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SECTION I: COWBIRD ECOLOGY: FACTORS AFFECTING THE ABUNDANCE AND DISTRIBUTION OF COWBIRDS

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Over the last decade, a great deal has been written about the distribution and abundance of Brown-headed Cowbirds (*Molothrus ater*) (e.g., Lowther 1993, Robinson et al. 1993, 1995a; Rothstein and Robinson 1994, 1998; Thompson 1994, Donovan et al. in press, Smith et al. in press). The intense interest in this subject has arisen mainly because cowbirds are a major conservation problem in some areas. Studying cowbird abundance and distribution is a logical first step in developing management plans to reduce brood parasitization. But, cowbirds are also of interest as one of the best case history studies demonstrating the need to consider multiple spatial scales. A common conclusion of most reviews of cowbird ecology is that continental, regional, and landscape scales influence the abundance and distribution of cowbirds as much as local factors such as distances from edges.

THE ORTHODOX VIEW

To some extent, an orthodox view has arisen from the studies and reviews published to date. This orthodoxy has recently been dominated by a series of studies from the American Midwest, a landscape dominated by row-crop agriculture in which landscape composition can easily be characterized (Robinson 1992, Donovan et al. 1995a,b, Robinson et al. 1995b, Brawn and Robinson 1996, Thompson et al. in press). This orthodox view can be summarized as follows (Robinson and Smith in press).

1. At the continental scale, cowbirds are extremely widespread, but are most abundant in the northern Great Plains; abundance declines with distance from this region (Lowther 1993, Peterjohn et al. in press, Thompson et al. in press, Wiedenfeld in press). For many widespread host species, parasitization also declines with distance from this center of abundance (Hoover and Brittingham 1993, Smith and Myers-Smith 1998). Presumably, the Great Plains forms the historical center of cowbird abundance (Mayfield 1965) and cowbirds are still relatively less abundant in newly invaded areas in the West, East, and South.

2. At the regional scale (e.g., the American Midwest), cowbird abundance is determined by the composition of landscapes within the region (e.g., percent of forest cover; Robinson et al. 1995b). The presumed mechanism underlying this pattern is that in mostly forested landscapes, cowbird populations are limited by feeding sites (e.g., for northern New England; Coker and Capen in press, Yamasaki et al. in press) , whereas in mostly agricultural landscapes, cowbird populations are limited by the availability of hosts (Robinson et al. 1995a).

3. At the landscape scale (operationally defined as a 10-km radius around a study site; Robinson et al. 1995b), cowbird abundance is strongly dictated by distance to feeding sites. A common result of many studies using radiotelemetry is that cowbirds commute up to 7 km between breeding and feeding sites, but that most flights are less than 2 km (e.g., Rothstein et al. 1984, Thompson 1994). As a result, cowbird abundance declines with distance from known feeding areas. In mostly agricultural landscapes in which feeding habitat is widespread, cowbirds may saturate all available breeding habitats (e.g., Thompson et al. in press), in which case parasitization does not decline as a function of distance from feeding areas. Recent studies from a saturated midwestern U.S. landscape, however, show that parasitization levels for some less-preferred hosts decline dramatically with increased distance (up to 1.5 km) from a particularly favored cowbird feeding site (a pig feedlot; Morse and Robinson, in press).

4. At the local scale (within a reserve or tract), patterns affecting the abundance and distribution of cowbirds are far less clear. Local edge effects may be pronounced (e.g., Temple and Cary 1988, Johnson and Temple 1990, Rich et al. 1994,) or absent (e.g., Robinson and Wilcove 1994), and may depend upon landscape context (Donovan et al. 1997). Thompson et al. (in press) argued that edge effects would be most pronounced in landscapes in which cowbird populations were low. Cowbird parasitization levels also may differ profoundly among habitats within a landscape (Hahn and Hatfield 1995), but it is not clear if cowbirds are more abundant in some habitats than they are in others. Cowbird parasitization can be related to tract size (Petit and Petit in press, Robinson et al. in press), but cowbirds can be abundant in large tracts (e.g., Trine, 1998, in press; Trine et al. 1998) and rare in small tracts (e.g., Roth and Johnson 1993, Hoover et al. 1996). Cowbirds appear to prefer sites and habitats where hosts

are more abundant, at least in landscapes in which cowbirds appear to saturate available habitat (Robinson et al. in press).

