GEOGRAPHIC VARIATION IN COWBIRD DISTRIBUTION, ABUNDANCE, AND PARASITISM

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Abstract. We evaluated geographical patterns in the abundance and distribution of Brown-headed Cowbirds (*Molothrus ater*), and in the frequency of cowbird parasitism, across North America in relation to habitat fragmentation. We found no distinctive parasitism patterns at the national or even regional scales, but the species is most abundant in the Great Plains, the heart of their original range, and least common in the southeastern U.S. This situation is dynamic, because both the Brown-headed and two other cowbird species are actively expanding their ranges in the southern U.S. We focused almost entirely in this paper on the Brown-headed Cowbird, because it is the only endemic North American cowbird, its distribution is much wider, and it has been much more intensively studied. We determined that landscape is the most meaningful unit of scale for comparing cowbird parasitism patterns as, for example, in comparisons of northeastern and central hardwood forests within agricultural matrices, and suburbanized areas versus western coniferous forests. We concluded that cowbird parasitism patterns were broadly similar within all landscapes. Even comparisons between prominently dissimilar landscapes, such as hardwoods in agriculture and suburbia versus coniferous forest, display a striking similarity in the responses of cowbirds. Our review clearly indicated that proximity of feeding areas is the key factor influencing presence and parasitism patterns within the landscape. We considered intensity of landscape fragmentation from forest-dominated landscapes altered in a forest management context to fragmentation characterized by mixed suburbanization or agricultural development. Our review consistently identified an inverse relationship between extent of forest cover across the landscape and cowbird presence. Invariably, the variation seen in parasitism frequencies *within* a region was at least partially explained as a response to changes in forest cover. The most salient geographic aspect of cowbirds' response to landscape fragmentation is the time since fragmentation occurred. Eastern landscapes generally experienced 200 years ago the development and fragmentation that western landscapes experienced less than 75 years ago. Consequently, there is a broad east-west contrast in which more numerous human settlements and smaller unbroken forest stands are found in the East, a difference that permits cowbirds to be more pervasive and ubiquitous. The locality of suitable feeding areas is a hallmark trait of the cowbirds' strategy in exploiting specific forest fragments. Host abundance influences parasitism patterns only secondarily at the landscape scale. These two limiting factors come into play differently in different landscapes. For example, cowbird abundance in unbroken forested landscapes are limited primarily by the availability of foraging areas rather than by host density, whereas cowbirds are limited primarily by host availability in landscapes that are extensively fragmented with feeding areas.

Key Words: Brown-headed Cowbird; cowbird parasitism; fragmentation; geographic variation; host defense; *Molothrus ater*.

The laying of eggs by one species in the nests of another species, allowing the host species to raise their young, is a fascinating evolutionary story (e.g., Rothstein and Robinson 1988, Ortega 1998:37–63). In North America, the Brown-headed Cowbird (*Molothrus ater*) is the primary nest parasite, although two other species are expanding their ranges in the southern U.S. (Cruz et al. 1998, Ortega 1998). The trait of parasitizing nests apparently developed in the Brown-headed Cowbird in the Great Plains. As reviewed below, this cowbird species expanded its range eastward in the 1800s and westward in the 1900s, and now occupies most states and provinces in North America (Rothstein 1994, Peterjohn et al. 2000). Parasitism, along with the cowbird's range expansion, has caused scientists to consider the role that cowbirds might be having in population declines of certain of their host species. Thus, the goal of our paper is to review cowbird abundance, distribution, and parasitism frequencies across North America so a better understanding of cowbird ecology and its impact on host species can be gained.

In this paper we assumed *no difference* in cowbird parasitism behavior by geographic location. We reviewed the literature (including unpublished manuscripts and reports) in order to characterize the relationship between host and parasite. Given the striking differences in environmental conditions across North America—including the distribution of bird species—we can presuppose that one can easily find some amount of difference in the frequencies of cowbird parasitism just by looking for it. And, in fact, we know this to be the case (see reviews by Ortega 1998, Trine et al. 1998). We were primarily interested in examining the *process* of parasitism. That is, are there fundamental differences in cowbird behavior in different regions that have ecological implications and evolutionary expla-

nations? In our review we considered both feeding behavior and host selection behavior.

