



COMMUNITY-LEVEL PATTERNS OF HOST USE BY THE BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*), A GENERALIST BROOD PARASITE

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ABSTRACT.—Quantifying community-level host use by generalist brood parasites is important because it provides a measure of the resources that parasites need for reproduction. During the 2002–2007 breeding seasons, we quantified host use by the Brown-headed Cowbird (*Molothrus ater*) at Konza Prairie Biological Station in northeast Kansas. Overall, 54.4% of nests ($n = 2,621$) of 22 passerine host species that typically accept parasitic eggs were parasitized, and parasitized nests contained an average of 1.9 ± 1.03 (SD) Brown-headed Cowbird eggs, nestlings, or both. Multiple parasitism was common on the study site in all years: 55.7% of parasitized nests ($n = 1,425$) received ≥ 2 Brown-headed Cowbird eggs. The Bell's Vireo (*Vireo bellii*; 70.5%) and the Dickcissel (*Spiza americana*; 69.6%) were parasitized at a significantly greater rate than the Red-winged Blackbird (*Agelaius phoeniceus*, 21.9%); collectively, these three species represented 85.8% of potential host nests found in all years. The host preference of Brown-headed Cowbirds did not appear to shift among the three species and instead they exhibited a consistent preference for Dickcissel nests over the course of the breeding season and among years. Both the rate and the intensity of parasitism on Dickcissels were significantly lower during the present study than in one conducted several decades earlier at the same site. Our results indicate that cowbirds in northeast Kansas differentially parasitize hosts, that most cowbird eggs are laid in the nests of a small number of host species, and that the Dickcissel appears to be preferred over other hosts. Received 20 August 2008, accepted 1 September 2009.

Key words: *Agelaius phoeniceus*, Bell's Vireo, brood parasitism, community-level parasitism, Dickcissel, host use, *Molothrus ater*, multiple parasitism, Red-winged Blackbird, *Spiza americana*, *Vireo bellii*.

Patrones Comunitarios de Uso de Hospederos por parte de *Molothrus ater*, un Parásito de Nido Generalista

RESUMEN.—La cuantificación del uso de hospederos a nivel comunitario por parte de parásitos de nido generalistas es importante porque representa una medida de los recursos que los parásitos necesitan para la reproducción. Durante los periodos reproductivos de los años 2002 a 2007, cuantificamos el uso de hospederos por parte de individuos de *Molothrus ater* en la Estación Biológica Konza Prairie en el noreste de Kansas. En total, el 54.4% de los nidos ($n = 2,621$) de 22 especies de hospederos paseriformes que típicamente aceptan huevos de parásitos estuvieron parasitados y los nidos parasitados tuvieron en promedio 1.9 ± 1.03 (DE) huevos y/o polluelos de *M. ater*. En todos los años, el parasitismo múltiple fue común en el sitio de estudio: 55.7% de los nidos parasitados ($n = 1,425$) recibieron ≥ 2 huevos de *M. ater*. Los nidos de *Vireo bellii* (70.5%) y de *Spiza americana* (69.6%) fueron parasitados con una tasa significativamente mayor que los nidos de *Agelaius phoeniceus* (21.9%). De forma colectiva, estas tres especies representaron el 85.8% de los nidos hospederos potenciales durante los años de estudio. La preferencia por parte de *M. ater* entre las tres especies de hospedero no pareció cambiar, y en cambio presentaron una preferencia consistente por los nidos de *A. phoeniceus* durante el periodo de cría y entre años. Tanto la tasa como la intensidad de parasitismo sobre *A. phoeniceus* fueron significativamente más bajas durante este estudio que durante uno realizado varias décadas antes en el mismo sitio. Nuestros resultados indican que los individuos de *M. ater* en el noreste de Kansas parasitan hospederos de forma diferencial, que la mayoría de los huevos de *M. ater* son puestos en nidos de un número pequeño de especies hospederas y que los nidos de *A. phoeniceus* parecen ser los preferidos con relación a los nidos de las otras especies de hospederos.

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MUCH RESEARCH HAS documented the effects of obligate avian brood parasites on host populations, especially endangered passerines that have small, geographically limited ranges (e.g., Robinson et al. 1995, Kosteke et al. 2005, Kus and Whitfield 2005). Because the entire host community has the potential to affect endangered host species used by generalist brood parasites (e.g., Grzybowski and Pease 1999), a key component of understanding the influence of brood parasites on their hosts is to document variation in host-use patterns across different spatial and temporal scales (Thompson et al. 2000, Chace et al. 2005, Jensen and Cully 2005b). The Brown-headed Cowbird (*Molothrus ater*; hereafter “cowbird”) is one of the most extreme generalists among avian brood parasites, its young having been raised by at least 144 of the more than 220 host species that it is known to have parasitized (Friedmann and Kiff 1985, Lowther 1993, Ortega 1998). Understanding cowbird host use is important because parasitism can lead to a complete loss of fitness for small hosts during a given breeding attempt, including several threatened species with small populations (Kosteke et al. 2005, Kus and Whitfield 2005, Kosciuch and Sandercock 2008). However, documentation of host use by cowbirds is challenging because individual female cowbirds may parasitize different host species within a given community (Alderson et al. 1999, Hahn et al. 1999, Woolfenden et al. 2004, Strausberger and Ashley 2005). Nevertheless, a growing body of work has provided a basis for understanding how cowbirds select hosts at the community level, and these studies have revealed that cowbirds typically parasitize a subset of available species nonrandomly and that parasitism frequency varies with local cowbird and host densities across different spatial and temporal scales (Hahn and Hatfield 1995, Strausberger and Ashley 1997, Strausberger 1998, Woolfenden et al. 2004, Chace et al. 2005, Patten et al. 2006). Despite these previous efforts, studies with robust sample sizes that are collected over an extended period of time (i.e., >5 years) at a single location are still lacking. This is important, because such studies would allow for a more complete understanding of interactions between brood parasites and their hosts at the community level and of how parasitism patterns may fluctuate over time.