5. Other conclusions of note from previous studies include the following: (1) Cowbird populations are generally stable or declining in many regions (Lowther 1993, Peterjohn et al. in press, Wiedenfeld in press) with the exception of the northern Great Plains, in which populations continue to increase, and in the Southeast, where several species of cowbirds are still invading new areas such as Florida (Cruz et al. 1998). (2) Cowbird presence may be affected by such features as local availability of perches in grasslands or marshes, cover around nest sites, and vertical strata within forested habitats. In general, however, there are few consistent patterns of cowbird abundance in relation to these microhabitat features (Robinson et al. 1995a). (3) Cowbirds may use certain natural edges such as streams as travel corridors (Gates and Giffen 1991). (4) Winter food availability may strongly determine cowbird populations, although evidence for this remains speculative (Brittingham and Temple 1983).

Now that the orthodox view has been established, I will examine how the papers in this volume, most of which are from western landscapes, fit the established pattern. Specifically, I will use the results presented in volume to check for consistency with the following predictions derived from research in the midwestern U.S.:

(a) Cowbird abundance and parasitization levels should decrease as distance from the Great Plains increases (Hoover and Brittingham 1983, Lowther 1993, Smith and Myers-Smith 1998, Thompson et al. in press).

(b) Cowbird abundance and parasitization levels should be much lower in mostly forested landscapes in which foraging opportunities are limited (Robinson et al. 1995a, Donovan et al. 1997). In landscapes with unlimited foraging habitat, cowbird abundance should be correlated with host abundance (Robinson et al. in press, Thompson et al. in press).

(c) Cowbird abundance should decrease with distance from feeding areas, and should be absent 7 km or further from feeding areas (Rothstein et al. 1984, Thompson 1994, Thompson and Dijak in press).

(d) Cowbirds should be less abundant in habitats with lower parasitization levels (Robinson et al. in press).

(e) At local spatial scales, cowbirds should be most abundant near edges and where hosts are more abundant, but these relationships are likely to vary with landscape context (Donovan et al. 1997).

FIT OF PAPERS TO THE ORTHODOX VIEW

Continental Scale

Most papers in this section support the prediction that cowbird abundance and parasitization levels are greatest in or near their historical center of abundance in the Great Plains. Cowbird abundance or levels of parasitization were generally higher in the midwestern U.S. (Robinson et al., Stribley and Haufler) and central Texas (T. E. Koloszar et al., pers. comm.) than in the Rocky Mountains (Chase and Cruz, Hejl and Young, Tewksbury et al., Wright, and Young and Hutto; C. P. Ortega et al., pers. comm.), California (Farmer, Purcell and Verner, Staab), and Washington (Vander Haegen and Walker). In heavily grazed riparian corridors in Colorado (C. P. Ortega et al., pers. comm.) and fragmented shrubsteppe habitats in Washington (Vander Haegen and Walker), levels of parasitization were generally much lower than in comparably fragmented habitats in Illinois (Robinson et al.). Nevertheless, within each region, cowbirds can be locally abundant in the vicinity of livestock and agriculture (Rocky Mountains; Goguen and Mathews, Hejl and Young, Tewksbury et al., Young and Hutto). Even in the Midwest, cowbirds may be largely absent from large forest tracts (Stribley and Haufler). Cowbird abundance and levels of parasitization in some western communities are at least comparable to those in the Midwest (Farmer, Hochachka et al., Staab and Morrison; see also Averill et al., Chace and Cruz, Greene et al., Kus, Sedgwick and Iko, Whitfield and Sogge from other sections in this volume). Cowbird abundance, therefore, is not solely determined by distance from the cowbird's historical range and conservation problems associated with cowbird parasitization are not confined to the Midwest.

Another challenge to the orthodox view comes from Chace and Cruz's analysis of historical patterns of American bison (*Bison bison*) distribution. Chace and Cruz argue that bison, and therefore cowbirds, may have been much more widely distributed, especially at high elevations, than previously thought. This result suggests the intriguing possibility that cowbirds and their western hosts may have been in contact for a much longer time than previously supposed (see also Rothstein 1994).

Regional Scale

Hochachka et al. provide strong evidence that the relationship between forest cover at the landscape scale and parasitization levels holds across all regions of the U.S. At least at the scale of a 10-km radius around study sites, parasitization

decreases within increasing percent forest cover within all regions of the U.S. for which there are data. The relationship weakens substantially (and may even be reversed) at a 50-km radius, which suggests a strong scale dependence when operationally defining a landscape. Nevertheless, Hochachka et al. provide strong support for the hypothesis that cowbirds may be limited by the availability of feeding sites within mostly forested landscapes (see Goguen and Mathews, Hejl and Young, Stribley and Haufler, Tewksbury et al., Wright, and Young and Hutto for additional evidence of the absence of cowbirds far from feeding sites in mostly forested landscapes).

