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Density-dependent habitat selection by brown-headed cowbirds (*Molothrus ater*) in tallgrass prairie

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Abstract Local distributions of avian brood parasites among their host habitats may depend upon conspecific parasite density. We used isodar analysis to test for density-dependent habitat selection in brown-headed cowbirds (*Molothrus ater*) among tallgrass prairie adjacent to wooded edges, and prairie interior habitat (>100 m from wooded edges) with and without experimental perches. Eight study sites containing these three habitat treatments were established along a geographical gradient in cowbird abundance within the Flint Hills region of Eastern Kansas and Oklahoma, USA. The focal host species of our study, the dickcissel (*Spiza americana*), is the most abundant and preferred cowbird host in the prairie of this region. Cowbird relative abundance and cowbird:host abundance ratios were used as estimates of female cowbird density, whereas cowbird egg density was measured as parasitism frequency (percent of dickcissel nests parasitized), and parasitism intensity (number of cowbird eggs per parasitized nest). Geographical variation in cowbird abundance was independent of host abundance. Within study sites, host abundance was highest in wooded edge plots, intermediate in the experimental perch plots, and lowest in prairie interior. Cowbirds exhibited a pattern of density-dependent selection of prairie edge versus experimental perch and interior habitats. On sites where measures of cowbird density were lowest, all cowbird density estimates (female cowbirds and their eggs) were highest near (≤ 100 m) wooded edges, where host and perch availability

are highest. However, as overall cowbird density increased geographically, these density estimates increased more rapidly in experimental perch plots and prairie interiors. Variation in cowbird abundance and cowbird:host ratios suggested density-dependent cowbird selection of experimental perch over prairie interior habitat, but parasitism levels on dickcissel nests were similar among these two habitats at all levels of local cowbird parasitism. The density-dependent pattern of cowbird distribution among prairie edge and interior suggested that density effects on perceived cowbird fitness are greatest at wooded edges. A positive relationship between daily nest mortality rates of parasitized nests during the nestling period with parasitism intensity levels per nest suggested a density-dependent effect on cowbird reproductive success. However, this relationship was similar among habitats, such that all habitats should have been perceived as being equally suitable to cowbirds at all densities. Other unmeasured effects on cowbird habitat suitability (e.g., reduced cowbird success in edge-dwelling host nests, cowbird despotism at edges) might have affected cowbird habitat selection. Managers attempting to minimize cowbird parasitism on sensitive cowbird hosts should consider that hosts in otherwise less-preferred cowbird habitats (e.g., habitat interiors) are at greater risk of being parasitized where cowbirds become particularly abundant.

Keywords Edge effects · Ideal free distribution · Isodar · *Molothrus ater* · *Spiza americana*

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Introduction

The effect of conspecific density on habitat choice is a persistent theme in habitat selection studies (Tregenza 1995; Morris 2003). As population sizes increase seasonally in migratory animals, intraspecific competition may cause resources to become depleted or less suitable within preferred habitats. Concomitant decreases in fitness or territoriality should then force newly arriving individuals or dispersers to settle in formerly unexploited, yet

accessible habitats (the *ideal free* and *despotic distributions* of Fretwell and Lucas 1970; Fretwell 1972). Patterns of density-dependent habitat selection have been observed in insects (Valladares and Lawton 1991; Krasnov et al. 2002), fish (Swain and Wade 1993; Marshall and Frank 1995; Bult et al. 1999), mammals (Meisser et al. 1990; Shenbrot and Krasnov 2000), and birds (O'Connor 1986; Fernández-Juric 2001; Shochat et al. 2002). Animal parasites should also exhibit density-dependent habitat selection (Krasnov et al. 2002) if host quality is inversely related to parasite density.

Obligate avian brood parasites provide an unstudied model system of density-dependent habitat selection. Although obligate brood parasites need only the nests of other birds in which to lay their eggs, patterns of habitat use in brown-headed cowbirds (*Molothrus ater*, 'cowbird' hereafter) and common cuckoos (*Cuculus canorus*) suggest that these brood parasites prefer particular vegetative habitats in which to parasitize host nests (Strausberger and Ashley 1997; Robinson et al. 1999; Vogl et al. 2002). Such habitat-use patterns are especially well studied in the cowbird (Robinson 1999), a host-species generalist (Friedman and Kiff 1985). Cowbirds are expected to be selective of host-habitat associations as host habitats appear to differ in host nest availability (e.g., nest density, vegetative cover, juxtaposition to cowbird surveillance perches or foraging habitat) and host suitability (e.g., variation in host defenses and life history traits; Martin 1995; Strausberger and Ashley 1997; Robinson et al. 1999; Hosoi and Rothstein 2000). As might be expected for any organism exploiting spatially-heterogeneous resources, cowbird density should also affect cowbird use of host-habitat associations (Robinson et al. 1999).