We investigated community-level patterns of cowbird parasitism at Konza Prairie Biological Station in northeast Kansas and used a large observational data set to address three objectives aimed at understanding host use by cowbirds at the community level. First, we quantified patterns of parasitism rate (i.e., the proportion of nests that contained at least 1 cowbird offspring) and parasitism intensity (i.e., the mean number of cowbird offspring per parasitized nest) among the primary hosts at Konza Prairie to determine variation in host use by cowbirds. We also assessed apparent cowbird preference to determine which host(s), if any, was preferred by laying females. Our second objective was to determine whether the apparent preference of cowbirds for particular hosts changed over the course of a breeding season. In the Great Plains, Dickcissels begin breeding ≥ 3 weeks later than most other passerine hosts (Fretwell 1986, Jensen and Cully 2005b), and our anecdotal observations suggested that parasitism shifted from the Red-winged Blackbird (hereafter “blackbird”) to the Dickcissel when the latter started to nest on the study site (see Table 1 for the scientific names of the cowbird hosts examined in this study). Therefore, we assessed temporal patterns of parasitism among four major host groups during our two most intensively studied

breeding seasons to determine whether a within-season shift in cowbird host preference occurred. Our final objective was to determine whether cowbird parasitism of a key host, the Dickcissel, changed over a period of several decades at Konza Prairie. To do this, we compared data on cowbird parasitism on Dickcissels that were collected during the current study period (2002–2007) with data from a study conducted by Zimmerman (1983) during 1965–1979 at the same location.

Because our study site is located near the center of cowbird abundance within recent historical times (Lowther 1993), it is notably different from most previous community-level studies of host use, which have been conducted in forested areas, cropped landscapes, or urban areas interspersed with trees and shrubs (Hahn and Hatfield 1995, Strausberger 1998, Robinson et al. 1999, Woolfenden et al. 2004). Although three previous studies have been conducted in grassland habitats within the current center of cowbird abundance, these studies were limited to relating the rates of parasitism on the five most abundant host species to habitat features (Patten et al. 2006) or were conducted over short periods (Elliott 1978, Fleischer 1986). Thus, our data add substantially to previous knowledge because we assessed apparent host preference and quantified cowbird parasitism over an entire community of potential hosts over six consecutive breeding seasons.

METHODS

Study location.—This research was conducted during the 2002–2007 breeding seasons at the 3,487-ha Konza Prairie Biological Station (hereafter “Konza Prairie”) in the northern Flint Hills region of northeast Kansas (39°05'N, 96°35'W), a region dominated by large expanses of tallgrass prairie. Konza Prairie is subdivided into ~60 experimental watersheds, each of which is assigned one fire treatment (i.e., fire applied at 1-, 2-, 4-, 10-, or 20-year intervals) and one grazing treatment (i.e., ungrazed or grazed by Domestic Cattle [*Bos taurus*] or American Bison [*Bos bison*]). Native warm-season grasses (e.g., Big Bluestem [*Andropogon gerardii*] and Indiangrass [*Sorghastrum nutans*]) dominate the vegetation, with woody shrubs—Roughleaf Dogwood (*Cornus drummondii*), American Plum (*Prunus americana*), and Coralberry (*Symphoricarpos orbiculatas*)—becoming established where fire is excluded for ≥ 4 years (Knapp et al. 1999). Most of the Konza Prairie is a prairie grassland matrix (~90%) interspersed with variable amounts of shrub habitat, with the remainder consisting of thin strips of gallery forest in mesic lowland areas (Briggs et al. 2005).

As noted above, Konza Prairie is located in an area of high cowbird density (Lowther 1993, Peterjohn et al. 2000, Jensen and Cully 2005b) and contains a varied host community that is dominated by grassland- and shrub-nesting passerines (Zimmerman 1993). In the present study, host nesting data were collected each year during the local cowbird breeding season (approximately 1 May–20 July) in watersheds that represented all combinations of fire and grazing treatments. Within these habitats, we used a combination of behavioral cues and systematic searches (Martin and Geupel 1993) to locate host nests; on a limited number of occasions, we also used rope dragging to find nests of ground-nesting birds. We determined the laying date of the first egg in each active nest (hereafter “nest initiation date”) and the maximum number of cowbird eggs or nestlings (or both) observed in the nest (hereafter

TABLE 1. Parasitism rate (i.e., proportion of total nests parasitized), parasitism intensity (i.e., mean number of cowbird offspring per parasitized nest), and total Brown-headed Cowbird offspring (i.e., eggs, nestlings, or both) found in host nests at Konza Prairie during the 2002–2007 breeding seasons. Species pooled for analysis as “other hosts” group are denoted by †, and species that typically eject cowbird eggs are denoted by*.

Host species	Parasitism rate	<i>n</i> ^a	Mean intensity	<i>n</i> ^b	Total offspring
Dickcissel (<i>Spiza americana</i>)	69.6%	890	2.09	619	1,295
Bell's Vireo (<i>Vireo bellii</i>)	70.5%	689	1.59	486	775
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	21.9%	670	1.75	147	257
Field Sparrow (<i>Spizella pusilla</i>) [†]	48.9%	141	1.62	69	112
Eastern Meadowlark (<i>Sturnella magna</i>) [†]	26.9%	67	2.00	18	36
Grasshopper Sparrow (<i>Ammodramus savannarum</i>) [†]	47.8%	46	1.50	22	33
Eastern Phoebe (<i>Sayornis phoebe</i>) [†]	18.2%	33	2.33	6	14
Lark Sparrow (<i>Chondestes grammacus</i>) [†]	70.6%	17	2.00	12	24
Eastern Towhee (<i>Pipilo erythrophthalmus</i>) [†]	100%	15	3.33	15	50
Northern Cardinal (<i>Cardinalis cardinalis</i>) [†]	66.7%	15	1.90	10	19
Common Grackle (<i>Quiscalus quiscula</i>) [†]	0%	9	—	—	0
Orchard Oriole (<i>Icterus spurius</i>) [†]	100%	7	2.86	7	20
Blue Grosbeak (<i>Passerina caerulea</i>) [†]	100%	4	2.25	4	9
Eastern Bluebird (<i>Sialia sialis</i>) [†]	25.0%	4	1.00	1	1
Yellow Warbler (<i>Dendroica petechia</i>) [†]	100%	4	1.5	4	6
House Finch (<i>Carpodacus mexicanus</i>) [†]	33.3%	3	1.00	1	1
Bobolink (<i>Dolichonyx oryzivorus</i>) [†]	0%	2	—	—	0
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>) [†]	100%	1	1.00	1	1
Common Yellowthroat (<i>Geothlypis trichas</i>) [†]	100%	1	1.00	1	1
Henslow's Sparrow (<i>Ammodramus henslowii</i>) [†]	100%	1	4.00	1	4
Indigo Bunting (<i>Passerina cyanea</i>) [†]	100%	1	3.00	1	3
Louisiana Waterthrush (<i>Seiurus motacilla</i>) [†]	0%	1	—	—	0
Brown Thrasher (<i>Toxostoma rufum</i>) [*]	9.6%	323	1.35	31	42
Gray Catbird (<i>Dumetella carolinensis</i>) [*]	5.2%	58	1.33	3	4
Scissor-tailed Flycatcher (<i>Tyrannus forficatus</i>) [*]	0%	3	—	—	0
Eastern Kingbird (<i>Tyrannus tyrannus</i>) [*]	0%	2	—	—	0
Great-tailed Grackle (<i>Quiscalus mexicanus</i>) [*]	0%	2	—	—	0
All species combined	48.5%	3,009	1.86	1,459	2,707
Acceptor hosts only	54.4%	2,621	1.87	1,425	2,661