Landscape Scale

The overwhelming conclusion of most papers in this section is that cowbird distribution and abundance within landscapes is limited by the availability and proximity of feeding sites (reviewed in Goguen and Mathews). Cowbirds were abundant in virtually all study sites in Illinois (with the notable exception of grasslands, see below) in which there are no areas more than 7 km from extensive cowbird feeding habitat. In Michigan, Stribley and Haufler only found cowbirds to be abundant within 3 km of agriculture. In Texas, cowbirds were strongly associated with recently grazed areas on Fort Hood (T. E. Koloszar et al., pers. comm.). In the northern Rockies, Young and Hutto's huge census data set showed that a landscape variable, distance to agricultural land, was by far the strongest correlate of cowbird abundance in multivariate models. Hejl and Young's census data from the same general areas also show that distance to agriculture is the key variable explaining cowbird abundance. In the Idaho wilderness, Wright also found cowbirds only in the vicinity of livestock and park stations. In another area of the northern Rockies, the Bitterroot Valley, Tewksbury et al. found that cowbirds were only found within 4 km of agriculture and that distance to large agricultural areas was the strongest predictor of cowbird occurrence. In a general overview, Goguen and Mathews found a strong association between cattle and cowbird abundance throughout much of the West. Chace and Cruz further argued that the restricted movements of cattle herds can create severe chronic local problems for hosts nesting nearby. Purcell and Verner came to similar conclusions for the southern Sierra Nevada; cowbirds are found mainly at lower elevations because of the proximity of cowbirds during the nesting season.

There were, however, some notable exceptions to this general pattern. Several papers found some evidence for breeding habitat preferences within landscapes (Hejl and Young, Robinson et al., Tewksbury et al., Young and Hutto), some of which may have been related to host density (see below). Farmer found that cowbirds were unaccountably rare at Vandenberg Air Force Base in central coastal California, even in areas where foraging habitat was present. Vander Haegen and Walker found very little parasitization in fragmented shrubsteppe even though there were extensive agricultural areas nearby and cowbirds occurred throughout most study areas. These data suggest that factors operating at a more local scale than the landscape may also be important (see below).

One of the most interesting results from several studies is the extent to which cowbirds may be more flexible in their home range use than generally thought. Many western breeding habitats also provide local foraging habitat as well, which reduces the need for long commutes (Goguen and Mathews 1998). Even more surprising was Goguen and Mathew's (1998) data showing that cowbirds in New Mexico routinely commute 12 km between breeding and feeding areas, a result that breaks the 7-km barrier of Rothstein et al. (1984) and Thompson (1994). The spatial scale at which we examine cowbird abundance and distribution, therefore, may need to be increased beyond the 10-km radius used previously (Robinson et al. 1995a, Hochachka et al. *this volume*). These results are somewhat discouraging for managers who want to eliminate cowbird parasitization by managing cattle herds (Goguen and Mathews *this volume*).

Local Scale

At the scale of the habitat tract or study area, cowbird abundance can be related to (1) habitat type, (2) host abundance, (3) distances from habitat edges, and (4) vegetation structure.

1. Several papers in this volume address the use of different vegetation types (hereafter referred to as habitats) by cowbirds. One of the most striking patterns throughout much of the West is the cowbird's tendency to be most abundant in riparian habitats (Farmer, Hejl and Young, Staab and Morrison, Tewksbury et al., Young and Hutto; see also Averill et al., Kus, Sedgwick and Iko, Spautz, Whitfield and Sogge from other sections of this volume). This result holds when controlling for distance to cowbird foraging habitat (Hejl and Young, Tewksbury et al., Young and Hutto), although many riparian corridors tend to be heavily grazed and therefore provide foraging habitat within them. Cowbird parasitization appears to be contributing to the population declines in and endangered status of Southwestern Willow Flycatchers (*Empidonax traillii extimus*) and Least Bell's Vireos (*Vireo*

bellii pusillus). It is unclear, however, whether cowbirds prefer riparian corridors because of some aspect of their vegetation structure (Staab and Morrison) or because hosts also tend to be most abundant in riparian corridors (Tewksbury et al.). Fortunately for conservation planners, there are riparian corridors in which cowbirds are rare (Farmer), and wider corridors with complex, multi-layered vegetation may be less heavily used by cowbirds (or at least may be more difficult for cowbirds to search; Farmer, and Staab and Morrison).

