Radio-Tracking Confirms a Unique Diurnal Pattern of Spatial Occurrence in the Parasitic Brown-Headed Cowbird

Author(s): Stephen I. Rothstein, Jared Verner and Ernest Steven

Source: Ecology, Vol. 65, No. 1 (Feb., 1984), pp. 77-88
Published by: Wiley on behalf of the Ecological Society of America
Stable URL: http://www.jstor.org/stable/1939460
Accessed: 11-06-2018 14:19 UTC

REFERENCES
Linked references are available on JSTOR for this article:
You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://about.jstor.org/terms

Wiley, Ecological Society of America are collaborating with JSTOR to digitize, preserve and extend access to Ecology
RADIO-TRACKING CONFIRMS A UNIQUE DIURNAL PATTERN OF SPATIAL OCCURRENCE IN THE PARASITIC BROWN-HEADED COWBIRD

STEPHEN I. ROTHSTEIN
Department of Biological Sciences, University of California, Santa Barbara, California 93106 USA

JARED VERNER
United States Forest Service, Forestry Sciences Laboratory, 2081 E. Sierra Avenue, Fresno, California 93710 USA

AND

ERNEST STEVENS
Department of Biological Sciences, University of California, Santa Barbara, California 93106 USA

Abstract. Brood-parasitic Brown-headed Cowbirds (Molothrus ater) in the eastern Sierra Nevada of California, breed and feed in almost totally disjunct areas that reflect local optima for finding host nests and food, respectively. Radio-tracking showed that five females and four of eight males spent mornings in host-rich habitats such as forests and then commuted 2.1–6.7 km to one or more prime feeding sites such as horse corrals and bird feeders for the rest of the day. The four noncommuting males, which were all yearlings and possibly socially subordinate, also showed high mobility but did not occupy the same area each morning. Since cowbirds lay eggs in the morning and were rarely seen feeding then, the disjunct areas visited by commuters can be characterized as morning-breeding (egg-laying) and afternoon-feeding areas. We found little evidence of territoriality on morning ranges, nor did we find evidence of prolonged pair bonds.

The morning ranges of commuters averaged 68 ha, and their total home ranges, including afternoon-feeding areas, averaged 442 ha. These are among the largest breeding home ranges described for passerines, and they equal those of certain raptors. Raptors require large areas to provide a sufficient prey base, and cowbirds require similarly large areas to provide a sufficient number of host nests. The cowbird’s commuting pattern, which is unique among passerines, involves a shift from largely asocial behavior in the morning to extreme sociality in the afternoon. Unlike related nonparasitic icterids that disperse from central breeding sites to feed, cowbirds do the reverse, dispersing from centralized feeding sites to breed. The commuting behavior of cowbirds is yet another example of the flexibility of a species’ behavioral ecology in response to the dispersion of resources essential for maintenance and reproduction.

Key words: brood parasitism; Brown-headed Cowbird; commuting; dispersion; diurnal; home range; icterid; Molothrus; pair bond; radio-tracking; Sierra Nevada; territoriality.

INTRODUCTION

The use of space by breeding birds is related to resources such as food, nesting sites, and mates. Most birds maintain territories or home ranges that satisfy the food requirements of adults and young in the same area, which is nearly always close to the nest, unless the species is highly mobile (e.g., swallows) or has offspring that can tolerate long periods of starvation (e.g., some seabirds). Parasitic birds, however, are not so limited because survival of their young depends on other species. If one area is not optimal for both locating host nests and feeding by adults, parasitic birds can feed and breed in separate areas. Using data from birds fitted with radiotransmitters, we show that parasitic Brown-headed Cowbirds (Molothrus ater) “commute” daily up to 7 km between disjunct feeding and breeding areas. We also show that this pattern is related directly to the cowbird’s parasitism and feeding niche.

Although previous studies suggested that cowbirds feed and breed in disjunct areas (Payne 1965, 1973a, Kennard 1978, Raim 1978, Rich 1978, S. I. Rothstein, personal observation) they provided no quantitative evidence. Recently, we showed that cowbird numbers at favored feeding sites in the Sierra Nevada of California, such as horse corrals, increase from an average of 1 or fewer in the early morning to 20 or 30 in the afternoon (Rothstein et al. 1980). Two reasons led us to hypothesize that these birds abandoned morning breeding ranges each day and “commuted” to feeding sites. Cowbirds usually lay eggs in the morning (Friedmann 1963) and are regularly found in the morning in Sierran habitats, such as riparian woodlands, that contain many potential hosts. Second, potential hosts oc-
Support for our “commuting hypothesis” was weak. First, the afternoon aggregation was demonstrated at only two sets of horse corrals. Second, we had no evidence that birds in these feeding aggregations were from habitats frequented by breeding cowbirds in the morning. We have since observed cowbird aggregations at other Sierran feeding sites (S. I. Rothstein, et al., personal observation). We have also collected birds from these groups and found that males have breeding-size testes and females have eggs in their oviducts (S. I. Rothstein et al., personal observation). In this paper, we present data from bird counts in breeding habitat throughout the day and on the movements of 13 radio-tagged cowbirds.