VALIDITY OF AN EAST-WEST COMPARISON OF BROOD PARASITISM

Our perception of geographic location is based in part on historic context and tradition. It is also difficult to lump large geographic areas under a common descriptor. Where does the East begin and the West end; where does the East becomes the Southeast? These geographical terms are frequently used subjectively and anthropocentrically in ways that are not supported by ecological characteristics that affect birds. Thus, dividing North America into "East" and "West" is an inappropriate means of examining an ecological relationship such as parasitism and fragmentation. This does not mean, however, that geographic differences do not occur in land-use practices and ecological processes and in the response of animals to these practices and processes. But establishing *a priori* boundaries constrains the analysis to preconceived categories and notions.

THE RESPONSE OF COWBIRD HOSTS TO FOREST FRAGMENTATION

In this section we set the stage for evaluating regional differences in cowbird parasitism by defining fragmentation and placing this concept into an ecological framework. The emphasis of this volume is on fragmentation, and from the perspective of cowbirds, the most important aspects of fragmentation are, first, that it affects the abundance and distribution of host species by altering their habitat and, second, that it alters the abundance and distribution of feeding areas associated with developments. These twin themes about the influence of fragmentation on hosts' breeding habitat and on feeding areas of cowbirds associated with human development recur throughout our review.

The classic description of fragmentation implies extensive landscapes of homogeneous vegetation, but this conception is an artifact of graphic art framed at a large spatial scale. Examined at finer resolutions, most ecological systems are actually a mosaic of different plant associations. Even changes of a few meters can change soils, slope, and aspect, and thus the associated plants. Further, these mosaics are dynamic and change, often rapidly, through succession, catastrophic events (e.g., fire, flood, wind), or development activities such as crop plantings or settlements (Meffe and Carroll 1997:274–275; Franklin et al. *this volume*).

The definition of "fragmented" habitat depends upon the spatial scale of observation. Our analyses use fragmentation at a scale relevant to selection of habitat by birds, particularly songbirds. Briefly, habitat selection is often viewed as a hierarchical process where individuals first select a broad geographic range, a decision that is largely innate. Within the geographic range the individual then makes a series of decisions based on increasingly refined combinations of vegetation structure, floristics, food resources, and nest sites (Johnson 1980, Hutto 1985).

Thus, in an analysis of brood parasitism, fragmentation is an ambiguous concept unless it is defined in spatial terms relevant to the series of responses a host makes. There are changes that take place in the environment at several scales of resolution (see also Angelstam 1996). Such descriptions of the environment and habitat selection are not restricted geographically, but should apply across eastern and western environs. Consequently, we would not expect different behavioral processes in either host species or cowbirds to be operating geographically. The proportion of birds that show a particular response to fragmentation (e.g., area sensitive, enhanced by edge) may differ geographically depending on the historic factors that formed the initial bird assemblage (e.g., Morrison et al. 1998:16–26). For example, fewer *Dendroica* warblers occur in the West than in central and eastern locations. This is apparently the result of Pleistocene and post-Pleistocene events (Mengel 1964, Morrison et al. 1998:18–21). Thus, there is simply a greater opportunity for fragmentation to cause negative impacts on these warblers in more eastern locations, and perhaps a proportionally more apparent impact to the bird assemblage due to fragmentation.

Fragmentation in managed forests can be considered dynamic in that stands are cut and reforested; stands are not retained in early successional conditions. This means the songbird communities that cowbirds parasitize continue to have extensive natural breeding habitat although the vegetation communities are less stable than they would be in unmanaged forest. In contrast, disturbances due to human development activities result in permanent or static fragmentation (McGarigal and McComb 1995). This eradicates some host-breeding habitat, leaving disjunct fragments separated by patches that have food for cowbirds. They concluded that it is unlikely that the empirical findings on forest fragmentation from urban and agricultural landscapes extend to the dynamic forest landscapes of the Pacific Northwest and elsewhere. Likewise, Keller and Anderson (1992) concluded that fragmentation in Wyoming could not be directly compared with fragmentation occurring in the Pacific Northwest. Freemark et al. (1995) also noted that most studies in the West have been con-