^aNumber of nests used to calculate parasitism rate.

^bNumber of parasitized nests used to calculate mean parasitism intensity.

“cowbird offspring”). If nests were found after laying ceased and we lacked data regarding hatching date (e.g., because of nest predation during incubation), we estimated the initiation date as the midpoint between the earliest and latest possible hatching dates, assuming that hosts laid modal clutch sizes as reported by Baicich and Harrison (1997). Unfortunately, we were unable to quantify nest survival of most cowbird hosts in the community because other ongoing research included manipulation of nest contents that may have potentially biased nest survival (e.g., Kosciuch et al. 2006, Rivers 2007).

We used data from Zimmerman's (1983) study of cowbird parasitism on Dickcissels at Konza Prairie during 1965–1979 to assess the extent to which parasitism rate and intensity varied over a period of several decades. Because changes to regional cowbird populations have the potential to influence local patterns of parasitism on Dickcissels (Jensen and Cully 2005a), we used data from 4 Breeding Bird Survey (BBS) routes close to Konza Prairie (see Acknowledgments) to document changes in Dickcissel and cowbird abundance during the present study and that of Zimmerman (1983). In addition, we used data from the 2002–2007 annual Konza Prairie breeding bird surveys (see Acknowledgments)

to assess possible changes in cowbird abundance at the study site during our study. Konza Prairie bird surveys were conducted each year during the first 2 weeks of June under favorable weather conditions by a single observer who recorded all birds detected by sight or sound along 1 or 2 transects per watershed (ranging from 343 to 1,637 m in total length) on a total of 17 watersheds (for details, see Zimmerman 1993). Cowbird abundance estimates at Konza Prairie were calculated for each year as the number of individual cowbirds detected per kilometer of transect within each experimental watershed unit, with each watershed considered a replicate for assessing changes in cowbird abundance over the course of the present study.

Data analysis.—Host species at Konza Prairie were first classified as “acceptors” or “rejecters” of cowbird eggs (*sensu* Rothstein 1975), and acceptor species were pooled into four primary groups based on the relative abundance of their nests: 34.0% of all nests of acceptor hosts were Dickcissel nests ($n = 890$), 26.3% were Bell's Vireo (hereafter “vireo”) nests ($n = 689$), 25.6% were blackbird nests ($n = 670$), and 14.2% were nests of 19 other species ($n = 372$) and hereafter pooled into the “other hosts” group. Although we recognize that pooling parasitism data from several hosts has

the potential to mask species-specific patterns of parasitism, the decision to pool uncommon hosts into one category was undertaken for two reasons. First, preliminary analyses found that two important life-history traits that could influence species-specific patterns of parasitism, adult mass and incubation period (Hauber 2003), were not related to either parasitism rate ($r^2 = 0.11$, $P = 0.361$ and $r^2 = 0.08$, $P = 0.421$, respectively) or parasitism intensity ($r^2 = 0.02$, $P = 0.666$ and $r^2 = 0.03$, $P = 0.645$, respectively) among the 10 acceptor species for which we located at least 15 nests. Second, limited sample sizes among several uncommon hosts prevented meaningful examination of cowbird parasitism for these species when examined alone. Nevertheless, because uncommon hosts on our study area represented suitable hosts that can raise cowbirds and that collectively may influence patterns of parasitism across the host community, they were combined in our analysis and are referred to hereafter as the “other hosts” group.

Parasitism rate and intensity were compared among the four host groups using general linear models. These included logistic regression for parasitism rate and Poisson regression for parasitism intensity, both performed using the GENMOD procedure in SAS, version 9.1 (SAS Institute, Cary, North Carolina). Initially, we restricted our analysis to assessing how both parasitism measures (i.e., rate and intensity) differed among the four host groups. When the host-group main effect was statistically significant ($P < 0.05$), we used follow-up pairwise comparisons to test for differences in parasitism among the host groups. In addition to this analysis, we expanded beyond the simple candidate model (host group) to explore the effect of nest initiation date and year as covariates for both parasitism measures among the host groups. Factors of the global candidate model included host group, year, nest initiation date (binned into 5-day periods; see below), and an interaction term between host group and nest initiation date to account for any seasonal patterns in cowbird use of particular host groups. Other candidate models included (1) host group and year; (2) host group and nest initiation date; (3) host group, year, and nest initiation date; and (4) host group, nest initiation date, and their interaction. Akaike's information criterion (AIC) was used to select the most parsimonious model from among candidate sets for parasitism rate and parasitism intensity.

We used the resource selection index of Williams and Marshall (1938; described in Krebs 1999) to quantify apparent cowbird host preference among the four host groups during the two most intensive years of study (2006–2007; see below). This approach provided an objective way to assess apparent preference by indexing resource use in relation to resource availability. We considered each host nest an available resource and each parasitized nest a use of that resource. Selection indices were calculated by dividing the proportion of the total pool of parasitized nests that belonged to each host group (i.e., “proportional use”) by the proportion of the total pool of host nests for that group (i.e., “proportional availability”; Krebs 1999). Ninety-five percent confidence intervals were calculated for these selection indices to test whether selection indices for each group were significantly different from 1. A selection index significantly less than or greater than 1 indicated an apparent avoidance of or preference for a host group, respectively, whereas an index not different from 1 indicated use of a host group in proportion to its availability (Krebs 1999). This approach assumed that the relative abundance of nests in our sample was

representative of the availability of nests in the local host community. Given that our nest-searching efforts were concentrated in the dominant grassland and shrubland habitats on Konza Prairie, averaged >600 passerine nests found per year, and included nest-searching effort comprising 28 search-years (where 1 search-year equates to 1 field researcher searching full-time for passerine nests over the entire breeding season), our effort appears to be comprehensive enough to provide a reasonably accurate representation of the available nests in the local host community.