METHODS

Bird counts and study areas

To determine if cowbird abundance declined in breeding habitat after morning, we conducted bird counts in June 1979 at 33 sites in or near Sierran forests and riparian zones. Count sites were ≥1.6 km apart and ≥0.5 km from areas where cowbirds were known to feed in the afternoon. All species seen or heard from a fixed point for 10 min during morning, afternoon, and late-afternoon periods (times in Fig. 1) were recorded. The three counts at each site were conducted by the same individual on a single day to control for confounding variables.

All count sites and areas where radio-tagged birds were studied were within 11 km of Mammoth Lakes, Mono County, California (altitudes 2220–2650 m), where most of our previous study (Rothstein et al. 1980) was done. This generally forested region has few human habitations and little foraging habitat for cowbirds. In and near the town of Mammoth Lakes, important afternoon feeding sites include horse corrals with a small adjacent horse pasture (Fig. 2: area A), a large horse pasture (area B), and several bird feeders stocked with “wild-bird seed” (areas E, F, and others noted in subsequent figures). The only feeding sites north of Mammoth Lakes are P, the Deadman Area Campground; N, a highway rest area; and H, the Glass Creek Campground where campers have fed cowbirds since at least 1955 (E. Eaton, personal communication).

The habitat southeast of Mammoth Lakes is mostly sagebrush (Artemisia sp.) scrub, with some areas of scattered Jeffrey pines (Pinus jeffreyi) and riparian woodland (mostly Salix and Populus). An open forest of Jeffrey pine, lodgepole pine (P. contorta), and white fir (Abies concolor) lies north and west of Mammoth Lakes.

Radio-tracking

Capture and processing of birds.—Cowbirds were trapped (dates in Table 1) at feeding site A in the after-
Table 1. Sex, age, capture data, and commuting pattern of radio-tagged Brown-headed Cowbirds. PST = Pacific Standard Time.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Age*</th>
<th>Transmitter</th>
<th>Site†</th>
<th>Date</th>
<th>Time (PST)</th>
<th>Tracked until</th>
<th>Commuting pattern‡</th>
<th>Min. no. days consistent commuting</th>
<th>Max. commuting distance (km)§</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>Y</td>
<td>496</td>
<td>A</td>
<td>10 June 79</td>
<td>1415</td>
<td>17 June</td>
<td>yes</td>
<td>5</td>
<td>2.1</td>
</tr>
<tr>
<td>F</td>
<td>AD</td>
<td>580</td>
<td>A</td>
<td>17 June 80</td>
<td>about 1130</td>
<td>26 June</td>
<td>yes</td>
<td>4</td>
<td>4.3</td>
</tr>
<tr>
<td>F</td>
<td>AD</td>
<td>511</td>
<td>A</td>
<td>17 June 80</td>
<td>afternoon</td>
<td>25 June</td>
<td>yes</td>
<td>6</td>
<td>3.5</td>
</tr>
<tr>
<td>F</td>
<td></td>
<td>749</td>
<td>Inyo Craters</td>
<td>3 July 80</td>
<td>1000</td>
<td>9 July</td>
<td>yes</td>
<td>4</td>
<td>3.8</td>
</tr>
<tr>
<td>F</td>
<td></td>
<td>659</td>
<td>Deadman</td>
<td>16 July 80</td>
<td>1020</td>
<td>23 July</td>
<td>yes</td>
<td>7</td>
<td>3.3</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>201</td>
<td>A</td>
<td>8 June 79</td>
<td>1745</td>
<td>25 June</td>
<td>yes</td>
<td>12</td>
<td>3.6</td>
</tr>
<tr>
<td>M</td>
<td>AD</td>
<td>301</td>
<td>A</td>
<td>13 June 79</td>
<td>1425</td>
<td>24 June</td>
<td>yes</td>
<td>6</td>
<td>4.5</td>
</tr>
<tr>
<td>M</td>
<td>AD</td>
<td>776</td>
<td>Inyo Craters</td>
<td>26 June 80</td>
<td>0920</td>
<td>29 June</td>
<td>yes</td>
<td>4</td>
<td>6.7</td>
</tr>
<tr>
<td>M</td>
<td>AD</td>
<td>861</td>
<td>Inyo Craters</td>
<td>2 July 80</td>
<td>0700</td>
<td>9 July</td>
<td>yes</td>
<td>5</td>
<td>3.6</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>096</td>
<td>A</td>
<td>9 June 79</td>
<td>1520</td>
<td>15 June</td>
<td>no</td>
<td></td>
<td>(1.9)</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>598</td>
<td>A</td>
<td>10 June 79</td>
<td>1235</td>
<td>21 June</td>
<td>no</td>
<td></td>
<td>(1.4)</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>705</td>
<td>A</td>
<td>17 June 80</td>
<td>1145</td>
<td>21 June</td>
<td>no</td>
<td></td>
<td>(1.4)</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>547</td>
<td>Inyo Craters</td>
<td>3 July 80</td>
<td>0645</td>
<td>9 July</td>
<td>no</td>
<td></td>
<td>(6.2)</td>
</tr>
</tbody>
</table>