TABLE 1. COMPARISON OF THE EFFECTS OF LANDSCAPE STRUCTURE ON NEOTROPICAL MIGRATORY SPECIES BREED-
ING IN NORTHEASTERN AND CENTRAL HARDWOOD FORESTS WITHIN AGRICULTURE AND SUBURBANIZED LANDSCAPES
VERSUS WESTERN FORESTS

Landscape structure	Northeastern and central vs. western comparison
Landscape composition	
Forest type	Same
Forest cover	Same; less severe in west
Habitat proportion	Same
Landscape configuration	
Patch size	Same; perhaps less severe in west
Patch shape	N/A[a]
Interpatch distance	Same
Nonforest edge	N/A
Habitat juxtaposition	Same

Note: Information summarized from Freemark et al. (1995).
[a] N/A = comparison not made or comparable.

ducted in forested landscapes fragmented by sil-
vicultural activities—which usually do not have
rich food sources for cowbirds—rather than in
agricultural and urban landscapes as in the East,
which do include sources of food (see also Hejl
et al. *this volume*).

Yet, Freemark et al's. (1995) extensive liter-
ature review of the response of breeding com-
munities of neotropical migrants to landscape
structure across much of North America does
show similarities in songbird responses. A sub-
jective comparison of communities nesting in
northeastern and central hardwood forests within
agricultural and suburbanized areas with com-
munities nesting in western coniferous forests
revealed similar responses of birds to broad
measures of landscape structure (Table 1). Par-
ticularly because this is a comparison among
very dissimilar landscape settings (i.e., hard-
woods within agriculture and suburbia versus
managed coniferous forest), the similarity in re-
sponse by breeding birds is striking.

Although there are similarities in the respons-
es of host communities in different regions to
fragmentation, Freemark et al. (1995) concluded
that birds in western (coniferous) forests have
not shown as strong a negative response to frag-
mentation as have birds in northeastern and cen-
tral hardwood forests. They attributed this sev-
eral factors: fragmentation is a more recent oc-
currence in the West; fragmentation has rarely
resulted in habitat isolation; and western forests
are naturally fragmented and human-induced
fragmentation has not had time to negatively im-
pact birds. The key insight here is that there are
not inherent differences in the response of bird
communities to forest fragmentation. The earlier
stage of fragmentation typical of western forest
means that many western coniferous forests are
actually "perforated" rather than fragmented
(Forman and Collinge 1996), or, as Freeman et

al. (1995) described them, "punctuated" by
clearcuts. Of course there are also numerous ex-
amples of both extensively forested areas and
forests perforated by logging and agriculture
outside of western environs (e.g., Robinson et
al. 1995a, Robinson and Robinson 1999).

McGarigal and McComb (1995), working in
the Oregon Coast Range, found that landscape
structure (composition and configuration) ex-
plained <50% of the variation in each species'
abundance among the landscapes. Species'
abundances were generally greater in areas with
a relatively fragmented distribution of habitat.
Note that from the cowbird's perspective this
means host abundance increases as fragmenta-
tion progresses. They cautioned, however, that
species sensitive to fragmentation at the scale of
their study may have been rare already and
therefore not subject to the approach they used.
Again from the cowbird's perspective the spe-
cies that drop out do not reduce the number of
host individuals available to cowbirds. They
concluded, however, that their results were gen-
erally similar to studies conducted in forest-
dominated landscapes in New Hampshire, Mis-
souri, Maine, and Wyoming. Thus, when com-
parisons are made between similar vegetation
types, birds respond in a similar manner across
broad geographic regions. They noted that ef-
fects of fragmentation in forest-dominated land-
scapes altered in a forest management context is
not comparable with fragmentation caused by
urbanization or agricultural development, which
is typically how eastern and western regions
have been compared in the literature.

