possess defenses against parasitism (Hosoi and Rothstein 2000, Peer et al. 2000), cowbird abundance does not seem to respond to changes in proportions of rejecter or mobbing species (Robinson et al. 1999).

Most studies of avian influences on cowbird distribution patterns use either host richness or abundance (Table 1), but each researcher tends to use a different measure: for example, all small to medium, open-cup-nesting passerines (Young and Hutto 1999); all species known to be parasitized (Purcell and Verner 1999); medium passerines that do not reject or abandon nests (Robinson et al. 1999); species that successfully fledge cowbirds (Ward and Smith 2000, Chace 2004); species with >10% of nests parasitized at the study site (Donovan et al. 2000, Thompson et al. 2000); or species with >15% of nests parasitized at the study site (Tewksbury et al. 1999); in some cases, hosts are not explicitly defined (Evans and Gates 1997). Although those subtle distinctions likely change the status of only a few species in any area, it could explain some of the disparities in the following results.

Host species richness and abundance are the most frequent measurements examined, but the relationship is not as obvious or consistent as previously assumed (Table 1; McGeen 1972; Rothstein et al. 1984, 1986; Thompson 1994; Robinson et al. 1995a). For example, Lownther and Johnston (1977) found that cowbirds were most abundant in shrub habitat, where host abundance was highest, even though host richness was highest in forest habitat; whereas Hahn and Hatfield (1995) found that cowbirds were most abundant in forest, where host richness was high but abundance was low. Those studies highlight the strong habitat–host confound and demonstrate that only very carefully designed studies can separate the relative importance of those two local factors.

Individual host species.—Warbling Vireo and cowbird abundances showed a negative correlation in the Sierra Nevada, but it is unclear whether (1) cowbirds avoid sites with Warbling Vireos, (2) cowbirds cause declines in local Warbling Vireo populations, or (3) both Warbling Vireo and cowbird numbers are correlated to some other confounding variable (Rothstein et al. 1980, Verner and Ritter 1983). Farmer (1999a) examined the relationship between cowbird distribution and the abundance of the four commonly used host species in coastal southern California: Yellow Warbler (*Dendroica petechia*), Wilson’s Warbler (*Wilsonia pusilla*), Common Yellowthroat (*Geothlypis trichas*), and Song Sparrow (*Melospiza melodia*). Cowbirds were positively associated with Yellow Warbler abundance in two different data sets, but not in the second year of the study, while there was a positive association with passerine abundance in both years.

Some studies focus on how changes in the local host community affects parasitism frequency. Barber and Martin (1997) discovered that Black-capped Vireo (*V. atricapilla*) parasitism frequency was most strongly correlated with Northern Cardinal (*Cardinalis cardinalis*) abundance. However, unparasitized nests of Northern Cardinals and Yellow-breasted Chats (*Icteria virens*) were within ~2 m, which suggests that actual local cowbird distribution did not change in response to Northern Cardinal density. Many species are aggressive toward cowbirds near their nests (e.g., Robertson and Norman 1976, Neudorf and Sealy 1992, Burhans 2000), but only Red-winged Blackbirds are reported to reduce parasitism by mobbing (Clark and Robertson 1979, Freeman et al. 1990, Strausberger 2001). However, cowbirds are not less abundant in habitats with high proportions of aggressive, mobbing species (Robinson et al. 1999). Those studies provide invaluable information on cowbird–host dynamics, but without a more explicit study design, parasitism studies cannot furnish data on whether cowbird distribution is influenced by local avian factors.

Vegetation strata.—Numerous studies have examined parasitism across host-nest strata
(i.e. ground, shrub, or canopy; Robinson 1992, Martin 1993, Hahn and Hatfield 1995, Robinson et al. 1995a, Farmer 1999a, Hahn and Hatfield 2000, Robinson et al. 2000). In Illinois (Robinson 1992; Robinson et al. 1995a, b, 2000) and southern coastal California (Farmer 1999a), parasitism did not differ among strata. However, cowbirds demonstrate a strong, consistent preference for ground-nesting birds in New York (Hahn and Hatfield 1995, 2000), low-nesting species (<3 m) in Arizona (Staab and Morrison 1999), and low-nesting Yellow Warblers rather than canopy-nesting Least Flycatchers (*E. minimus*) in Manitoba (Briskie et al. 1990). Those studies suggest that cowbirds may prefer to breed in areas with a high abundance of low-nesting species, though they certainly do not avoid canopy-nesting birds (Robinson et al. 1995a, 2000). We know of no study that analyzes the pattern of cowbird distribution on the basis of host, passerine, or total species nesting strata, an aspect that warrants further attention.