* Y = yearling; AD = adult, i.e., bird 2 yr old or older.
† A = horse corrals within feeding site A. Inyo Craters and Deadman were in breeding habitat. See Fig. 2.
‡ Yes, if bird consistently occurred in the same area on at least four mornings and if this area was disjunct from areas it occupied in the afternoon.
§ Distance is the longest straight line between any point in a bird's morning range and any feeding site it visited. Figures in parentheses are distances, for noncommuters, between feeding sites and an area that was sometimes occupied in the morning. Male 598 was never located in the morning.
|| These birds were captured and banded at site A in previous years: 580 as an unsexed juvenile (bird of the year) on 3 August 1978, 776 as a yearling male on 6 July 1979, 861 as an adult male on 7 July 1979, and 598 as an unsexed juvenile on 18 August 1978.

noon or netted at breeding sites in the morning (Fig. 2). Radiotransmitters weighing 2.5 g (11 birds) or 5 g (2 birds), with a trailing 20-cm wire antenna (Wildlife Materials, Carbondale, Illinois), were fitted to the birds' backs, using a combination of Raim's (1978) and Martin and Bider's (1978) methods. Transmitters had frequencies between 159.096 and 159.861 MHz, and birds are referred to by their sex and transmitter frequency. Transmitters had a range up to 1.6 km and a life span of 1–2 wk. Radio-tagged cowbirds behaved normally, as found by Dufty (1982) and Raim (1978).

All birds were banded with plastic color bands. Seven of eight males were aged via plumage (Selander and Giller 1960) as either yearlings or adults; females cannot be aged reliably. The remaining male (301) was designated an adult by virtue of its long wing (107.5 mm). Adults have longer wings than yearlings (Johnson et al. 1980); 27 yearlings captured by the same bander who measured male 301 had a mean wing length of 102.8 mm, and none of their wing lengths was as large as that of male 301.

Recording and processing of data.—We often made visual and radio contact with tagged birds, but the former was difficult because birds frequently flew long distances over hilly terrain. The locations of contacts were noted on United States Geological Survey topographical maps with a scale of 1:62500.

For data analyses, we divided the day into 15-min periods (0500–0515, 0515–0530, etc., all times Pacific Standard Time, PST) and graphed a bird's location (if known) during each period, preparing a separate graph for each tracking day. Unsuccessful attempts to locate a bird at a site where it sometimes occurred (negative information) were also graphed. We present summary graphs (e.g., Fig. 3) of the number of days a bird was located at a site during each 15-min period. Detailed "daily" graphs, showing detections of two birds during each of two full days (Fig. 4) illustrate the data base for the summary graphs. Negative data are discussed but are of uncertain significance because radio signals were sometimes undetectable from 200 m or less due to uneven topography.

RESULTS

Bird counts

Thirty cowbirds were detected in the morning but only four and six in the afternoon and late-afternoon periods, respectively. Cowbird detections were noted only in the morning at 13 (68%) of the 19 sites at which the species was found, and clearly declined later in the day (Fig. 1). None of the 11 other common passerine species showed a pattern like the cowbird's. For eight of these species, the most common pattern was detection during all three count periods (Fig. 1: MAL). The number of other passerines declined only moderately, averaging 6.9, 5.3, and 5.5 species detected during the morning, afternoon, and late afternoon, respectively.
Activity patterns of radio-tracked cowbirds

Areas visited by cowbirds were easily designated as either (1) morning ranges (in breeding habitat) or (2) feeding sites. Morning ranges lacked food sources, and cowbirds there were highly mobile and usually perched or flew high above the ground. Cowbirds rarely foraged in morning ranges. By contrast, at feeding sites cowbirds were relatively sedentary, feeding on the ground or on bird feeders; less commonly they rested, perching on the ground, fenceposts, or plants.

Five cowbirds were captured at two sites in breeding habitat, eight at feeding site A (Fig. 2, details in Table 1). Birds captured in breeding areas usually reappeared there on subsequent mornings and visited known feeding sites. Birds captured at the feeding site tended to return on subsequent afternoons, but several days of searching were usually required to find their morning ranges. A bird’s radio frequency was monitored until either its transmitter fell off or its signal failed. Birds were monitored for 4–17 d (x̄ = 8.0 d) after being released.

The 13 birds fell into three categories: (1) commuting females, which moved between predictable morning ranges and disjunct feeding sites; (2) commuting males; (3) noncommuting males, which did not occupy consistent morning ranges.

Females

Habits in morning ranges.—Female 496 had a morning range in a riparian corridor mostly <100 m wide (Fig. 2). Ranges of the other females were in open coniferous forest with some patches of shrubs or small aspens.

Daily movements.—Before the hours of 1100 to 1200, detections were mostly in the morning ranges (Fig. 3). Afterwards they were mostly at feeding sites, except at dusk when the females returned to their morning ranges. Once a female’s morning range was discovered, she was found there nearly every morning before 1100. The morning range of female 496, for example, was not found until 13 June, but she was located there subsequently on 3 d before 1100. By contrast, the females were rarely located at feeding sites before 1100. A receiver was within reception distance of feeding sites A, B, E, or F (Fig. 2) before 1100 during 31 15-min periods; there were only two detections of the four radio-tagged females that used these sites (females 496, 511, 580, and 749). By contrast after 1100 we located the same females at these feeding sites during 123 (64.4%) of 191 15-min blocks. This difference is highly significant (χ² = 34.1, P < .001 for 2 of 31 vs. 123 of 191). Unsuccessful attempts to locate females after 1100 do not necessarily mean these individuals were absent, since the birds were usually on the ground and their signals were thus easily blocked.