In conclusion, the same ecological processes
associated with fragmentation seem to operate
regardless of geographic region. It is the longev-
ity of those land-use changes that precipitated
fragmentation that causes any geographic differ-
ences in current responses by birds. Verner

(1986) concluded that in western forests fragmentation was in the early stage and tended to produce two-dimensional islands (clearcuts) in three-dimensional seas (forests), while in eastern forests (as in European forests) the later stages of fragmentation have resulted in three-dimensional islands (forest fragments) in two-dimensional seas (e.g., agricultural lands). Askins et al. (1990) likewise concluded that the longer history of fragmentation in Europe has resulted in the extirpation of most area-sensitive species, a situation now in progress in North America. The localized abundance, breeding success, and survival of birds is related primarily to factors of habitat quality such as resource availability and predator-competitor activity, but these factors can be overridden when patches becomes very small (<10–20 ha) and isolated.

In summary, landscape fragmentation affects the songbird communities that cowbirds parasitize. At one level of intensity, fragmentation refers to the transformation of extensive forests into smaller stands, with the consequence for cowbird hosts of smaller, often shifting, breeding areas, and habitats with a greater edge to interior ratio. As fragmentation progresses, it evolves to a heterogeneous landscape composed of a mix of patches of breeding habitat with patches of development activities such as agriculture and settlements. With these twin aspects of fragmentation—smaller forest stands and increasing food sources associated with development—an increase in cowbird abundance and parasitism is likely.

HISTORIC DISTRIBUTION OF BROWN-HEADED COWBIRD AND POPULATION TRENDS

Peterjohn et al. (2000) described the continental decline in cowbird numbers in North America since the mid-1960s. Maximum cowbird abundance occurs in the northern Great Plains. Regionally, numbers are declining in the southern plains and throughout most of the East. The decline in the East is attributed to substantial increases in forest cover. There appears to be an overall steady abundance of cowbirds in the West. Within the region there is perhaps a slight decrease in the Pacific Northwest, while the Central Valley of California showed perhaps the greatest proportional increase in cowbird numbers in North America.

While there is consensus that the ancestral range of cowbirds in the Great Plains is still the area of their greatest abundance, other aspects of the extent and timing of their range expansions both eastward and westward are less certain. Rothstein (1994) suggested that cowbirds have been in the East in small numbers since at least the 1700s, the earliest era of European colonization. In the West, cowbirds may not be recent additions to the avifauna. While their colonization up the Pacific Coast from southern California to Oregon and Washington has been well documented over the course of the 20th century, there is also evidence of earlier populations in the northwest (Rothstein 1994). They apparently occurred historically, however, across the Great Basin to the eastern edge of the Sierra Nevada (Rothstein 1994). Thus, contrary to popular belief, the cowbird did occur historically in western North America. The Sierra Nevada-Cascade mountain ranges may have served as a barrier to widespread expansion onto the Pacific slope. There is also fossil evidence that cowbirds (of unknown breeding behavior) occurred along the edges of the species' current range in California, Oregon, and Florida in the late Pleistocene (Lowther 1993). Chace and Cruz (1999) suggested that cowbirds formerly ranged to near timberline in the Rocky Mountains because of the historic presence of bison (*Bison bison*). Cowbirds retreated from these elevations with the extirpation of bison from these mountains. The addition of cattle to former bison range is now allowing cowbirds to return to the mountains. If this is the case, we would expect that birds in at least some regions of the Rocky Mountains have had a longer exposure to cowbirds than our recent data indicate, and they may still express behavioral traits that evolved during the bison-cowbird period.

SUBSPECIES DIFFERENCES

Differences among the three subspecies of the Brown-headed Cowbird have been little studied. Rothstein (1994) speculated that the smaller southwestern subspecies, the "dwarf" cowbird, *M. a. obscurus*, might be more vagile or more competitive than *M. a. artemisia*, found to the north, east of the Rockies, because the westward range expansion of the species to the Pacific and up the west coast seems to have been driven by *obscurus*. At some point later *artemisia* appears also to have crossed the Rockies into northern California such that the two have subsequently intermixed as cowbirds moved north into Oregon and Washington.