To assess whether apparent host preference by cowbirds changed during the breeding season, we calculated a relative selection index for each of the four host groups in relation to nest initiation date during the breeding season. This index was similar to the selection index described above but differed in that the relative contribution of each host group was determined by dividing the selection index for a given host group by the sum of all selection indices over all host groups (for details, see Krebs 1999). This approach allowed for an assessment of the relative selection of each host group on a scale from 0 to 1. Relative selection indices were calculated in 5-day increments across the breeding season, because most host species at Konza Prairie have a laying period of ≤ 5 days for a given nesting attempt during which cowbird parasitism typically occurs. In this analysis, we included only 5-day intervals that contained at least 5 parasitized nests per host group, and we assumed that the number of nests found in any time interval likely reflected nest availability. After relative selection indices were calculated, we used linear regression to assess how relative selection indices changed over the course of the breeding season for each host group. In addition, we also used linear regression to assess how the proportion of the total cowbird offspring in each host group changed over the same time period. Because anecdotal observations of within-season changes in cowbird host use were made before 2006, our nest-searching efforts during the 2006–2007 breeding seasons were structured so that they were conducted on the same study plots, employed a similar amount of nest-searching effort, and focused on collecting parasitism and nest-initiation data from as many host nests as possible.

Because parasitism data from Zimmerman (1983) were summarized by week and therefore nest-initiation data for individual nests were unavailable, we used linear regression to assess how parasitism rate and parasitism intensity varied across breeding seasons in both this study and that of Zimmerman (1983), in lieu of the categorical regression used above. In addition, chi-square and t -tests were used to compare cowbird parasitism on Dickcissels between the present study and that of Zimmerman (1983), and t -tests were used to compare the mean numbers of cowbirds and Dickcissels detected on BBS routes between the two periods. Finally, linear regression was used to assess trends in cowbird abundance at Konza Prairie during 2002–2007. Statistical tests were two-tailed, the significance level for all statistical tests was $P < 0.05$, and means \pm SE are reported for response variables unless otherwise noted.

RESULTS

No significant changes in cowbird abundance at Konza Prairie were detected from breeding surveys conducted between 2002 and 2007 ($r^2 = 0.018$, $F = 1.52$, $df = 1$ and 82 , $P = 0.221$). Fresh cowbird eggs were observed in host nests as early as 1 May (in 2002)

and as late as 27 July (in 2006), which indicated a minimum 12-week period for the cowbird laying season. However, cowbirds began laying eggs before our field work started (~1 May) in some years, because the earliest initiation date for a parasitized host nest was backdated to 13 April (Eastern Phoebe, in 2005). However, only 2.2% of acceptor nests were initiated before 1 May, and rates of parasitism on these nests were relatively low (i.e., only 16 of 57 acceptor nests parasitized) compared with rates from later in the season. Therefore, these nests were included in all subsequent analyses because their inclusion did not influence general patterns of cowbird parasitism.

Over all years, we located 3,009 active nests belonging to 27 passerine species. The five species ($n = 388$ nests) that typically eject cowbird eggs from their nests (see Table 1) were excluded from further analyses because their actual rates of parasitism could not be determined because of potential removal of cowbird eggs by hosts. This reduced the data set to 22 species ($n = 2,621$ nests) known to accept cowbird eggs. Of these, 90.3% were found during the laying or incubation stages and 72.9% had a known initiation date. Nearly all the acceptor species that we monitored were parasitized by cowbirds (19 of 22 species), and 54.4% of 2,621 acceptor nests were parasitized, with a mean of 1.9 ± 1.03 (SD) (range: 1–7; $n = 1,425$ parasitized nests) cowbird offspring per parasitized nest (Table 1). Multiple parasitism occurred at 55.7% of parasitized nests ($n = 1,425$) of acceptor species.

When data from all years were combined, parasitism rate ($\chi^2 = 465.1$, $df = 3$, $P < 0.001$) and parasitism intensity ($\chi^2 = 38.99$, $df = 3$, $P < 0.001$) were significantly different among the four host groups. Rates of parasitism in vireos (70.5%, $n = 689$ nests) and Dickcissels (69.6%, $n = 890$ nests) were similar ($\chi^2 = 0.18$, $df = 3$, $P = 0.672$) and were significantly greater than rates of parasitism in the other hosts group (46.5%, $n = 372$ nests), and these three groups had significantly greater parasitism rates than the blackbird (21.9%, $n = 670$ nests; $P < 0.001$ for all other pairwise comparisons). Parasitism

intensity in Dickcissels (2.1 ± 0.04 cowbird offspring) was similar to that in the other hosts group (1.9 ± 0.08 cowbird offspring; $\chi^2 = 1.71$, $df = 1$, $P = 0.191$) but significantly greater than that in blackbirds (1.8 ± 0.08 cowbird offspring; $\chi^2 = 6.91$, $df = 1$, $P = 0.009$) and vireos (1.6 ± 0.05 cowbird offspring; $\chi^2 = 35.74$, $df = 1$, $P < 0.001$). Parasitism intensity in the other hosts group was similar to that in blackbirds ($\chi^2 = 1.43$, $df = 1$, $P = 0.232$) but was significantly greater than that in vireos ($\chi^2 = 8.53$, $df = 1$, $P = 0.004$). Levels of parasitism intensity in blackbirds and vireos were not significantly different from each other ($\chi^2 = 1.63$, $df = 1$, $P = 0.201$).