Overview of avian influences.—The relationship between cowbirds and host abundance or richness is neither as obvious nor as straightforward as is commonly assumed. A simplistic analysis of Table 1 shows that 58% of studies found a positive relationship between cowbirds and measures of host richness and abundance (richness: 6 of 9 studies; abundance: 8 of 15), and 83% of studies found a positive relationship between cowbirds and overall avian species measures (richness: 2 of 3; abundance: 3 of 3). In all studies, there was a positive relationship between cowbirds and passerine measures (richness: 5 of 5; abundance: 4 of 4). Those results strongly suggest that cowbird distribution is not finely tuned to the composition of the host community; rather, cowbirds may use passerines as indicators of breeding sites. Future studies clearly need to incorporate different community levels and both abundance and richness measures to test that hypothesis.

Donovan et al. (1997) established that local-scale effects depend on landscape context, and Farmer (1999a) showed that host cues used by cowbirds vary temporally. Although elaborate multiscale studies may not be logistically feasible, enough descriptive detail and actual numerical results (i.e. cowbird abundance measures) need to be provided for other researchers to qualitatively evaluate the results considering all the factors discussed above.

**Density-dependent habitat selection.**—Spatial patterns of cowbird parasitism exist within and among host communities but may vary regionally. Although cowbird habitat-use patterns depend on locally available habitats, those patterns may also be affected by geographic—and perhaps temporal—variation in cowbird density (Robinson et al. 1999, Jensen and Cully 2005a). As cowbird density increases, we can expect cowbirds to spatially broaden their host use within or among host communities (Robinson 1999). Density-dependent habitat selection in cowbirds is evident from Midwestern forests (Donovan et al. 1997, 2000; Thompson et al. 2000), where cowbirds expand their distribution from forest edges to forest interior as cowbird density increases with the degree of forest fragmentation by agriculture. Similarly, in prairie landscapes, as cowbird density and parasitism increase, cowbirds move farther from the prairie–woodland edges and parasitize more hosts in the prairie interior (Jensen and Cully 2005a).

The competitive mechanism driving density-dependent habitat selection in cowbirds is not clearly known, but cowbirds may distribute themselves in an ideal free manner (Fretwell and Lucas 1970, Fretwell 1972) in response to variation in their own conspecific density and resulting effects on their fitness (Winslow 1999, Jensen and Cully 2005a). Several lines of evidence suggest that cowbirds exhibit a free settlement pattern, in which cowbird laying ranges overlap rather than displace one another (despotic distribution) as cowbird density increases: (1) multiple parasitism of single host nests by different female cowbirds (Fleischer 1985, Hahn et al. 1999, McLaren et al. 2003, Strausberger and Ashley 2003) where local cowbird densities are high (Robinson et al. 2000), (2) cowbird territory dissolution (Elliott 1980), (3) cowbird eggs apparently laid randomly with respect to previous parasitism (Johnsgard 1997), and (4) cowbird abundance within host habitats negatively and linearly correlated with distance from cowbird foraging areas (Goguen and Mathews 2000). As the incidence of multiple parasitism within primary host habitats (e.g. habitat edges) increases with increasing cowbird density, cowbird egg and nestling survival decrease (McGeen 1972, Hatch 1983, Trine 2000, Jensen and Cully 2005a). Density-dependent responses by cowbirds in selecting...
host habitats may be reinforced by negative effects of multiple parasitism on cowbird fitness (i.e., incentive to exploit secondary-host habitats). It follows that variation in cowbird: host ratios among habitats should not be used to reject ideal free distribution in cowbirds if cowbird fitness is density-dependent or if habitat suitability varies (e.g., variation in host life histories [Martin 1995], availability of perches or cowbird feeding habitat, etc.).