Recent evidence of the range expansion of the eastern subspecies *M. a. ater* into the Florida peninsula makes it feasible that *ater* may be as successful as *obscurus* was in colonizing the Pacific west coast. Cruz et al. (1998) noted that *ater* has spread rapidly since the 1950s and now has breeding records confirmed halfway down the peninsula, with non-breeding sightings reported throughout the state. The expansion of the Brown-headed Cowbird into Florida is ex-

pected to have significant negative consequences for the indigenous breeding passerines, many of which are patchily distributed and breeding in small populations. The character of natural habitats and human settlements in Florida consists of mangrove on the west coast and dunes and beach on the east coast, with relentless human settlement along both coasts. The central section of the peninsula is higher and drier and agricultural and livestock developments are pervasive. Two mangrove-obligate species, the Black-whiskered Vireo (*Vireo altiloquus*) and the Florida subspecies of Prairie Warbler (*Dendroica discolor*), are already reflecting local population extirpation due to parasitism (W. Pranty, pers. comm.).

OTHER COWBIRD SPECIES: RECENT NORTH AMERICAN INVADERS

While it is only speculative to compare the invasive character of Shiny (*Molothrus bonariensis*) and Bronzed (*M. aeneus*) cowbirds to Brown-headed Cowbirds at this stage, recent developments in their respective range expansions suggest that both may be successful and increasingly widespread in the United States. Both are also host generalists, although perhaps not as extreme as the Brown-headed Cowbird (Rothstein et al. 2002). The rapid and impressive northward range expansion of the Shiny Cowbird across the Caribbean and into North America makes it a likely candidate to become established in the southeastern U.S. in the next few decades. While no breeding records have yet been recorded in Florida, the Shiny Cowbird is expected to become established there with little difficulty (Stevenson and Anderson 1994; W. Pranty, pers. comm.). Nothing is known about the extent of habitat specialization for either Brown-headed or Shiny cowbird within Florida.

The Bronzed Cowbird has only recently shown marked range expansion, apparently in association with loss of songbird breeding habitat in lower Rio Grande Valley in Texas. However, it has expanded both eastward and westward and could thus become a factor in regions of the U.S. (Cruz et al. 1998). In Texas, the Bronzed Cowbird parasitizes over 23 species, and at this stage it appears to prefer larger host species than does *M. ater*. The bronzed is thought to have contributed to the extirpation of Audubon's Oriole (*Icterus graduacuada*) in portions of lower Rio Grande Valley. Together with the brown-headed, the bronzed may also have contributed to declines of the Orchard (*I. spurius*), Hooded (*I. cucullatus*), and Northern (*I. galbula*) orioles in south Texas (Cruz et al. 1998).

HOST BEHAVIOR AND GEOGRAPHY

Much interest has focused on the question why most host species of the Brown-headed Cowbird do not show effective anti-parasite behavior. Rothstein's (1975) early experimental study of twelve eastern species used artificial eggs colored to resemble cowbird eggs and showed that only a few species regularly ejected the parasite eggs. Since then a large number of studies have been conducted in a variety of sites both east and west, showing that parasitism defenses (i.e., egg ejection, egg burial, or nest desertion) occur occasionally and unpredictably among species.

Some western-residing species and subspecies show effective anti-parasite behaviors that prevent or minimize deleterious effects of parasitism, which may have developed after contact with cowbirds, or which may have been present as pre-adaptation. For example, the Black-throated Gray Warbler (*Dendroica nigrescens*) regularly buried cowbird eggs in its nests in the Inyo-White mountains of eastern-central California (J. Keane and M. Morrison, unpubl. data), and Rich and Rothstein (1985) showed that Sage Thrashers regularly rejected cowbird eggs throughout their western range.

Egg-ejection behavior is one of the best-studied anti-parasite behaviors, yet a thorough summary of the proportion of acceptor and rejecter species by geographic region is still lacking because that would require systematic comparative studies of different populations of a large number of host species. Although evidence for egg rejection exists for many species, the quantitative estimates of frequency of this behavior can usually only be confirmed through experimentation, usually with artificial eggs (Ortega 1998:19). Of the >225 species known to be parasitized by Brown-headed Cowbirds, fewer than 20 are known to regularly eject parasitic eggs (Ortega 1998:19–20). Despite the obvious advantages to hosts of removing cowbird eggs, there are also many reasons why birds accept them (Ortega 1998:23–27). The most prominent reason is that parents risk breaking their own eggs when they try to move the cowbird egg.