The movements of the remaining female (659) were less predictable, although she too occurred mostly in forested areas (morning ranges 1, 2, and 3) before 1100 and at feeding sites (H and P) at later times (Figs. 2 and 3). This female’s pattern reflects the presence of feeding site P within her morning range. She made brief visits to P before 1100 on four of the five mornings she was tracked and was foraging on the ground at campsites each of the three times she was seen. This feeding may have enabled her to remain longer on her
morning ranges, as she occurred there after 1100 more often than other females (Fig. 3). Fig. 4 shows 2 d of tracking data for female 659. The first day, 20 July, was the only day she failed to commute to feeding site H. The second day, 22 July, was the only day she failed to visit feeding site P before 1100; it was also the only time she flew to feeding site H before 1100.

Because we rarely checked morning ranges after 1000, we cannot dismiss the possibility that birds returned there briefly in the afternoon. However, all females were followed continuously at feeding sites for 1 h or more during midday on at least two days, and none ever left the feeding areas. Females returned to their morning ranges just before dark. Except for one failure to locate female 659 after 1900, each female was located on her morning range just before dark on every occasion she was sought (two to five evenings for each female, see also Fig. 3). The two females whose exact evening locations were determined apparently roosted alone in parts of their morning ranges closest to feeding areas.

Interactions with conspecifics, and other behavior.—All females, except 496, were followed on their morning ranges and observed frequently for at least 1.5 h on two or more mornings. The females were generally silent during the morning and usually flew frequently, often quickly crossing their entire morning range (Fig. 4). Occasionally they remained in one spot for 10–20 min. Because of the females' mobility, the sizes of morning ranges increased little after the first day or two of tracking. By contrast, females showed little movement in their morning ranges later in the day. For example, female 749 stayed in her morning range on 6 July until at least 1300, and from 1121 to 1300 she perched in the location at which she roosted on two nights; she later commuted to feeding site E. At feeding sites, females usually foraged silently on the ground or at a feeder with 5–30 or more other cowbirds.

Females showed varying degrees of association with males. In their morning ranges, females 580 and 511 were usually accompanied by one and at times two or three males. The males gave occasional flight whistles, songs (see Friedmann 1929:166), and single-syllable flight calls and several times appeared to chase the females. Another female and two males were often in the vicinity of female 749, but she apparently traveled alone on her morning range, even though a male whose morning range partially overlapped hers commuted to the same bird feeders (male 861, Figs. 5 and 6). Only female 659 associated with an identifiable (banded) male. This male, PY (no radio), was banded at feeding site A in 1978 as an independent juvenile. He and female 659 foraged together with no other birds two
Commuting males

Habitats in morning ranges.—Three of the four males had morning ranges in areas of open coniferous forest with varying amounts of shrubby openings. The fourth, male 301, occupied a morning range that included a shrubby slope with scattered Jeffrey pines and a riparian association of tall aspens, willows, and scattered conifers.

Daily movements.—As with the females, detections before 1100–1200 were mostly in morning ranges (Figs. 5 and 6). Later in the day, nearly all detections were at feeding sites, most of which were bird feeders. Male 301 roosted alone in the same patch of brush on each of the three nights his morning range was checked after 1900 (Fig. 6). The other males were not located at nightfall, but all had morning ranges with topography that could have blocked radio signals. As with females, the low temporal overlap in the commuting male’s detections at morning ranges and feeding sites (Fig. 6) was not due to our field techniques. Once a male’s morning range was known, attempts to locate him there before 1100 were nearly always successful. By contrast, attempts to locate these males before 1100 at feeding sites usually failed. However, male 301, whose morning range was near feeding site A (Fig. 5), occasionally made brief trips to the site before 1100 (Fig. 6). Males were highly mobile both in the morning and afternoon; e.g., male 301’s movements on 22 and 23 June (Figs. 4 and 5) covered 510 and 550 ha, respectively.

Male 776 was the only bird hindered by a transmitter. On 28 June, he was found in his morning range unable to fly, his bill tangled in threads securing the transmitter. After his transmitter attachment was strengthened, male 776 flew off normally but was never detected after 29 June, suggesting that he again became disabled. Although we have only four days of data, we have designated male 776 as a commuter because he occurred in the same breeding area and commuted long distances to feed at sites A, B, and D (Figs. 5 and 6) each day. The two 15-min blocks showing male 776 in his morning range in the late afternoon (Fig. 6) occurred on the day of his capture, when he may have been affected by our handling.