**Management Applications**

In conclusion, we offer a synthesis showing how knowledge of factors affecting distribution and abundance of cowbirds at different spatial scales might be used in reducing parasitism levels on hosts of conservation concern (Fig. 2). However, before management is initiated—or continued—at any scale, two initial considerations must be addressed. First, will reduction or elimination of cowbird parasitism significantly affect population growth rates of the species of interest? Before time and financial resources are devoted to cowbird management, possibly at the expense of alternative management strategies, it should be demonstrated that such management can have a measurable effect on projected population growth (Rothstein and Cook 2000). Also, there needs to be some structure or mechanism for measuring success, so that management actions are scientifically evaluated. Second, management may be more effective for reducing parasitism at some spatial scales than at others; thus, managers need to concentrate management activities at a variety of spatial scales to achieve their goals.

**Management Considerations at the Continental Scale**

Establishment of preserves for hosts in regions where parasitism levels are low could protect possible host source populations, especially if populations that are determined to be parasitism-driven sinks occur in less manageable regions or landscapes. For example, although grassland songbird populations of concern (Vickery et al. 1999) in much of the Midwest are limited to small patches of highly fragmented grassland, cowbird parasitism of those populations is rare (Strausberger and Ashley 1997; Kershner and Bollinger 1998; Robinson et al. 1999, 2000; Peer et al. 2000). Toward the center of the cowbird’s distribution in the Great Plains, the same species are heavily parasitized (Elliott 1978, Hatch 1983, Zimmerman 1983, Koford et al. 2000, Jensen 2003). If regional variation in cowbird parasitism has significant effects on population persistence of grassland bird species, the more fragmented eastern populations may be globally valuable if grassland fragments are large enough to minimize nest predation (Herkert et al. 2003). Managers must also realize that geographic patterns of cowbird parasitism of a species may be highly variable within states or provinces, independent of variation in habitat structure at local or landscape scales (Jensen and Cully 2005b).

There has been speculation that cowbird control at large winter congregations could reduce parasitism pressure at the continental scale (Griffith and Griffith 2000, Ortego 2000). There is no clear evidence that cowbirds are limiting any host population, and no need for cowbird control at this scale has been demonstrated (Rothstein and Cook 2000, Ortega et al. 2005). Cowbirds congregating in dense winter flocks disperse widely to breeding habitats (Dolbeer et al. 1982); therefore, large winter kills of cowbirds may not have the intended effect of reducing pressure on the few hosts cowbirds actually limit.

**Management at the Regional and Landscape Scales**

Management of cowbird abundance and parasitism becomes somewhat feasible at regional and landscape scales, at which cowbird occupation of host habitats is ultimately limited by availability of cowbird foraging habitat. At the largest scales studied in fragmented Midwestern forests (<10-km radii around forest fragments), cowbird abundance and parasitism declined with increasing forest cover (Donovan et al. 1995, 2000; Robinson et al. 1995b; Thompson et al. 2000). Because cowbirds can commute great distances (≤15 km) from their foraging habitats in pasture and agricultural areas to a diversity of host habitats, management to completely omit parasitism from host communities would require landscapes within 15 km to be free of cowbird foraging areas. However, most cowbirds commute shorter distances from foraging areas into host habitat, and relatively few cowbirds penetrate...
**Fig. 2.** Adaptive management to match cowbird ecology across spatial scales. Management should be scale-appropriate and cognizant of implications at broader and finer scales.
deep into host habitat (Goguen and Mathews 2000). Also, cowbirds that travel considerable distances into host habitats from feeding areas produce fewer eggs than cowbirds commuting relatively short distances and may not pose a serious threat to habitat interior birds (Curson and Mathews 2003). Therefore, cattle removals or reforestation at landscape scales have the potential to reduce parasitism, but they would be most effective at large spatial scales. Cowbird foraging areas should be displaced as far as possible from critical host habitats.

Reducing the number or spatial extent (or both) of cowbird foraging sites becomes especially problematic when suburban backyards, school playing fields, and golf courses are the foraging locations (Farmer 1999a, Chace et al. 2003). Urban planning may assist in reducing future cowbird foraging opportunities at the suburban edge. Maintaining large open spaces and promoting clustered homes on smaller lot sizes in new developments would reduce cowbird foraging area, creating buffers between residential areas and nature reserves that increase the distance cowbirds need to travel (J. J. Walsh and J. F. Chace unpubl. data). Educational efforts can encourage voluntary compliance—through curtailing of bird feeding during the breeding season and increasing of native vegetation at the expense of short, shaded, and well-watered lawns—with the goal of reducing cowbird feeding opportunities (Chace et al. 2003).