Another dramatic difference in cowbird use of habitats occurs in the Midwest in which cowbirds are less abundant in grasslands, even heavily grazed ones, than they are in other adjacent habitats, even when controlling for host density (Robinson et al.). The reasons for this apparent avoidance are unclear, although grasslands have few perches from which to search for hosts and many hosts may have effective defenses against parasitization (egg ejecting; Peer et al.; or mobbing cowbirds). The much lower community-wide levels of parasitization in midwestern shrublands and savannas (when compared with forests) does not appear to be a result of lower cowbird abundance in these habitats (Robinson et al.). Rather, these habitats appear to contain a much higher proportion of unsuitable hosts. A similar result was obtained by Vander Haegen and Walker, who found very low levels of parasitization in shrubsteppe habitats in which cowbirds were widespread and relatively common. A lack of suitable perches and the timing of cowbird versus host breeding may explain some of the enigmatically low parasitization levels in fragmented shrubsteppe and other shrublands (e.g., Ellison), but it is also possible that many hosts within these communities have defenses against parasitization. For these reasons, the cowbird:host ratio (Robinson et al. in press, Thompson et al. in press) may not be a good predictor of parasitization levels among habitats.

Otherwise, few consistent patterns of differential habitat use have been documented when controlling for distance to cowbird feeding habitat. Cowbirds avoided steep-sided canyons in the Bitterroot Valley of Montana (Tewksbury et al.). Hejl and Young and Young and Hutto found no consistent association between forest types and cowbird abundance in Montana where cowbirds were not more abundant in logged forests. Robinson et al. found no differences in cowbird abundance (controlling for host abundance) among upland, floodplain, and coniferous forests in Illinois. Purcell and Verner found that cowbirds were most abundant at lower-elevation forests, probably because of proximity to cowbird feeding habitats and host abundance rather than preferences for particular vegetation types (see below).

2. When controlling for proximity to feeding habitat, cowbirds tend to be most abundant in habitats in which hosts are most abundant (Robinson et al., Tewksbury et al., Young and Hutto). Purcell and Verner, however, found that species richness (including non-hosts) was a better predictor of cowbird abundance than host population densities in the Sierra Nevada. The cues used by cowbirds to select habitat is a promising area for future study (see below).

3. Few studies in this volume address the issue of cowbird abundance in relation to edges. Farmer found cowbirds to be most abundant along edges, which is the basis of the recommendation that riparian corridors be as wide as possible. Hejl and Young and Young and Hutto found no evidence that cowbirds were more abundant near silvicultural openings. Many studies, however, showed cowbirds to be most abundant near large agricultural openings (Hejl and Young, Stribley and, Young and Hutto) and near openings in which cowbirds feed (Goguen and Mathews, Wright).

4. The effects of vegetation structure on parasitization is the subject of only one paper in this section. Staab and Morrison found that nests were less likely to be parasitized in riparian corridors with distinct canopy and shrub layers. It is not clear, however, if this difference results from reduced cowbird abundance, or greater difficulty of finding nests in multilayered vegetation (see also Spautz for a discussion of vegetation structure).

Other Factors

Many western hosts may escape parasitization because cowbirds arrive too late in the season (Ellison, Purcell and Verner, Vander Haegen and Walker). Breeding of many western species may be triggered by seasonal rains that occur before the cowbird breeding season, especially in California (Ellison). The timing of cattle movements may also keep cowbirds out of some areas during the host nesting season (Goguen and Mathews, Purcell and Verner).

Cowbirds do not necessarily feed equally in all pastures or other agricultural areas. Cowbird abundance therefore may depend additionally on the kinds of pastures available within a site (Goguen and Mathews; T. E. Koloszar, pers. comm.) and in some areas, row crops may provide suitable cowbird feeding habitat (Thompson 1994, Robinson et al.)

FUTURE RESEARCH QUESTIONS

1. What cues are used by cowbirds to select breeding habitat? There is some evidence that

both host density and overall species richness are used as cues in habitat selection, but definitive experimental studies are lacking. This question is particularly important because there is growing evidence that cowbirds are often attracted to poor habitats with few suitable hosts and high predation rates (e.g., in Illinois shrublands, Robinson et al. *this volume*; the Central Valley of California, Farmer *this volume*; and the northern Great Plains, Davis and Sealy in press, Wiedenfeld in press). Such regions and habitats may act as ecological traps (sensu Gates and Gysel 1978) for cowbirds and might help explain why cowbird populations nationwide are stable or even decreasing through negative feedback on overall populations, as suggested by Rodenhouse et al. (1997).