Best-fit models for parasitism rate and parasitism intensity that incorporated temporal covariates were global models that included all explanatory factors (i.e., host group, year, nest initiation date, and interaction between host group and nest initiation date), with ΔAIC values of 14.9 and 3.0 for next best-fit models for parasitism rate and parasitism intensity, respectively. Both parasitism rate and parasitism intensity varied significantly among host groups, across years, and with nest initiation date within years in these models (Table 2). Ninety-five percent confidence intervals for the slopes of both parasitism measures over year and nest initiation date were significantly negative (Table 2), which indicated declines across both time scales. Additionally, there was a significant interaction between host group and nest initiation date for parasitism rate (Table 2), which indicated differences in parasitism among the host groups as the breeding season progressed. The slope of parasitism rate over nest initiation date in the other hosts group did not differ significantly from zero, whereas parasitism levels in all other host groups were significantly negative (Table 2). The rate of parasitism tended to decline more steeply over the nesting season for blackbird nests than for vireo nests (Table 2).

During the two most intensive years of study (2006–2007), 71–77% of all cowbird offspring were found in either Dickcissel or vireo nests. Selection indices for cowbird use of Dickcissel nests were significantly >1 in both years (Fig. 1), which suggested an

TABLE 2. Summary statistics from general linear models comparing parasitism rate (i.e., proportion of total nests parasitized) and parasitism intensity (i.e., mean number of cowbird offspring per parasitized nest) by Brown-headed Cowbirds on host nests at Konza Prairie during 2002–2007. Ninety-five percent confidence intervals (CI) are provided for slope parameters (β) of numerical variables.

Explanatory terms per response	95% CI for β^a	χ^2	df	P
Parasitism rate				
Host group		136.96	3	<0.001
Year	–0.169 to –0.055	14.93	1	<0.001
Nest initiation date	–0.415 to –0.280	191.73	1	<0.001
Host group * nest initiation date ¹		103.43	3	<0.001
Bell’s Vireo	–0.276 to –0.155			
Dickcissel	–0.302 to –0.185			
Other hosts group	–0.022 to 0.071			
Red-winged Blackbird	–0.415 to –0.280			
Parasitism intensity				
Host group		12.67	3	0.005
Year	–0.050 to –0.003	5.01	1	0.025
Nest initiation date	–0.077 to 0.007	16.14	1	<0.001
Host group * nest initiation date ¹		4.85	3	0.183

^aNinety-five percent confidence intervals for slopes of parasitism levels over nest initiation date per host group.

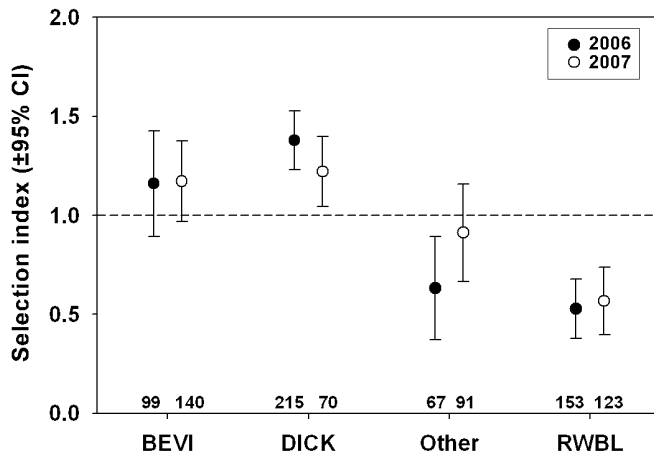


FIG. 1. Selection indices and 95% confidence intervals for preference of the Brown-headed Cowbird for the four primary host groups during 2006 (filled circles) and 2007 (open circles) at Konza Prairie. A selection index significantly less than 1 indicates an apparent avoidance of a host group, an index significantly more than 1 indicates an apparent preference for a host group, and an index not different from 1 indicates use of a host group in proportion to its availability (shown by dashed line). Abbreviations for the four host groups: BEVI = Bell's Vireo, DICK = Dickcissel, Other = other hosts group, and RWBL = Red-winged Blackbird. Sample sizes for each year are noted below point estimates.

apparent preference for the Dickcissel over other available hosts. In both years, selection indices for the vireo were not different from 1, which suggested use in proportion to availability, whereas selection indices for the blackbird and the other hosts group suggested apparent avoidance by cowbirds (Fig. 1). Examination of temporal patterns of cowbird parasitism during 2006–2007 indicated that apparent preference of cowbirds for Dickcissels as hosts did not change in relation to apparent preferences for the other three host groups over the course of the breeding season. In 2006, there was a nonsignificant positive slope between relative selection index and nest initiation date for Dickcissels ($P = 0.570$, $n = 10$) and the other hosts group ($P = 0.857$, $n = 12$), a nonsignificant negative slope for vireos ($P = 0.217$, $n = 12$), and a significantly negative slope for blackbirds ($P = 0.002$, $n = 12$; Fig. 2A). A similar relationship was found in 2007 for Dickcissels ($P = 0.214$, $n = 11$), other hosts ($P = 0.308$, $n = 15$), and blackbirds ($P = 0.003$, $n = 15$); however, the slope in vireos was significantly negative ($P < 0.001$, $n = 15$; Fig. 2B). The slope of the relationship between nest initiation date and the proportion of total cowbird offspring in nests of each host group was significantly different from zero in 3 of 4 groups in both 2006 (vireo: $P = 0.019$, $n = 12$; Dickcissel: $P = 0.015$, $n = 10$; blackbird: $P = 0.005$, $n = 12$; Fig. 2C) and 2007 (Dickcissel: $P = 0.002$, $n = 11$; blackbird: $P = 0.017$, $n = 15$; other hosts: $P = 0.022$, $n = 15$; Fig. 2D). Of note, in both years the slopes of the relationship between proportion of total cowbird offspring and nest initiation date were positive for the Dickcissel, whereas the slopes for the other three groups were negative, indicating that the proportion of cowbird young in Dickcissel nests increased while the proportion of cowbird young in the three other groups decreased during the breeding season (Fig. 2C, D). However, the increase in the

proportion of cowbird offspring in Dickcissel nests over the breeding season was positively correlated with the proportion of new Dickcissel nests that was available for parasitism in both years of intensive study (2006: $r^2 = 0.67$, $P = 0.050$, $n = 9$; 2007: $r^2 = 0.91$, $P < 0.001$, $n = 11$). Taken together, these results indicate that cowbirds' apparent preference for Dickcissels did not increase and their preference for other available hosts decrease, but instead cowbirds exhibited a consistent preference for Dickcissel nests over the course of the breeding season.