The regional and landscape scales of management require the longest-term investment and greatest incentives to private landholders. Removal of cattle grazing at large scales could entail considerable expense. Purchasing land at such scales is also expensive, and land acquired by donation—though economical—is not likely targeted specifically for cowbird-free, high-quality habitats for threatened cowbird hosts. Reforestation of agricultural areas on a regional scale relies on economic changes outside the scope of cowbird management.

**Management at the Local Scale**

Options for reducing cowbird parasitism at local scales are limited to (1) manipulations of habitat structure and (2) reducing local cowbird abundance as compared with host abundance, though those options are not mutually exclusive. Diversity of hosts, host communities, and vegetative habitats throughout the range of the cowbird limit our ability to generalize about habitat manipulations that might reduce parasitism across regions. Reductions in the amount of “edge” habitat in forests and prairies might reduce local parasitism levels, but that may not be effective where cowbird density is particularly high (e.g. in much of the Great Plains). Cowbird preference for certain vegetative and associated host communities vary regionally.

Manipulation of the vegetation structure of important host habitats might reduce parasitism levels by physically reducing host-nest detectability. It is possible that habitat enhancement of cowbird-preferred avian communities that have large proportions of rejecter species (e.g. eastern shrublands) might create local cowbird population sinks (Grzybowski and Pease 1999, Robinson et al. 1999), but those models need to be tested. Managed vegetation structure may allow hosts to build nests at heights that allow for reduced parasitism. Elevated perches (e.g. trees, shrubs, or snags) can facilitate cowbird parasitism in open habitats, and could thus be reduced or eliminated from targeted areas. However, alteration of vegetative habitats may adversely affect habitat quality for other species (Staab and Morrison 1999). Habitat manipulations that increase the amount of host habitat, and thus host abundance, may indirectly reduce parasitism by decreasing local cowbird:host ratios, if cowbird populations remain stable or are reduced (Rothstein et al. 2003). In the latter case, reductions in local cowbird population size may occur if host habitat enhancement also reduces cowbird feeding areas. That would be preferred, because increases in local host abundance or diversity might promote a functional or numerical response in cowbird parasitism and density (Table 1) if foraging habitat remains accessible to cowbirds.

Cowbird trapping programs are frequently employed to reduce cowbird abundance and parasitism of hosts (Hayden et al. 2000). However, cowbird trapping presents only a temporary solution—if it affects host population persistence at all—and may divert financial resources from more efficacious management strategies (Rothstein and Cook 2000, Wiedenfeld 2000, Rothstein et al. 2003). Continuous trapping effort would be required to counter cowbird dispersion from
outside designated cowbird trapping areas. Conversely, if host populations are restored through cowbird trapping efforts, further trapping might not be needed if cowbird:host ratios are lowered to the point where parasitism no longer has an effect on host population growth (Rothstein et al. 2003). Therefore, host habitat restoration is preferred over cowbird trapping, but trapping programs may be a necessary first step in recovery of very small, highly parasitized populations (Rothstein and Cook 2000).

Management to thwart cowbird parasitism of hosts at a fine-grain, local scale is less straightforward than recommendations at larger landscape scales. Management recommendations are further complicated by inconclusive results from research conducted at local scales. That does not mean that local vegetative habitats cannot be managed for improved nesting success by reducing nest depredation. However, cowbird distribution and parasitism at local scales seem more dependent on geographic and landscape patterns in cowbird abundance.

Interactions among Scales

Patterns of cowbird abundance at larger spatial scales (continental, regional, landscapes) may affect spatial patterns of parasitism at finer scales. Those complicated interactions must be appreciated when considering cowbird management options. Cowbird host-use patterns among habitats—and host species (Woolfenden et al. 2003)—may change with variation in cowbird density. Thus, management activities to reduce cowbird abundance at landscape scales may only reduce parasitism at local scales in secondary cowbird habitats, or on secondary hosts, because the residual cowbird population still uses primary cowbird habitats and hosts (Robinson et al. 1999, Jensen and Cully 2005a). A similar concentration of parasitism on primary hosts could result from management to reduce cowbird abundance at local scales (e.g. trapping). Similarly, if cowbird density increases (naturally or anthropogenically), cowbirds may use secondary hosts in habitats they otherwise appear to avoid (e.g. grassland or forest interior). Those patterns of density-dependent habitat selection at the local scale are also expected across regional and continental gradients in cowbird abundance.