Little is known about the degree to which egg-ejection behavior is genetically based or learned. Briskie et al. (1992) concluded that some anti brood-parasitic defenses are probably genetically determined. Robertson and Norman (1977) thought that the presence and intensity of aggression should vary widely geographically depending on the length of exposure to brood parasitism. For example, they compared aggression in an area of long-term host-cowbird sympatry (Manitoba) with an area (Ontario) of more

recent sympatry. They found that the Manitoba host populations showed more aggression towards a model cowbird, and concluded that this was because of the longer history of sympatry. Hobson and Villard (1998) studied the response of American Redstarts to model cowbirds in western Canada and found that they exhibited more vigorous nest defense in fragmented forests where cowbirds are more common than in extensively forested landscapes.

There is a widespread assumption that all hosts would evolve measurable anti-parasite behaviors given long enough sympatry with cowbirds. According to this hypothesis, some species along the Pacific slope may not have had adequate exposure to parasitism to evolve regular ejection behavior (Rothstein 1975). As discussed above, however, additional evidence must be gathered before any analysis of geographic trends in egg-rejection behavior. We suggest that the variability and relative rarity of anti-cowbird defenses reflects the inconsistent selection pressure exerted by cowbird parasitism in those landscapes where parasitism is relatively low and where the level of parasitism on individual species and communities varies from year to year. In several areas where long-term studies of cowbird parasitism have been conducted and where parasitism pressure is both high and consistent on particular species in the community (such as central Illinois, the Edwards Plateau in Texas and Oklahoma, and southern California), the study populations should be tracked for the emergence of anti-parasite behaviors. Similarly, the evolution of defenses by forest interior birds should be watched in the context of fragmentation in both east and west.

COWBIRD PARASITISM AND GEOGRAPHY

We present a summary of patterns of cowbird parasitism in relation to vegetation structure, host community, and degree of landscape development based on studies conducted across North American a variety of vegetation types in different geographic regions (Table 2).

Our review indicates that proximity of feedings areas is the key factor influencing which host community a local cowbird population will parasitize. Although Payne (1973, 1977) discussed the importance of temporal mismatch of breeding seasons (i.e., differing lengths of exposure, *sensu* Mayfield 1965) and documented the phenomenon for the birds of northern California, temporal mismatch is often overlooked. It is a notable phenomenon in eastern and western locations. The local abundance of cowbirds resulting from fragmentation and feeding opportunities further correlated with parasitization (Payne 1973, 1977).

It is commonly stated that the heavily parasitized riparian communities in the western and southwestern United States are physiographically unique because of the often abrupt change from the relatively mesic riparian vegetation and the xeric surrounding landscape (Ortega 1998: 267, Farmer 1999). However, cowbirds frequently use riparian areas in eastern and central, as well as western regions for passage, nesting, and foraging. Riparian corridors allow passage by cowbirds into an otherwise less suitable landscape matrix, including both eastern and western forests. The primary development impact to western riparian areas is loss of area and fragmentation (isolation), which is the same pattern seen in eastern deciduous forests (i.e., isolated patches of forest in a matrix of different vegetation). Several riparian obligate species in the West and Southwest have been nearly extirpated because of habitat loss. The isolation of these species into small patches exacerbated the effect of cowbird parasitism on their host populations. This situation, however, is not restricted to riparian vegetation of the West and Southwest. In three eastern regions where small and restricted species or subspecies occur in conjunction with a unique and limited habitat, development has created the classic situation in which cowbird parasitism (and nest predation) accelerate the decline of the resident species. In northern Michigan, in jack pine (*Pinus banksiana*) habitat, the species at risk is the Kirtland's Warbler (*Dendroica kirtlandii*). In the coastal mangrove forests of Florida, the species at risk are Black-whiskered Vireo and Prairie Warbler (Cruz et al. 1998, Stevenson and Anderson 1994). In Central Texas and Oklahoma, on the Edwards Plateau, the species at risk are the Golden-cheek Warbler (*Dendroica chrysoparia*) and Black-capped Vireo (*Vireo atricapillus*).