Patterns of cowbird distribution within Midwestern forest fragments suggest that cowbirds might use host habitats in a density-dependent manner (Donovan et al. 1997, 2000; Thompson et al. 2000). As the ratio of cowbird to host abundance increases with the degree of forest fragmentation by agriculture, cowbirds expand their distribution from forest edges to forest interior (Donovan et al. 1997, 2000; Thompson et al. 2000). In New Mexico, Curson and Mathews (2003) found that cowbirds experienced reduced clutch size and follicle degeneration as commuting distance from cowbird foraging areas (with bison *Bos bison*) into host habitat increased. Thus, there must be some competitive incentive to drive cowbirds deeper into host habitat interior as their population density increases (Goguen and Mathews 2000).

Cowbird distribution may be 'free' or 'despotic' (Fretwell 1972; Winslow 1999). That is, their breadth of habitat distribution may be affected solely by density effects on fitness within habitats or to some degree by despotic ('dominance') territoriality. Density effects on cowbird fitness may result from multiple parasitism of single host nests by different female cowbirds (Fleischer 1985; Hahn et al. 1999; McLaren et al. 2003; Strausberger and Ashley 2003; Woolfenden et al. 2003) as local cowbird densities increase (Robinson et al. 2000; Jensen

2003). Reduced cowbird egg and nestling survival in host nests parasitized by multiple cowbirds (McGeen 1972; Hatch 1983; Trine 2000; Dearborn and Litchenstein 2002) might promote a response by female cowbirds to exploit alternative host habitats with fewer conspecifics as local cowbird densities increase. Additionally, dominant cowbirds may prevent conspecifics from settling in primary habitats. There is evidence of dominance hierarchies and territoriality in cowbirds (reviewed by Rothstein et al. 1986), though cowbird territory dissolution may occur at especially high cowbird densities or in certain habitats (Elliott 1980).

Cowbirds may exhibit density-dependent habitat selection within North American grasslands. In certain areas of the Midwestern United States, grassland songbird nests are rarely parasitized (Strausberger and Ashley 1997; Kershner and Bollinger 1998; Winter 1999; Peer et al. 2000). When parasitism on these hosts does occur, most nests are parasitized near wooded edges, rather than in prairie interior (Johnson and Temple 1990; Winter et al. 2000). Elevated branches of trees and shrubs may provide brood parasites with adequate vantage points from which to find ground-nesting hosts (Normon and Robertson 1975; Freeman et al. 1990; Johnson and Temple 1990; Alvarez 1993; Øien et al. 1996; Clotfelter 1998; Hauber and Russo 2000). Grassland songbirds, however, are moderately to heavily parasitized in the center of the cowbird's geographic distribution in the Great Plains (Elliott 1978; Zimmerman 1983; Koford et al. 2000), where cowbirds are especially abundant (Peterjohn et al. 2000). In this region, nests are commonly parasitized far into prairie interior (Jensen and Finck 2004).

Here we examined density-dependent cowbird distribution and parasitism of a single grassland-nesting host species (the dickcissel, *Spiza americana*) among wooded edge, experimental perch (described below), and interior habitats of tallgrass prairie using the isodar method of Morris (1988). The dickcissel is the most abundant (Zimmerman 1993) and heavily parasitized cowbird host (Elliott 1978; Jensen 1999) in the relatively simple avian community of the tallgrass prairie in central North America (Zimmerman 1993). We tested for a pattern of density-dependent habitat selection in cowbirds by establishing study sites, each including the three aforementioned habitats of interest, along a geographical gradient in cowbird abundance apparent from North American Breeding Bird Survey (BBS) data (Fig. 1). Cowbird abundance, cowbird:host ratios, and parasitism levels on dickcissel nests (described below) were used as measures of cowbird density that were compared among habitat pairs along this geographical gradient in cowbird abundance. We then explored multiple parasitism effects on cowbird reproductive success within dickcissel nests as a possible density-dependent effect on cowbird fitness. Examination of this possible density-dependent effect provides insight on two aspects of density-dependence in cowbird habitat selection: (1) the occurrence of such a density-dependent effect could provide an incentive for cowbirds to sequentially exploit secondary habitats with

increasing density in a primary habitat (Fretwell and Lucas 1970), and (2) once adjacent habitats have been occupied, a stronger density-dependent effect observed in certain habitats may explain why other habitats are occupied at higher cowbird densities as overall cowbird density increases (Morris 1988). Unlike previous studies that speculated about the role of competition for space and hosts as a mechanism driving local cowbird distribution (e.g., Donovan et al. 1997; Thompson et al. 2000), we explicitly designed our study to test for density-dependent habitat selection in cowbirds, independently of landscape fragmentation effects.