The overall rate of parasitism on Dickcissel nests was significantly lower during the present study (69.6%, $n = 890$ nests) than during the earlier study by Zimmerman (1983) (84.7%, $n = 235$ nests; $\chi^2 = 21.45$, $df = 1$, $P < 0.001$). For parasitized Dickcissel nests found during laying and assumed to have complete clutches, parasitism intensity was significantly lower during the present study (2.1 ± 0.06 cowbird eggs per parasitized nest, $n = 489$ nests) than during the earlier study (2.9 ± 0.16 cowbird eggs per parasitized nest, $n = 96$ nests; $t = -5.51$, $P < 0.001$). In addition, the proportion of multiply-parasitized Dickcissel nests found during laying and assumed to have complete clutches was also significantly higher in the earlier study (63.2% of 125 nests) than in the present one (44.3% of 690 nests; $\chi^2 = 15.09$, $P < 0.001$). The proportion of Dickcissel nests that were unparasitized or contained a single cowbird egg was higher during our study than in the earlier one, whereas the proportion of Dickcissel nests that contained >3 cowbird eggs was lower than earlier levels (Fig. 3A). During both periods, there was a significant decrease in parasitism rate (Fig. 3B; 1965–1979: $P = 0.007$, $n = 8$; 2002–2007: $P = 0.005$, $n = 14$) and mean parasitism intensity (Fig. 3C; 1965–1979: $P < 0.001$, $n = 9$; 2002–2007: $P = 0.005$, $n = 11$) over the course of the breeding season. During most periods across the breeding season, parasitism rate and intensity were lower in the present study than in the earlier one (Fig. 3B, C). A comparison of the mean number of detections on BBS routes between the two periods of study found no significant difference in the numbers of Dickcissels detected (1967–1979: 92.7 ± 4.04 Dickcissels year $^{-1}$; 2002–2006: 104.8 ± 4.88 Dickcissels year $^{-1}$; $t = -1.67$, $P = 0.114$), but significantly fewer cowbirds were detected during the period of the present study than in the earlier period (1967–1979: 55.9 ± 3.70 cowbirds year $^{-1}$, 2002–2006: 32.6 ± 2.30 cowbirds year $^{-1}$; $t = 3.74$, $P = 0.002$).

DISCUSSION

General patterns of cowbird parasitism.—We found that cowbirds parasitized nearly all available acceptor host species at Konza Prairie, that more than half of all acceptor host nests were parasitized by cowbirds, and that the majority of parasitized nests contained ≥ 2 cowbird offspring. These findings concur with previous research that found high levels of cowbird parasitism (i.e., rate and intensity) in the northern Flint Hills, which is likely attributable to both the high density of individuals and the overlapping laying ranges of female cowbirds in this area (Elliott 1980, Peterjohn et al. 2000, Jensen and Cully 2005b). Unlike research conducted in areas where cowbirds are less abundant (Hahn and Hatfield 1995, Strausberger and Ashley 1997, Woolfenden et al. 2004), our study found that cowbirds at Konza Prairie heavily parasitized both abundant and uncommon species. Whether cowbirds at this site select hosts in a density-dependent manner remains unknown,