Interactions with conspecifics, and other behavior.—Unlike females, males at feeding sites were vocal, often directing song-spreads and other displays to males and females. All four males were followed on their morning ranges for 2 h or more on at least two days. Like fe-
Table 2. Numbers and spatial spread of feeding sites visited by radio-tagged Brown-headed Cowbirds. PST = Pacific Standard Time.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Age</th>
<th>Transmitter</th>
<th>No. days located after 1000 (PST)</th>
<th>Total no. feeding sites visited</th>
<th>Total no. feeding sites + sites between 1000</th>
<th>No. feeding sites visited each day*</th>
<th>Max. distance between feeding sites (km)</th>
<th>Area of total home range (ha)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td></td>
<td>496</td>
<td>6</td>
<td>1</td>
<td>0.17</td>
<td>1.00</td>
<td>0.0</td>
<td>70</td>
</tr>
<tr>
<td>F</td>
<td>AD</td>
<td>580</td>
<td>8</td>
<td>2</td>
<td>0.25</td>
<td>1.25</td>
<td>1.5</td>
<td>435</td>
</tr>
<tr>
<td>F</td>
<td></td>
<td>511</td>
<td>6</td>
<td>2</td>
<td>0.33</td>
<td>1.17</td>
<td>1.5</td>
<td>325</td>
</tr>
<tr>
<td>F</td>
<td></td>
<td>749</td>
<td>5</td>
<td>2</td>
<td>0.40</td>
<td>1.60</td>
<td>0.3</td>
<td>285</td>
</tr>
<tr>
<td>F</td>
<td></td>
<td>659</td>
<td>5</td>
<td>1</td>
<td>0.20</td>
<td>1.00</td>
<td>0.0</td>
<td>405</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>201</td>
<td>10</td>
<td>4</td>
<td>0.40</td>
<td>1.60</td>
<td>2.5</td>
<td>385</td>
</tr>
<tr>
<td>M</td>
<td>AD</td>
<td>301</td>
<td>10</td>
<td>5</td>
<td>0.50</td>
<td>1.70</td>
<td>2.5</td>
<td>695</td>
</tr>
<tr>
<td>M</td>
<td>AD</td>
<td>776</td>
<td>3</td>
<td>3</td>
<td>1.00</td>
<td>2.33</td>
<td>1.5</td>
<td>1025</td>
</tr>
<tr>
<td>M</td>
<td>AD</td>
<td>861</td>
<td>5</td>
<td>2</td>
<td>0.40</td>
<td>1.80</td>
<td>0.3</td>
<td>350</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>096</td>
<td>4</td>
<td>2</td>
<td>0.50</td>
<td>1.25</td>
<td>1.2</td>
<td>205</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>598</td>
<td>8</td>
<td>2</td>
<td>0.25</td>
<td>1.13</td>
<td>2.1</td>
<td>300</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>705</td>
<td>2</td>
<td>3</td>
<td>1.50</td>
<td>1.50</td>
<td>1.9</td>
<td>195</td>
</tr>
<tr>
<td>M</td>
<td>Y</td>
<td>547</td>
<td>4</td>
<td>3</td>
<td>0.75</td>
<td>1.25</td>
<td>1.1</td>
<td>575</td>
</tr>
</tbody>
</table>

P (Mann-Whitney U tests) for females vs. males .43 < .01 < .01 .02 .14 .26

* Figures are the mean for the number of sites per day at which each bird was located, counting only days on which it was located after 1000.
† Area, to nearest 5 ha, of a polygon enclosing all the points (morning ranges, feeding sites, and roost) at which each individual was located.

Males, the males showed great mobility, often quickly flying across their entire morning range. Unlike females, males were highly vocal, giving frequent flight whistles, songs, and single-syllable calls.

Males often traveled with females while on their morning ranges. The most closely watched male, 201, was with a female roughly 60% of the time, and on four brief occasions, two females were in his immediate vicinity. Male 201 often directed songs towards the female from 2 m or less, but he sometimes deserted her, flying long distances, so no permanent bond was suggested. Although other males frequently occurred in morning ranges, they only occasionally precipitated agonistic interactions. Most interactions occurred when no females were present and, except for one fight involving pecks and feather pulling, involved exchanges of head-up and song-spread displays (Norman et al. 1977).

Noncommuting males

Four males did not show regular morning visits to a particular area of breeding habitat. Male 096, for example, visited a potential breeding area on one morning but a meadow 3 km away the next two mornings. We designated this meadow a feeding site, rather than a morning range, because male 096 was feeding every time he was seen there. Similarly, male 705 was in one meadow on two consecutive mornings but was not detected there the next four mornings. These noncommuting males were sedentary and rarely vocalized while in potential breeding habitat. Unlike the commuters, the four noncommuters were detected in the morning at feeding sites as often as in potential morning ranges. Three of the noncommuters occurred at a nocturnal blackbird roost. The roost was on a steep, brush-covered hillside 2.3 km southwest of feeding site A and was used mostly by Brewer's Blackbirds (Euphagus cyanocephalus). Males 547 (in 1980), 598 (in 1979), and 096 (in 1979) used the roost on at least one, two, and three nights, respectively. None of the females or commuting males was detected at the roost. Thus the noncommuting males differed from the commuters by their: (1) lack of a consistently occupied morning range; (2) silent, sedentary behavior; (3) frequent morning detections at feeding sites; and (4) use of a communal roost.

Persistence of commuting patterns

The nine commuters showed consistent patterns for at least 4–12 d. Since all but one commuter, male 776, continued its pattern until its transmitter failed, we suspect that once a morning range is established, most birds commute regularly for much or all of the breeding season. Stability is further suggested by sight records. Male 201 was seen in his morning range 11 d after we ceased tracking him and was recaptured the next day at feeding site A (Fig. 6). In our only attempt to locate a bird in a subsequent year, female 659 was quickly found in July 1981 feeding alone at site P during the late morning, just as she had done in 1980.