Materials and methods

Study area and habitat treatments

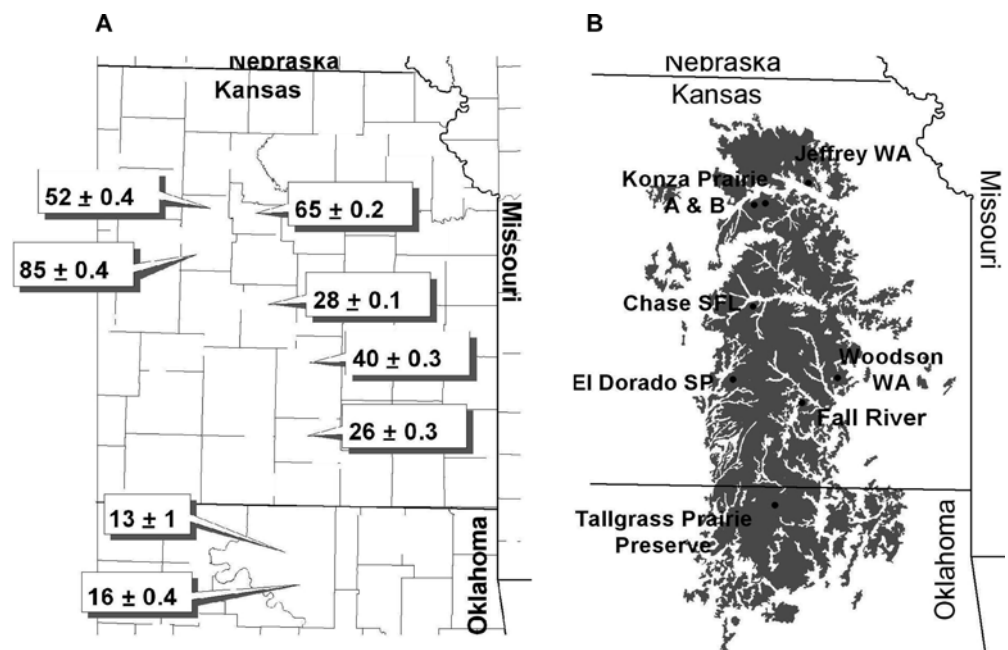
The study area was the Flint Hills tallgrass prairie region, stretching from northeastern Kansas to northeastern Oklahoma within the central Great Plains of North America (Fig. 1). This region is dominated by treeless expanses of remnant tallgrass prairie, the soils of which are typically too thin for cultivation. This prairie is dominated by the grasses *Andropogon gerrardii*, *Panicum virgatum*, *Sorghastrum nutans*, *Schizachyrium scoparium* and numerous other grass and forb species. Gallery forests and other woodlands form wooded edges of tallgrass prairie, but cover only a small percentage of the region's landscape (Cully et al. 2002). The amount of forest in prairie landscapes surrounding the study sites was not related to local cowbird densities or parasitism levels (Jensen 2003). Six study sites were monitored in each of two years (2001 and 2002) and were located across the latitudinal extent of the Flint Hills, from Konza Prairie Biological Station, Kansas (The Nature Conservancy,

Kansas State University) in the north to Tallgrass Prairie Preserve, Oklahoma (The Nature Conservancy) in the south. Other study sites were managed by the Kansas Department of Wildlife and Parks or the US Army Corps of Engineers. The 2001 Konza Prairie study site was relocated to the other side of that preserve (approximately 4 km away) in the second year of the study due to a late spring season fire in 2002. The Fall River Lake area was discontinued due to a lack of cowbirds and its small area, which resulted in low nest samples sizes in 2001. This site was replaced with the nearby Woodson Wildlife Area in 2002. Thus, there was a total of eight study site replicates across the Flint Hills region (Fig. 1). The prairie of each site was ungrazed to prevent domestic cattle (*Bos taurus*) damage to experimental perches (described below), and to allow for maximum nest densities—and thus maximum nest sample sizes—within each habitat plot per study site. Some sites were mowed in mid-July each year for hay.

Three habitat treatment plots were established within each study site. Naturally occurring “wooded edge” treatments were areas of tallgrass prairie ≤ 100 m from wooded edges. An earlier study indicated that wooded edge effects of cowbird parasitism on dickcissel nests may extend this far into tallgrass prairie in Kansas (Jensen and Finck 2004). The woodlands forming edges with prairie were strips of riparian woodlands, consisting mainly of *Ulmus*, *Populus*, *Quercus*, and *Salix* tree genera, ranging from 3 m to over 20 m in height. Wooded edge was expected to be the cowbird's primary habitat due to the highest availability of perches and potential hosts (Fig. 2).

We then selected two equivalently-sized areas (approx. 5–15 ha) of tallgrass prairie interior >100 m from wooded edges. An experimental perch treatment was randomly assigned to one of these plots, yielding “experimental perch” and “prairie interior” habitat treatments. The experimental perches were originally established to test

Fig. 1 Flint Hills region of eastern Kansas and northeastern Oklahoma, USA, depicting **a** geographical variation in count (mean number per route \pm SE) of brown-headed cowbirds (*Molothrus ater*) across counties of the region from the North American Breeding Bird Survey (1966–2002) and **b** the distribution of study sites across the contiguous tallgrass prairie of the region (gray shaded area) as depicted by The Nature Conservancy