VALIDITY OF GEOGRAPHICAL COMPARISONS OF COWBIRD PARASITISM

One of the most important aspects of geography in analyzing the impact of cowbirds is the use of different spatial scales. Robinson (1999) noted that cowbird ecology can be analyzed at continental, regional, and landscape scales as much as at a local scale in relation to factors such as distances from edges. In this section, we discuss the findings of investigators who analyzed patterns at different scales. Hochachka et al. (1999) emphasized that investigators must define the scale they are using when predicting cowbird abundance and parasitism level.

Several investigators have considered whether aspects of cowbird parasitism vary on a conti-

TABLE 2.   FACTORS CORRELATED WITH INCREASED COWBIRD PRESENCE, ABUNDANCE, OR PARASITISM

Factor	Location	Source
Temporal mismatch	E. Washington	1
	Arizona/California	11
Proximity of feeding	E. Washington	1
	N. Rockies	2, 3, 5
	Sierra Nevada	6, 10
	N. Michigan	7
	Midwest	8, 13, 14, 15
	Vermont	9
	Florida	16, 17
	New Mexico	18
	Texas	19
	Pennsylvania	20
	Virginia	21
Local stand factors[a]	N. Michigan	7
	New York	22
Presence of riparian corridor	N. Rockies	2, 3, 5
	Coastal California	4
	Southern California	23
	Sierra Nevada	10
	Missouri	12
Host density	N. Rockies	2, 5
	Midwest	13
	Nationally	24
Species richness	Sierra Nevada	6
Fragmentation	Illinois	8
	Arizona/California	11a
	Florida	17
	Tennessee	25
Original range	Nationally	26
	Northeast	27

Sources: 1: Vander Haegen and Walker (1999); 2: Young and Hutto (1999); 3: Hejl and Young (1999); 4: Farmer (1999); 5: Tewksbury et al. (1999); 6: Purcell and Verner (1999); 7: Stribley and Hauffler (1999); 8: Robinson et al. (1995a); 9: Coker and Capen (1995, 1999); 10: Lynn et al. (1998); 11: Rosenberg et al. (1991:265, 335); 11a: Rosenberg et al. (1991:282–283); 12: Thompson et al. (1992); 13: Donovan et al. (1997); 14: Thompson (1994); 15: Trine et al. (1998); 16: Cruz et al. (1998); 17: W. Pranty, pers. comm.; 18: Goguen and Mathews (1999); 19: Eckrich et al. (1999); 20: E. Morton, pers. comm.; 21: J. Karr, pers. comm.; 22: Hahn and Hatfield (1995); 23: Kus (1999); 24: Hahn and O'Connor (2002); 25: Miles and Buehler (1999); 26: Smith and Myers-Smith (1998); 27: Hoover and Brittingham (1993).
[a] When in close proximity to feeding areas.

nental scale (Smith and Myers-Smith 1998, Robinson 1999). At a national scale, Hahn and O'Connor (2002) found that the most important factor predicting cowbird abundance is the presence of their preferred mix of host species (i.e., the seventeen most common hosts identified by Friedmann [1963]; Table 2). Landscapes in which host communities are found in close proximity to feeding areas typically occur where considerable habitat fragmentation occurs, that is, intrusion of agricultural activities, including concentrated livestock grazing, into a formerly undisturbed area. When they examined ancestral versus invaded ranges separately, they found that the predictive value of these host species actually operated only in the invaded ranges. Robinson et al. (1995b) suggested that because some western coniferous forests are more open than eastern forests, it was unclear whether or not western and eastern cowbirds differed in their preferences for forests, or if host distribu-

tion or some other factors influenced habitat occupancy by cowbirds. Our review indicates that the relationship between the openness of forests and cowbird abundance holds regardless of region. In fact, the variation seen in parasitism rates *within* a region was at least partially explained as a response to changes in forest cover. Further, many western forests have interlocking canopies with dense understories (e.g., Pacific Northwest, many western riparian forests). Again, sweeping generalizations regarding East and West seem unwarranted.