Comparisons among radio-tracked birds

All females but only half of the males commuted. This difference is probably related to age, as all three
adult males but only one of five yearlings maintained morning ranges, a difference that was suggestive but not significant (P = .07 for 3 of 3 vs. 1 of 5, Fisher Exact Test [Siegel 1956]). Significantly fewer yearling males than females maintained morning ranges (P ≤ .025 for 1 of 5 vs. 5 of 5), suggesting the influence of both age and sex.

Males visited more feeding sites than did females. Considering only feeding sites that were disjunct from morning ranges, females visited a mean of 1.6 sites and males a mean of 3.0 (Table 2). Bias in this comparison is unlikely because individuals of each sex were located after 1000 (when most feeding began) on similar numbers of days (Table 2). Both the number of feeding sites visited and the number of sites per day located after 1000 are significantly greater for males (Table 2). Even on a daily basis, males visited more sites. For example, one male visited three different feeding sites on each of 2 d (Fig. 4), whereas females usually stayed at a site. The number of sites visited each day a bird was tracked, 1.00–1.60 sites for females and 1.13–2.33 sites for males, was significantly different (Table 2). Males tended to travel farther between feeding sites. The maximum distance between sites averaged 1.1 km for the three females that visited more than one site and 1.6 km for the eight males, but the difference was not significant (Table 2). A last measure of the larger feeding ranges of males is the size differences between morning ranges (Figs. 2 and 5) and total home ranges (Table 2). The difference is 325–970 ha for commuting males and 30–385 ha for females and is significant (P = .03, Mann-Whitney U test), although the total home ranges of males and females were similar in size (Table 2).

**DISCUSSION**

**Bird counts**

At most sites, cowbirds were detected only during the morning, whereas other species were usually detected during all three time periods. The decline in cowbird detections after morning was not due to retreat during all three time periods. The decline in the morning, whereas other species were usually detected male cowbirds showed they are highly vocal reduced conspicuousness because observations of radio-tracking (Bailey et al. 1953) travel between disjunct breeding and feeding areas, but these species differ from the cowbird in important ways: (1) the birds commute shorter distances; (2) they are social throughout the day; (3) they make many round trips each day; (4) they do not abandon their breeding areas for half or more of the day. Also because these species breed colonially, they occur with the least predictability (Horn 1968) and in the smallest group sizes while feeding, whereas cowbirds are most predictable in occurrence and most aggregated when feeding. Essentially, nonparasitic icterids disperse from clustered breeding sites to feed, whereas cowbirds do the reverse.

The cowbird’s commuting pattern is related both to its parasitic breeding and to its preference or requirement for special foraging habitat. The importance of freedom from parental care is suggested by the fact that early in the breeding season before eggs are present, nonparasitic icterids such as Red-winged Blackbirds (Agelaius phoeniceus) show a commuting pattern similar to the cowbird’s, abandoning breeding marshes for long periods to travel to rich feeding habitat (Orians 1961). Commuting is absent in some parasitic birds. Males of some honeyguides (Friedmann 1955, Cronin and Sherman 1977), all or most of which are parasitic, and viduines (Payne 1973b, Payne and Payne 1977) occupy call sites throughout the day and feed near these sites, although females are more mobile. This lack of commuting in other parasitic birds shows that the cowbird’s pattern is due to both liberation from parental duties and the use of special feeding sites. Other species of parasitic cowbirds also feed preferentially with large

...
mammals (Friedmann 1929). Whether these cowbirds commute is unknown but likely, because they are highly mobile (R. Fraga and P. Mason, personal communication). Similarly, the parasitic Common Cuckoo (Cuculus canorus), which also exploits a special food source, hairy caterpillars, may also be a commuter. However, the limited radiotelemetry data available (Wyllie 1981) indicate that commuting is much more irregular in Common Cuckoos than in Sierran cowbirds.

Geographic variation in cowbird dispersion patterns

The commuting behavior of the Brown-headed Cowbird varies geographically in response to the distribution of hosts and feeding sites. A radio-tracking study on the west slope of the Sierra Nevada, where a different race exists (Molothrus ater artemisiae on the east slope, M. a. obscurus on the west (Grinnell and Miller 1944)), found that cowbirds there also show considerable mobility and commuting (J. Verner, personal observation). Some, however, stay near their morning ranges all day because of adjacent good feeding habitat: lush meadows with grazing livestock. Smith (1981) suggested that cowbirds breeding on small offshore islands near Vancouver Island feed on larger islands up to 7 km away. From the cowbird’s perspective, the Sierra Nevada may also be an island system, but the islands are scattered feeding sites in a “sea” of breeding habitat.

In most regions outside of the Sierra Nevada and true island systems, agriculture is so widespread that much of the habitat rich in hosts is relatively close to preferred feeding sites. Although studies in other regions suggest that commuting sometimes occurs (Payne 1965, 1973a, Kennard 1978, Raim 1978, Rich 1978), the behavior is generally less pronounced. Raim (1978: 330), for example, noted that radio-tagged cowbirds in the Midwest, USA, “. . . flew about 1.5 km to afternoon flock-feeding areas. . . .” By contrast, the shortest commuting distance in our study was 2.1 km (Table 1), and the mean was 4.0 km. Furthermore, temporal and spatial overlap of breeding and feeding activities is probably greater outside of the Sierra Nevada. For example, cowbirds radio-tracked in New York spent much of the late afternoon in their breeding ranges and also fed there (Dufty 1982). Similarly, S. I. Rothstein (personal observation) found that a color-marked pair, but rarely other cowbirds, fed together throughout the day for at least half the breeding season in a suburban habitat at Santa Barbara, California. Clearly, cowbirds are opportunistic in their use of feeding sites; even in the present study female 659, the only bird with a feeding site (P, Fig. 2) adjacent to a morning range, fed at the site in the morning (Figs. 2, 3, and 4).