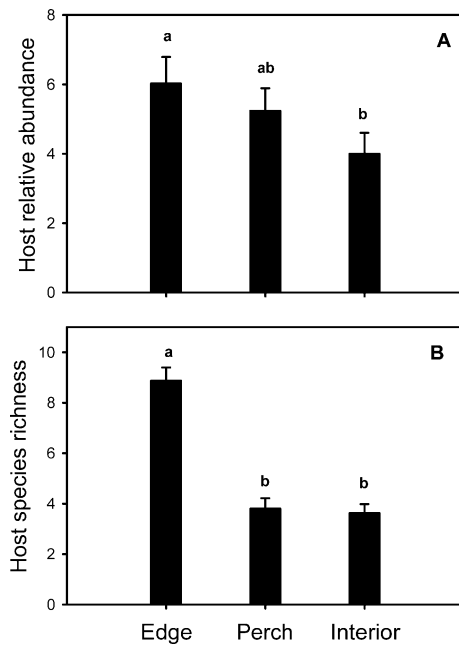


Fig. 2 a Mean (\pm SE) relative abundance (detections per sampling period) and b species richness of potential cowbird hosts within three habitat plots (*Edge* = wooded-edge plot, *Perch* = experimental-perch plot, *Interior* = prairie interior plot) across eight study sites as determined from 100-m radius point count surveys. Different letters above bars indicate significant ($P < 0.05$) differences among habitat treatments

for the importance of elevated perches to cowbird parasitism of grassland hosts (Jensen 2003). However, this experimental habitat also provided what was predicted to be a secondary cowbird habitat, as it was thought to have elevated perches but host density and species richness inferior to that offered by wooded edge habitat (see Fig. 2). The experimental perches were dried stems of *Cornus drummondii* (a woody shrub), ranging from 1.5 to 2.5 m high, attached to re-bar stakes with duct tape. The *Cornus* stems had branching near their apices for birds to alight upon. These perches were spaced every 40 m in rectangular grid arrays ranging from 4.2 to 13 ha per plot. Perch plots were established after dickcissels had apparently established territories in late May, although dickcissels on one site in 2002 did not settle until early June after the perch plot was established. A nest was considered to be within a perch plot if it was located within 50 m of an experimental perch. The remaining prairie interior treatment (>100 m from wooded edges) was relatively free of naturally occurring perches, of inferior host availability and species richness (Fig. 2), and thus was predicted to be the tertiary cowbird habitat. Although nest search effort within prairie interior plots was concentrated in areas of similar size to those of experimental perch plots, nests found incidentally outside of designated prairie interior plots, but >100 m from woodland vegetation, were still included as “prairie interior” nests. Thus, the experimental perch treatment had fewer nests due to lower nest search effort (area sampled) within that treatment (see Results below).

Although the size of the habitat plots for parasitism data varied depending upon the available area per habitat type per study site, parasitism frequency and intensity measures (described below) are proportions of cowbird eggs to nests found, and so were independent of habitat area. Count data (data collection described below) were collected within standardized, 100-m radius circles per habitat treatment plot within each study site.

Data collection

Data were collected during the dickcissel breeding season (mid-May to late July). The relative abundances of female cowbirds and males of potential cowbird hosts within each plot were measured using single 10-min, 100-m radius point count surveys per plot. These were centered within the experimental perch and open plots, whereas wooded-edge points were randomly positioned along the length of the wooded edges, where count circle points were centered directly on the prairie-woodland edge. Although woodlands comprised a portion of the wooded edge treatment count circles, birds were counted within a full 100-m radius circle comprising the woodland vegetation. As these woodlands were relatively thin, linear strips or diffuse, we felt that most female cowbirds within the woodlands, or in prairie on the opposite side of woodland strips from the observer, (but ≤ 100 m from the observer) could be seen or heard within a 10-min period. Most female cowbirds detected gave chatter calls (81 of 103 female cowbirds detected during point counts) and thus were heard even if not seen. Moreover, the isodar slopes of cowbird relative abundance and area-independent cowbird:host ratios (described below) and parasitism levels were similar among habitat treatment pairs (described below), suggesting that detection biases in determining cowbird relative abundance in wooded edge plots were insignificant. Five surveys were conducted per site across all treatment plots each year from 27 May to 30 June, between 0600 and 1000 each day. All birds seen or heard that were perched within habitat of the count circles, or flushed by the observer (W.E.J.) upon approaching or departing each count circle (i.e., flyovers excluded), were recorded by gender. Aside from sexual dimorphism in cowbird plumage, cowbird males have unique vocalizations so are easily discriminated from female cowbirds. The movements of individual birds within plots were noted to avoid double-counting individuals. However, individuals could not be discriminated among different sample periods.