Hochachka et al. (1999) evaluated the relationship between forest coverage and parasitism among eastern, central, and western regions of the United States to provide a biological explanation for differences in the relationship between forest coverage and rates of cowbird parasitization across the continent. They also examined if variation in forest coverage was associated with the presence or absence of

cowbird parasitization in a study area, and, where cowbirds were present, if the frequency at which nests were parasitized was associated with forest coverage. They obtained data on parasitization rates of forest birds from the Breeding Biology Research and Monitoring Database (BBIRD), with data from 23,448 individual nests being analyzed. There were 26 study sites on which the nesting success of forest-nesting birds was monitored.

Hochachka et al. (1999) reported that the conclusions of previous research suggested that larger proportions of forest cover will result in a lower impact of Brown-headed Cowbirds on their hosts. They further suggested that the relationship between forest coverage and parasitization might differ away from the Midwest for a number of reasons. They offered that variation in cowbird abundance may not only affect absolute rates of parasitization, but also the pattern of variation in parasitization rate with varying forest coverage. Cowbirds in different parts of the continent encounter communities of hosts with different lengths of exposure (e.g., Mayfield 1965) and responses (e.g., Briskie et al. 1992) to parasitization, and host species with longer exposure to cowbirds may be resistant to parasitization regardless of the proportion of forest in a landscape. This appears true, but we do not see any evidence of this varying predictably by region in our review—all host responses are seen across the country, and all responses were seen within different localities within a region.

Hochachka et al. (1999) continued that the relationship between cowbird parasitization and forest coverage may also vary as a function of the local area over which forests were measured. Within local areas, forest coverage varied in its power to predict parasitization, depending on the size of the area over which forest coverage was measured (Tewksbury et al. 1998, Donovan et al. 2000). It is clear that vegetated patches surrounded by agriculture are different than those surrounded by more forest; this holds regardless of region.

Hochachka et al. (1999) failed to find any substantial differences in the behavior and habitat requirements among the races of Brown-headed Cowbirds (Lowther 1993). They concluded that although cowbird abundance declined westward—away from the center of the cowbird's range—the lower abundance of cowbirds in the West should result in a lower rate of parasitization, but not in a complete reversal of the relationship between parasitization rate and forest coverage. In the analyses by Hochachka et al. (1999), we see the importance of examining parasitization in a spatially explicit

manner. Local factors, such as presence of agriculture and patch size, will usually override relatively region-wide factors, such as absolute forest coverage and host density, in determining parasitization rates. Our review shows that the major factors determining the impacts of cowbirds on hosts operate continent-wide (Table 2). Fragmentation increases the degree of local sympatry between cowbird and host. Peterjohn et al. (2000) found no evidence to suggest that changes in cowbird populations differentially influenced population changes in cowbird hosts and rejecter species. Trends from BBS data showed that both cowbird host species and species rarely parasitized showed the same pattern of direct association with trends in cowbird abundance, and all of the correlations were low. The general direct relationship between cowbird trends and trends of neotropical migrants reflected the broad regional patterns of increasing bird populations in western North America and declines in the southern United States. They concluded that large-scale changes in weather patterns, land use practices, and habitat availability were primarily responsible for the direct associations they found between population trends in cowbirds and their host species. The strong influence of weather was also used by Johnson (1994) to explain the numerous range expansions of western birds.

Lowther (1993) concluded that fragmentation of eastern deciduous forest leads to increased parasitism by cowbirds. Further, he summarized that similar patterns were becoming evident in western montane areas as human settlement expand. We agree, and conclude that geographic differences in the response of birds to fragmentation—and thus our characterizations of the assemblage of birds in different locations (e.g., species richness)—are largely determined by the time since fragmentation occurred, rather than any inherent differences in the response. Cowbirds respond in distribution to fragmentation first by the location of suitable feeding areas, and secondarily to host abundance. As aptly summarized by Robinson et al. (1995a), cowbirds in heavily forested landscapes appear limited primarily by the availability of foraging areas rather than by host density. In fragmented landscapes, however, cowbirds appear limited primarily by host availability because feeding areas are readily available as a result of the fragmentation.