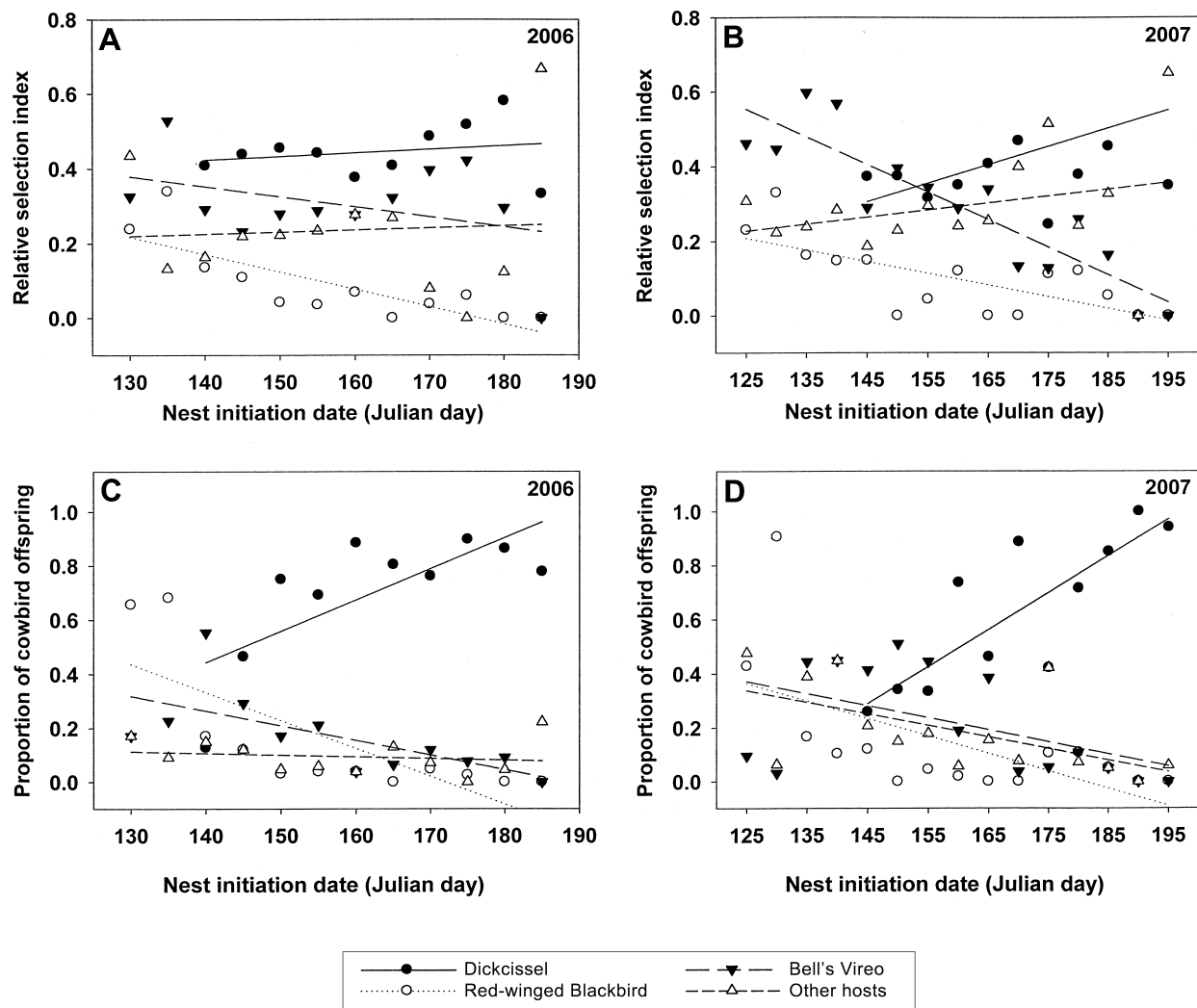


FIG. 2. Relationships between (A, B) relative selection indices and nest initiation date and (C, D) between the proportion of total Brown-headed Cowbird offspring in each host group for each nest initiation period for the 2006–2007 breeding seasons at Konza Prairie. Values were calculated for newly initiated nests for each host group over 5-day intervals of the breeding season during which at least 5 nests were found. Regression lines in all panels are shown for the Dickcissel (solid line, filled circle), Red-winged Blackbird (dotted line, open circle), Bell's Vireo (short dashed line, filled triangle), and other hosts (long dashed line, open triangle).

although available data suggest that this may be the case given the spatial patterns of cowbird parasitism on the Dickcissel (Jensen and Cully 2005a). Despite the gaps in our knowledge of the mechanisms used by cowbirds to select nests for parasitism, it is clear that levels of parasitism at Konza Prairie are relatively high with respect to parasitism rate and intensity across a host community (Ortega 1998), which suggests that laying strategies of females at this location may differ from those at other sites.

Our analyses revealed that the Dickcissel is the most preferred cowbird host on Konza Prairie, both over the course of our 6-year study and within individual breeding seasons. Cowbirds parasitized many acceptor hosts before Dickcissels began nesting on our study site, which typically commenced in the third week of May. However, shortly after Dickcissels began breeding, cowbirds parasitized them at high rates, with a modest decline over

the remainder of the breeding season. In addition, there was an increase in the proportion of all cowbird offspring that were found in Dickcissel nests as the season progressed. These results are explained in part by the finding that Dickcissels typically breed later than other host species at Konza Prairie (Zimmerman 1993) and make up a significant proportion of the host nests available for parasitism later in the breeding season. Nevertheless, these data indicate that cowbirds consistently preferred Dickcissels and consequently parasitized them at a high rate and intensity when they were available. Furthermore, the data do not indicate a change in apparent preference by cowbirds for Dickcissel nests over other hosts, as had been suggested by our anecdotal observations and by other authors working in northeast Kansas (Fretwell 1977, Fleischer 1986). Other studies of laying decisions by cowbirds have documented individual females using different hosts within

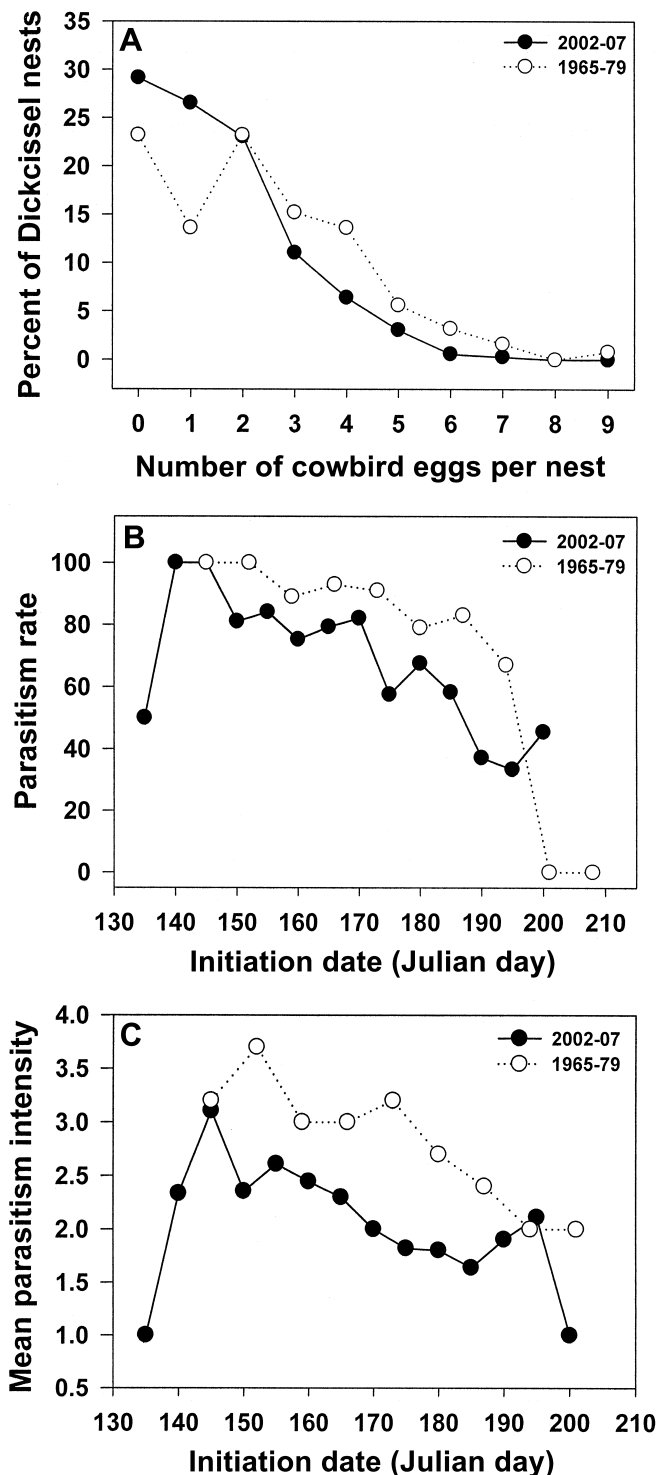


FIG. 3. (A) Percentage of nests at each level of number of cowbird eggs per nest at Konza Prairie during the present study (2002–2007, filled circles) and a previous study (1965–1979, open circles). (B) Relationship between parasitism rate (percentage of nests parasitized) and (C) mean parasitism intensity (mean number of cowbird offspring per parasitized nests) in relation to nest initiation date during 2002–2007 (filled circles) and 1965–1979 (open circles).

a season (Fleischer 1985, Alderson et al. 1999, Woolfenden et al. 2003, Strausberger and Ashley 2005), although only Strausberger and Ashley (2005) examined cowbird host use in a community where an important cowbird host began nesting several weeks after other hosts in the community. Therefore, additional research to determine whether parasitism decisions of individual female cowbirds change with the arrival of Dickcissels in this breeding community would be fruitful.