Female cowbird ‘density’ was approximated with two measures. First, mean relative abundance of female cowbirds (“cowbird relative abundance”) was measured as the average number of female cowbirds heard or seen across sampling periods per habitat plot. This approximates cowbird density per unit of area sampled. Second, a mean ratio (Krebs 1989) of cowbird to host relative abundance was also calculated (“cowbird:host ratio”). ‘Host species’ for this ratio were determined as all

potential host species that cowbirds may attempt to parasitize, which excluded excessively large or aggressive hosts and cavity nesters (Robinson et al. 1999). As cowbirds in the study region do lay eggs in nests of species that commonly desert parasitized nests or remove parasitic eggs (Parker 1999; William E. Jensen, personal observation), this host designation was deemed to be a reasonable index of the availability of perceived hosts. The relative abundance of hosts was measured as the average number of males heard or seen across sampling periods per habitat plot. Male host abundance was assumed to approximate the number of host territories and nest availability, as surreptitious behavior or sexual monomorphism complicates the detection of females (we have no estimates of densities of all nests in the host community). This ratio was also used because hosts are the limiting resource for cowbirds within parasitism habitats, rather than area per se, thus providing the best ‘density’ approximation from count data. The cowbird:host ratio has been shown to be a good index of nest parasitism rates elsewhere (Robinson et al. 2000).

Note that the cowbird:host ratio is somewhat different from a consumer:resource ratio fitness index, and thus can be used as a measure of cowbird density. There is some upper limit to parasitism opportunity based on host nest availability, but host nests are not ‘consumed’ by cowbirds, rather single nests can be utilized by several female cowbirds. Cowbird fitness could be similar among habitats despite unequal cowbird:host ratios if density effects of this ratio—and thus multiple parasitism—differ among habitats and host species. Thus, we might not expect the cowbird:host ratio to index fitness similarly in all habitats. This is not to say that cowbirds do not include host quantity in their perceptions of habitat suitability, only that depletion of resources is not necessarily paralleled by the availability or quality of host nests in all habitats. Moreover, changes in cowbird:host ratios among habitats with increasing cowbird density indicates how habitat quality is perceived by cowbirds.

Searches for dickcissel nests were done from mid-May to mid-July by following females to nests or accidentally as observers walked through study plots. Blue surveyor flags were placed 5 m from each nest. Nest contents were monitored every 3–4 days until nest completion (fledging, desertion, or depredation). Most nests were monitored through nest completion, but monitoring was discontinued for some nests due to mowing for prairie hay (92 of 466 nests). Nests that failed prior to incubation were not included because the window of parasitism opportunity during host egg laying and early incubation stages (Lowther 1993; Johnsgard 1997) is incomplete for such nests. Two measures were used to approximate cowbird egg ‘density’ across dickcissel nests: (1) parasitism frequency per plot was measured as the percent of nests containing ≥ 1 cowbird egg or nestling, and (2) parasitism intensity was measured as the number of cowbird eggs or nestlings per parasitized nest. Indices of cowbird reproductive success compared to parasitism intensity within habitat treatments were: (1) the hatchability of cowbird

eggs (proportion of eggs not lost during incubation that produced nestlings in nests that survived to the nestling stage), and (2) daily mortality rates of parasitized dickcissel nests (number of nest losses per total nest observation days; Mayfield 1975) examined separately for incubation and nestling stages. Nest mortality rates measure mortality of all cowbird eggs and nestlings per nest. Losses of individual cowbird eggs and nestlings during incubation and nestling stages, respectively, were rare and therefore could not be analyzed in relation to parasitism intensity among habitats.

Statistical analyses

Geographic variation in cowbird abundance across the study region may have reflected the level of host resources. If so, then geographic variation in cowbird density might have negligible effects on cowbird fitness and thus provide no incentive for density-dependent habitat selection. To compare cowbird abundance to host abundance across the region, relative abundance estimates of cowbirds, all potential hosts, and dickcissels were averaged across point count circles within each study site. The mean relative abundances of female cowbirds were then compared to the mean relative abundances of all hosts and dickcissels across study sites using Pearson correlation analysis.

To compare host availability per habitat plot, mean relative abundances of all potential hosts and host species richness (the latter an index of nest asynchrony diversity and thus continuity of nest availability to cowbirds) were compared among habitat treatments using blocked analyses of variance, with study sites as blocks containing the three treatments (habitat plots are less independent within—rather than among—study sites due to juxtaposition and similar grassland management regimes). Post-hoc comparisons of mean relative abundances and species richness estimates among treatments were then done using Duncan’s multiple range tests.

Isodar analysis (Morris 1988) can be used to explore patterns of density-dependent habitat selection. This method uses pairwise plots of densities of a species among adjacent habitats, where densities in predicted primary and secondary habitats are placed on the ordinate and abscissa, respectively. Each point represents a locality containing the adjacent habitats along a spatial gradient in local population sizes. Thus, local population sizes increase as the points stray from the origin. A regression line (“isodar” line) among these points models density between the two habitats, where actual fitness is expected to be equal in both habitats at any point on this line (i.e., organisms are optimally distributed among the two habitats). Isodar lines extending from the origin with of slope = 1 indicate that densities between habitats are equal at all population sizes (i.e., habitat selection is independent of density). A positive regression intercept (y) along the primary habitat axis (ordinate) verifies that this habitat is indeed primary at the lowest population size, and that the

resources in this habitat are quantitatively superior. The slope of the isodar line indicates changes in relative density as population size increases, and reflects the resource quality (i.e., the efficiency of resource utilization per unit of resource). If the slope is equal to one (i.e., densities increase at equal rates in primary and secondary habitats) it is assumed that relative fitness within each habitat does not change as population density increases, because resource quality is similar among the habitats (i.e., *parallel regulation*; Morris 1988). If the slope is greater or less than one, this indicates a greater increase in settlement frequency within the habitat that the regression line tends toward. It is therefore assumed that density effects on perceived fitness are greater in the habitat from which the isodar line tends away.