Elliott (1980) found no spatial separation of breeding and feeding activities in prairie habitat. The prairie, which constitutes continuous feeding habitat, was the original center of cowbird abundance in North America (Mayfield 1965). Currently, cowbirds in the prairie are highly mobile (Elliott 1980), and under primeval conditions they may have followed herds of bison over even larger areas (Friedmann 1929). Starting with this high mobility, the cowbird may have developed, or at least accentuated, its commuting pattern over the last 200–300 yr as it expanded over much of the continent.

Commuting and colonization of the Sierra Nevada

Cowbirds began to colonize the Sierra Nevada only ≈50 yr ago and did not reach some areas until 1968 (Rothstein et al. 1980). Our data suggest that Sierran cowbirds require manmade feeding habitat. Thus human influence at a single site, such as at a pack station or bird feeder, may allow commuting cowbirds to occupy a large area of otherwise natural Sierran habitat. Because of the rapid increase in area with distance from a site, many birds should show commuting distances that approach the maximum for the population. Since no bird we studied commuted >7 km (Table 1), it is likely that few individuals commuted longer distances. However, few sites in our overall study area were farther than 7 km from a manmade food source, so 7 km may not represent a cowbird’s maximum capability. In the winter, icterids sometimes commute 40 km or more between feeding sites and social roosts (Meanley 1971, Bray et al. 1979).

Possible costs of commuting

The temporal and spatial separation of feeding and breeding sites imposes energetic costs. The cowbirds we studied rarely fed for the first 5 h or more after sunrise. This problem is exacerbated by the nightly demands of thermoregulation, which are relatively great in our high-altitude study area. Frost is common, and temperature minima average 4°C during the cowbird’s peak laying period in June. A related species, the Tri-colored Blackbird (Agelaius tricolor), which breeds at low altitudes, appears to benefit from early morning feeding since there is a mass feeding flight at dawn (Orians 1961).

Some commuters that had morning ranges near feeding sites (females 496 and 659, male 301) visited these sites briefly in the morning, suggesting that they were stressed by the lack of feeding. If food stress occurs, it is likely to be more severe for females because their energetic costs of reproduction are probably greater (King 1972). This may explain why females spend more time at feeding sites and less time traveling between them (Table 2). Also only females show a significant peak in feeding just before dark (Rothstein et al. 1980: Fig. 2b).

Defense of space and local dominance

Because they fed communally, our cowbirds clearly did not defend territories for the entire day. Moreover,
we have no clear evidence of territoriality for just the morning period. Groups of males, and less frequently of females, occurred in morning ranges, and there were only occasional agonistic interactions between members of the same sex. Most interactions among males occurred while females were not nearby, and thus they were not over immediate access to mates. We suggest that individuals of both sexes attempt to establish local dominance in morning ranges and may even succeed in excluding some socially subordinate birds. The critical resources contained in morning ranges are almost certainly host nests for females and females in the case of males.

Site-based dominance and spatial exclusion of subordinates may explain why adult males seem to maintain morning ranges more regularly than yearlings. In some nonparasitic icterids, adult males typically dominate yearlings, and many of the latter do not win breeding territories (Willson 1966, Searcy 1979). Yearling cowbirds in our study may have been subordinate, as suggested by Friedmann (1929:87) for the Shiny Cowbird (M. bonariensis). The irregular behavior of the yearling noncommuters suggests that they were "prospecting" for breeding ranges. Previous studies have produced conflicting evidence on differential dominance and mating success of yearling and adult male cowbirds (Payne 1973a, Darley 1978, Ankeny and Scott 1982, Dufty 1982). Such differentials are especially likely in our area, since the degree to which males outnumber, and hence compete for, females seems most extreme there (Rothstein et al. 1980).

The apparent lack of territoriality in our study differs from studies in the eastern United States (Dufty 1982), which have shown that females (but not males) defend territories. In Kansas, Elliott (1980) like us found little evidence for territoriality. Thus the degree of spatial defense and exclusiveness shown by cowbirds, especially females, varies geographically. Sierran cowbirds may show reduced territorial defense because cowbird density is low and the available "host habitat" is not filled up. Thus female cowbirds may conform to a widespread trend (Davies 1978), with territoriality most prevalent at moderate cowbird densities such as prevail in the eastern United States. At high densities, as in Kansas (Van Velzen 1972), defense of space may be too costly. At low densities, as in the Sierra Nevada, defense may provide too few benefits.