Has parasitism of the Dickcissel changed over a decades-long time scale?—It is unclear why the parasitism rate and parasitism intensity in Dickcissels declined significantly over the 22-year period between Zimmerman's (1983) study and our own, but more than one factor may be responsible. Declines in cowbird abundance over this period, as indicated by the BBS data from the Flint Hills, likely contributed to reduced parasitism rates and intensities. On the other hand, BBS data gave no indication of an increase in Dickcissel numbers over the same period, and it is therefore unlikely that increased numbers of Dickcissels resulted in a more diffuse distribution of cowbird eggs among nests. That the Dickcissel has been and remains the most abundant songbird on the study site (Zimmerman 1993, Powell 2006, J. W. Rivers et al. unpubl. data) suggests that the population in this area is able to withstand intense parasitism pressure over time, perhaps because of immigration or the ability of Dickcissels to raise some of their own offspring even when heavily parasitized (Hatch 1983, Rivers et al. 2003, Jensen and Cully 2005b).

An additional, nonexclusive explanation for the decline in parasitism on Dickcissels over time is based on a marked increase in woody vegetation at Konza (Briggs et al. 2005). Because obligate shrub-nesting species require woody vegetation for breeding, the minimal amount of shrub habitat on Konza during the period of Zimmerman's (1983) study (J. M. Briggs pers. comm.) likely resulted in a markedly smaller population of shrub-nesting hosts than currently observed at Konza Prairie, perhaps to the point where they played a very minor role as cowbird hosts. Indeed, BBS data from areas near the study site indicate a significant, positive increase in the number of vireos since the time of Zimmerman's study (K. L. Kosciuch et al. unpubl. data), and this species is currently a heavily used host at Konza Prairie (Table 1). All else being equal, if the increase in woody vegetation led to changes in cowbird host use, the rate and intensity of parasitism on grassland species should have been greater during the period of Zimmerman's study. In support of this idea, Elliott (1978) described rates and intensities of parasitism on Eastern Meadowlarks and Grasshopper Sparrows in an area immediately adjacent to Konza Prairie that were higher than those found in the present study. Nevertheless, because distinguishing between the relative importance of a decline in the local cowbird population and the increase in extent of woody vegetation at Konza is not possible, we suggest that the combined effect of both factors may have led to the observed decrease in parasitism on Dickcissels since Zimmerman's study.

The relative importance of hosts to the local cowbird population.—Hosts may be important to cowbirds because of their influence at the level of the individual or as a consequence of their effect on the overall cowbird population. We cannot address the former because we lack nest survival data for most cowbird hosts at Konza Prairie. However, we can examine how hosts might influence the overall cowbird population at Konza by assessing several

important traits of members of the host community: the degree of size disparity between cowbird and host nestlings (a function of both body size and incubation period), the behavioral response of the host to cowbird eggs (i.e., accept or reject), the number of cowbird offspring that a host can raise from its nest, and the ability to reduce cowbird parasitism via nest defense. Because 86% of cowbird offspring were observed in Dickcissel, vireo, and blackbird nests, our analysis is restricted to these hosts.

Vireos are smaller than cowbirds, and their incubation period is 3 to 4 days longer than that of the parasite (Baicich and Harrison 1997). Cowbird young thus have a strong competitive advantage, which typically results in the death of any nestling vireos that hatch (Parker 1999, Kosciuch and Sandercock 2008). In contrast to other hosts at Konza Prairie, vireos do not raise >1 cowbird per parasitized nest and they often desert heavily parasitized nests (Budnik et al. 2000, Kosciuch and Sandercock 2008). Finally, vireos are unable to deter parasitism by laying cowbirds (Sharp and Kus 2004). Similarly, the Dickcissel's incubation period is slightly longer than that of the cowbird (Baicich and Harrison 1997) and its nestlings are also smaller than cowbird young (J. W. Rivers et al. unpubl. data). But unlike vireos, Dickcissels can fledge up to 5 cowbirds from a single nest (Hatch 1983) and they do not typically abandon heavily parasitized nests (J. W. Rivers and W. E. Jensen unpubl. data). Little is known about nest defense against cowbirds by Dickcissels (Temple 2002), but high levels of parasitism in our population suggest that nest defense against cowbirds is poor (e.g., Zimmerman 1983). Blackbirds have incubation periods similar to those of cowbirds (Baicich and Harrison 1997), they do not reject cowbird eggs, and their young are slightly larger than cowbird young (J. W. Rivers et al. unpubl. data). Although we lack data on the number of cowbirds that can fledge from blackbird nests at our study site, Weatherhead (1989) found that at least 2 cowbirds can fledge from a blackbird nest. Finally, blackbirds effectively defend their nests against brood parasitism in at least some populations (e.g., Strausberger 2001), which may have contributed to their relatively low parasitism rate. Taken together, differences among the most common hosts in our study suggest that the Dickcissel is the most important host to the local cowbird population, followed by the vireo and the blackbird. Nevertheless, because we lack measures of relative reproductive success of cowbirds with each host, we suggest that the relative fitness payoffs that cowbirds receive from parasitizing these hosts be examined by future researchers.

Because they are logistically challenging, investigations of community-level patterns of brood parasitism over long periods are rarely conducted. However, studies of this nature are critical to our understanding of how generalist brood parasites select among potential hosts within a community. Our study found that cowbirds parasitized a wide range of species, that the majority of cowbird eggs were laid in the nests of a small number of host species, and that one species, the Dickcissel, appeared to be preferred over other hosts in the community. Nevertheless, gaps remain in our knowledge of community-level host use by cowbirds that should stimulate further study. For instance, we lack nest survival data that would allow the critical determination of the relative profitability of all hosts available for parasitism which, in turn, would help determine which host(s) provide the best fitness return for a laying female. In addition, we lack an understanding

of the proximate cues that female cowbirds use when making laying decisions, although it seems intuitive that host density and the ease with which cowbird females find host nests likely play important roles. Additional research along these lines will provide us with a better understanding of how generalist brood parasites select hosts within a community, both from the perspective of individual females and from that of the local cowbird population.

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