Geometric mean regression (Ricker 1973) was used to derive isodar functions of female cowbird relative abundance, cowbird:host ratios, parasitism frequencies, and parasitism intensities of dickcissel nests among habitat treatment pairs along the predicted cowbird habitat preference hierarchy (i.e., wooded edge vs prairie interior, wooded edge vs experimental perch plots, and experimental perch plots vs prairie interior). Intercepts and slopes of regressions were tested for differences from 0 and 1, respectively, by using 95% confidence intervals around parameter estimates. Intercepts and slopes were considered significantly different from 0 and 1, respectively, if their confidence limits did not include 0 or 1. Note that as individual cowbirds were not uniquely-marked, nor was molecular maternity analysis of cowbirds eggs possible (see below), we examined the effect of cowbird density on the distribution of cowbird occurrence and parasitism events, not the distribution of individual cowbirds or their territories.

We attempted to identify a density-dependent effect of multiple parasitism intensity on cowbird reproductive success, and if this effect differed among habitats in accordance with the predictions from the isodar analyses. Simultaneous estimates of reproductive identity and success of individual female cowbirds is not yet attainable using current molecular technology (Strausberger and Ashley 2001). Moreover, finding a representative sample of all host species nests per female cowbird to estimate individual fitness would be a daunting task at such large spatial scales, especially from species that reject cowbird eggs (Rothstein et al. 1986). We could, however, explore cowbird egg success within nests of the dickcissel, the most regionally abundant and preferred cowbird host. We examined cowbird egg success across nests covering the range of parasitism intensity across all plots within habitat treatments. By doing so, we could predict changes in cowbird habitat suitability at hypothetical levels of average parasitism intensity within habitats. This provides insight to density-dependent fitness levels potentially 'perceived' by cowbirds, not experienced fitness. If parasitism intensity did not interact with habitat type in affecting cowbird egg success, we would expect levels of parasitism intensity to be equalized across habitats at all cowbird densities (from isodar analysis described above).

If parasitism intensity affected cowbird egg success differently depending upon habitat type, then we would expect parasitism intensities in isodar analysis to become higher in those habitats where parasitism intensity effects on cowbird egg success are weaker. Cowbird egg hatchability and daily mortality rates of parasitized nests during incubation and nestling stages were compared to parasitism intensity levels of nests using logistic regression (PROC LOGISTIC; SAS Institute). Comparisons of all indices of reproductive success to parasitism intensity involved the same sample of nests by measuring parasitism intensity as the maximum number of cowbird eggs present within nests (1 to ≥ 6 cowbird eggs per nest). A second explanatory variable, 'habitat,' was added to test for differences in parasitism intensity effects on cowbird success among habitats that might correspond to density-fitness functions predicted from isodar analyses. Candidate models of all possible main effects and interactions (including at least parasitism intensity) were compared using Akaike's Information Criterion (AIC). Models with the lowest AIC values were considered best fit, but models with ΔAIC values < 2 with the fewest explanatory terms were considered most parsimonious.

We also assessed to what extent host selection in cowbirds might be affected by avoidance of previously parasitized nests (Ortega et al. 1994). This was examined by comparing the observed versus expected distribution of cowbird eggs across nests using the method of Mayfield (1965). If cowbird eggs were distributed in a Poisson fashion, then we could conclude that cowbird eggs were laid randomly with respect to previous parasitism. Observed versus expected distributions of cowbird eggs across nests were compared within each study site using χ^2 goodness of fit tests. Only nests that were active during incubation were used in this analysis.

Justification for pooling data across years, for all analyses, is as follows. Only a single year of data was available for four of the eight study site replicates due to site relocations. Moreover, in 2001, nests were either heavily parasitized (parasitism rates from 68 to 85%), or not parasitized at all (of 48 nests at Tallgrass Prairie Preserve and 19 nests at the Fall River site), which would have provided little variation for isodar analyses. However, 8% of the 61 dickcissel nests found on the Tallgrass Prairie Preserve in 2002 were parasitized. On sites sampled in both years where parasitism was observed, parasitism rates did not differ significantly among years (with sites as blocks, Cochran-Mantel-Haenszel $\chi^2=2.07$, $df=1$, $P=0.15$). Also, five or fewer nests were found in perch plots in some years on some study sites that were sampled in both years. Between five and ten nests were found on some prairie interior treatment plots on those study sites. As these were considered small nest sample sizes for individual years, pooling data among years was seen as the only reasonable remedy. Thus, we assumed that pooling data among years did not result in the loss of important information.