Sizes of morning ranges

Home range in birds and mammals increases with body mass and is largest for species that take the highest proportion of animal foods (McNab 1963, Schoener 1968, Baker and Mewaldt 1978, Harestad and Bunnell 1979). The morning ranges of our nine commuting cowbirds averaged 68 ha. By contrast, a bird with the diet and mass of the cowbird (35-37 g for females, 40-45 g for males, based on locally captured birds) should have a range of 1-3 ha (Schoener 1968: Fig. 2). This disparity is even greater if the total home ranges (\( \bar{x} = 405 \) ha, Table 2) are considered. Among the passerines in Schoener's (1968) analyses, only the largest, the Common Raven (Corvus corax), has a range size that exceeds the morning ranges in our study. Among the passerines Schoener excluded, some colonially nesting species, such as the Tricolored Blackbird, may have larger ranges than cowbirds. Tricolors travel up to 6.4 km from their colonies (Orians 1961), giving a potential maximum (i.e., circular) home range of nearly 13 000 ha. However, such colonies usually have > 1000 females, so the area per bird is < 13 ha. By contrast our female cowbirds had morning ranges averaging 78 ha.

The unexpectedly large home ranges in cowbirds, on both absolute and per bird bases, seem clearly related to resources. Food is the major determinant of most avian home range sizes (Schoener 1968), but for Sierran cowbirds the important resource is host nests. If cowbird breeding ranges were the same size as those of similar-sized passerines (i.e., \( \leq 3 \) ha), only one or two host nests of each host species would be available, since none of the hosts is a colonial breeder (Rothstein et al. 1980). Because there are only six to seven species per site, such small morning ranges would limit female cowbirds to roughly 10-15 host nests per season. By contrast, cowbirds lay from 15 to 40 or more eggs per season (Payne 1965, 1973a, 1976, Scott and Ankeny 1979, 1980). We suggest that the cowbird's use of space is analogous to that of avian predators. The morning ranges of our cowbirds were nearly as large as the ranges of accipiter hawks (Craighead and Craighead 1956), which also exploit passerines in wooded or brushy areas. Although accipiters and cowbirds occupy different trophic levels, their home range sizes may be similar because reproduction of both depends on the same trophic group, passerines.

The morning ranges in our study are considerably larger than the mean of 20.4 ha that Dufty (1982) found for the "non-feeding ranges" of New York cowbirds. This difference probably relates to two factors. First, cowbirds are much less common in the Sierra Nevada than in most lowland regions (S.I. Rothstein, personal observation), and morning range size may be inversely correlated with the density of conspecifics. Second, host density was probably greater in Dufty's study. Dufty worked in deciduous forest and old-field habitats with higher bird densities than the open coniferous forests used by most of our birds. Significantly, the smallest morning range in our study (female 496, Fig. 2) was in dense riparian vegetation. Cowbirds probably prefer such habitat. Elsewhere, they preferentially parasitize birds in habitats that have the highest host densities (Gates and Gysel 1978), and our counts (Rothstein et al. 1980) show that cowbird density is greater in riparian habitat than in open coniferous forests.
Mating system

Cowbirds are variously reported to be monogamous (Friedmann 1929, Laskey 1950, Darley 1978), polygynous (Payne 1973a, West et al. 1981), or promiscuous (Elliott 1980). Ankney and Scott (1982) suggest that this variation is an artifact of different research methods, but we believe that some of it is real. Dufty’s (1981, 1982) New York study, which also used radiotelemetry, suggests long-term monogamy due to mate guarding by males (type 3 monogamy of Wüstenberg and Tilson [1980]), whereas our observations suggest little monogamy. Males in both studies followed females, but we often saw males desert females, an event Dufty rarely saw. Dufty’s females were closely accompanied by males except in the morning when they were sometimes stationary and presumably watching hosts. By contrast, our females were often alone while they moved over their morning ranges and sometimes for long periods while feeding. Also, the two females seen at night-fall apparently roosted alone. The large distances over which Sierran cowbirds move may make it difficult for males to guard females continuously or to maintain the site-based dominance necessary for exclusive access to a female (Dufty 1982).

Males visited more feeding sites than did females (Table 2), perhaps enabling them to maximize their opportunities for copulations by establishing temporary bonds with many females. Also, demonstrating dominance to both males and females at feeding sites may have given males greater access to females at later times. Even relatively subordinate males might benefit by visiting a large number of feeding sites since they may eventually find a site that at least temporarily lacks males that dominate them.

Acknowledgments

We thank L. Bevier, P. Lehman, T. Martin, and especially G. N. Fugle for assistance with fieldwork. The manuscript was improved greatly via the comments of G. W. Cox, A. Cruz, A. M. Dufty Jr., H. Friedmann, and R. B. Payne. D. Mustard provided a heroic typing effort during preparation of the manuscript. We thank numerous residents of Mammoth Lakes, campers, and especially the operators of pack stations for tolerating our frequent visits. Housing and facilities were provided by the Valentine Eastern Sierra Reserve maintained by the University of California. Funding was provided by the United States Forest Service Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA. Trade names and commercial enterprises or products are mentioned in this article solely for information. No endorsement by the United States Department of Agriculture is implied.

Literature Cited


Friedmann, H. 1929. The cowbirds, a study in the biology of social parasitism. C. C. Thomas, Springfield, Illinois, USA.
Grinnell, J., and A. H. Miller. 1944. The distribution of the birds of California. Pacific Coast Avifauna 27, Cooper Ornithological Society, Los Angeles, California, USA.