2. What agricultural lands (row crops, pasture, and open range) provide the best foraging conditions for cowbirds? Our understanding of what makes optimal foraging habitat for cowbirds is still in its infancy. If we are to reduce parasitization through managing cattle movements and agricultural practices, we need more studies such as those of T. E. Koloszar et al. (pers. comm.) and Morris and Thompson (1998). In some areas, row crops may provide high-quality feeding habitat (Thompson 1994, Thompson and Dijak in press).

3. To what extent do cowbirds use foraging sites other than open range, pastures, and row crops? During the symposium, participants listed a wide variety of foraging habitats that cowbirds used when not feeding with cattle or in row crops. Cowbirds may be able to increase their home ranges enormously if they can supplement their diet with food obtained on or near breeding areas.

4. Can cowbirds use human residential areas exclusively, even if there are no cattle or row crops nearby? Anecdotal observations from urban areas in the Midwest suggest that cowbirds spend the afternoon feeding in mowed grass (S. K. Robinson, unpubl. data). If this pattern is widespread, human habitations may be replacing cattle as a feeding habitat in many parts of the country where cattle ranches and farms are being replaced with suburban developments.

5. How flexible are commuting distances of cowbirds? With the results of papers in this section, we now know that there is no 7-km barrier beyond which cowbirds cannot commute (Goguen and Mathews 1998). Yet, many studies show that most cowbird breeding-feeding flights are less than 3 km. Even in the "saturated" Midwest, parasitization levels of some hosts drop to very low levels 1.5 km from cowbird feeding sites (Morse and Robinson in press). In contrast, parasitization levels in some sites in New Mexico can be very high even far (>5 km) from the closest feeding area (Goguen and Mathews 1998). Cowbirds in different regions of the country may respond differently to landscape structure. Additional studies using telemetry to define cowbird home ranges would help determine how cowbirds modify their commuting patters in different landscapes.

6. Do cowbirds select habitats and hosts more efficiently in areas where cowbird abundance is low? Many studies showing less-than-optimal habitat selection and host selection come from regions in which cowbird populations may saturate the landscape (e.g., Robinson et al. *this volume*). In such landscapes, many cowbirds may be forced to use less optimal habitats and hosts. Experimental reduction of cowbird abundance might provide answers to this question.

7. Do cowbirds select breeding home ranges based on foraging habitat or on breeding habitat? The high abundance of cowbirds in many host-poor habitats (e.g., Farmer *this volume*) suggests that cowbirds may be selecting habitats based on foraging rather than breeding. If so, then cowbirds may be highly susceptible to ecological traps (sensu Gates and Gysel 1978).

8. Are there cryptic or as-yet unstudied defenses of many host species that confound our ability to calculate cowbird:host ratios and are such defenses more likely to occur in historical cowbird habitat? To address this question, we need more studies of the ways in which hosts defend their nests against parasitization.

9. Can cowbird parasitization be reduced by altering range management practices? Experimental manipulations of cattle may enable us to develop methods of reducing cowbird abundance in critical habitats during the breeding season (Goguen and Mathews *this volume*).

10. Can cowbird parasitization be reduced through local vegetation management? Removal of woody vegetation from grasslands, maintaining a dense shrub layer in riparian corridors, and promoting complex, shrubby edges have all been proposed as ways of reducing parasitization (e.g., Johnson and Temple 1990, Staab and Morrison *this volume*). Many of these variables can be manipulated as a test of vegetation-based management.

11. Are there enough cowbird-free areas of the West to balance losses in cowbird-dominated landscapes? In the midwestern and eastern U.S. there are huge forest tracts in which cowbird parasitization is not a problem (Robinson et al. 1995b, Coker and Capen in press, Yamasaki et al. in press). There are also areas in the West in which cowbirds are extremely rare, but cattle ranching is also pervasive in the West. Large-

scale spatial models of cowbird abundance may tell us a great deal about the potential balance of sources and sinks for sensitive hosts (Green et al. *this volume*).

12. At what spatial scale can cowbird abundance best be predicted? Hochachka et al.'s (*this volume*) analysis suggests that the scale at which a landscape is defined may be critical for predicting cowbird abundance and levels of parasitization.

13. To what extent are cowbird populations limited by winter food availability? This topic remains poorly studied.

14. To what extent are cowbird populations limited by nutrient (mainly calcium) availability? Some differences in cowbird abundance (and fecundity) may result from regional differences in nutrient availability, which may limit cowbird reproduction (Ankney and Scott 1980, Holford and Roby 1993).