Results

A total of 466 dickcissel nests were found that survived past the laying stage (Table 1) across the 24 habitat plots comprising three habitat treatments, across the eight study sites sampled in 2001 and 2002. Overall nest mortality was due mostly to predation (58.5% of all nests), and less so to nest desertion (5% of all nests). Parasitism frequencies varied widely among study sites (0–85% of nests parasitized, across years). As noted above, dickcissel nests were not parasitized by cowbirds on the Fall River area, nor were any female cowbirds detected on point counts from that site. As cowbirds were not present on this study site to select habitats, zero values of parasitism and cowbird relative abundance were omitted from isodar analyses. Similarly, female cowbirds were not detected during point counts in the experimental perch and prairie interior habitats on the Tallgrass Prairie Preserve and Woodson Wildlife Area. Therefore, zero values of cowbird relative abundance and cowbird : dickcissel ratios from those habitat plots (i.e., not edge plots) were also omitted from isodar analyses.

The mean relative abundance of female cowbirds across study sites of the region varied independently of the abundances of all hosts ($r=0.52$, $P=0.19$) and dickcissels ($r=0.09$, $P=0.83$). Among habitat plots, the mean relative abundance of potential hosts was highest in edge habitat and lowest in prairie interior, being intermediate in the experimental perch habitat ($F_{7,14}=5.34$, $P=0.02$) (Fig. 2a). The mean species richness of potential hosts also differed among the habitat treatments, being higher in the edge habitat than either of the other two habitats ($F_{7,14}=50.83$, $P<0.0001$, respectively) (Fig. 2b). Thus, the wooded edge habitat had the highest quantity of hosts, and the experimental perches did not significantly alter the host community within prairie interior.

Cowbirds exhibited a pattern of density-dependent selection of wooded edge versus experimental perch and prairie interior habitats. Isodar y -intercepts were significantly positive along the wooded edge axes when cowbird relative abundance, cowbird:host ratio, parasitism frequency, and parasitism intensity were independently regressed among the wooded edge and prairie interior habitats (Figs. 3a, b and 4a, b). In fact, female cowbirds were only detected in—and only parasitized nests in—the primary wooded edge habitat on the Tallgrass Prairie Preserve, where overall female cowbird detections and parasitism rate were lowest (positive points lying directly on the y axis in Figs. 3a and 4a). In the first year of study (2001),

no cowbirds or cowbird eggs (in any of 50 dickcissel nests) were found on that site. Isodar y -intercepts were also significantly positive along the wooded edge axes when cowbird:host ratio, parasitism frequency, and parasitism intensity were regressed among the wooded edge and experimental perch habitats (Figs. 3d and 4c, d). The y -intercept was nearly significantly positive along the wooded edge axis when cowbird relative abundance was regressed among the wooded edge and experimental perch habitats (Fig. 3c). However, isodar slopes were significantly positive, but less than one, when cowbird relative abundance, cowbird : host ratio, parasitism frequency, and parasitism intensity were regressed among the wooded edge versus both the experimental perch and prairie interior habitats (Figs. 3a–d, and 4a–d). Thus, although cowbird density was higher near wooded edges than the other habitats when overall cowbird density was low, cowbird density increased more rapidly within the experimental perch and prairie interior habitats as local cowbird density increased geographically.

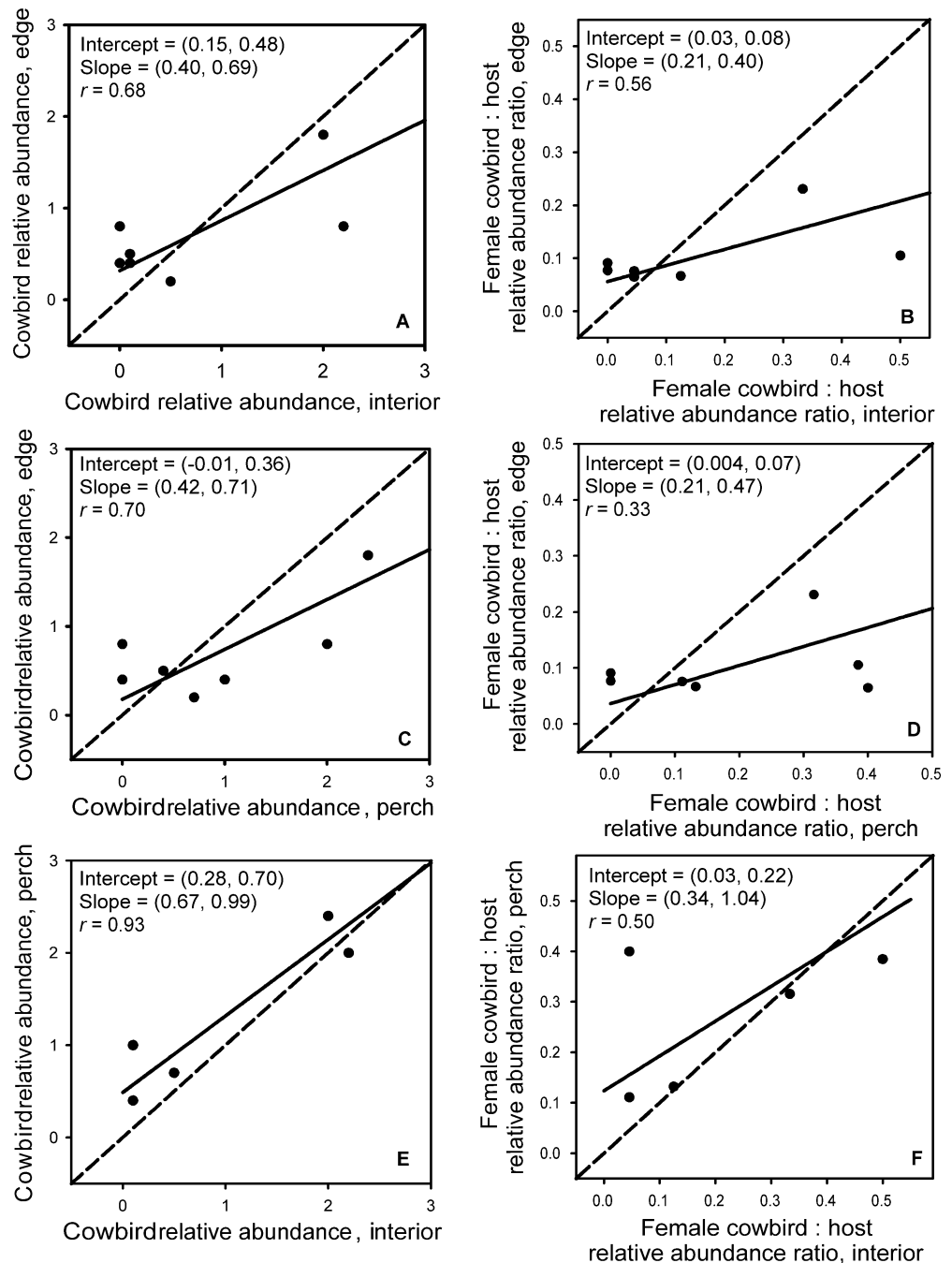
There was not consistent evidence that cowbirds selected the experimental perch over the prairie interior habitat at any level of local cowbird density. Cowbirds did use the experimental perches. From 40-point count surveys in experimental perch habitats, there were 34 and 48 detections of female and male cowbirds, respectively, alighting upon experimental perches. Female cowbirds were observed sitting on the experimental perches for several minutes without feeding or copulating, possibly watching host activity (including two females for entire 10-min count periods), whereas others would only alight temporarily or were flushed from perches upon observer approach or departure from point counts. On several occasions, several male cowbirds were observed courting one to three females on a single perch. As many as seven cowbirds were observed using a single perch at a time. The isodar y -intercepts of cowbird relative abundance and cowbird:host ratios were significantly positive along the experimental perch axes when these measures were regressed among the experimental perch and prairie interior habitats (Fig. 3e, f). Thus, cowbirds were more abundant (relative to area sampled and host abundance) in the experimental perch habitat than prairie interior at sites of lower overall cowbird abundance. The isodar slope of cowbird relative abundance was also significantly greater than zero, but less than one (albeit slightly). Thus, there was indication that cowbird relative abundance expanded from the experimental perch to the prairie interior habitat as local cowbird abundance increased geographically. The

Table 1 Number of dickcissel (*Spiza americana*) nests surviving to incubation, percent and number of nests parasitized by brown-headed cowbirds (*Molothrus ater*) (nests containing ≥ 1 cowbird egg or nestling), and parasitism intensity (number of cowbird eggs or

nestlings per parasitized nest) across three habitat plots in tallgrass prairie (≤ 100 m of wooded edges, experimental perch plots, and prairie interior >100 m from wooded edges)

Habitat plot	Nests (n)	Percentage of parasitized (n)	Parasitized intensity (n)
Wooded edge	170	60.6 (103)	2.5 (255)
Experimental perch	123	44.7 (55)	2.5 (140)
Prairie interior	173	45.7 (79)	2.6 (207)

Fig. 3 Isodar plots of female cowbird relative abundance (mean number counted per 10-min, 100-m radius point counts) and mean ratio of female cowbird:host relative abundances between locally-adjacent habitat pairs of **a, b** edge and interior, **c, d** edge and perch, and **e, f** perch and interior. *Edge* is prairie ≤ 100 m of a wooded edge. *Interior* is prairie >100 m from a wooded edge. *Perch* is an experimental perch plot containing artificial perches for cowbirds. Each point is an abundance coordinate between adjacent habitats on a particular site, averaged across years. *Solid lines* are geometric mean regressions correlating these measures among habitat pairs, where *dashed lines* passing through the origin with a slope of one reference isodar slopes equal to one (i.e., hypothetical density-independent habitat selection). The 95% confidence limits for regression intercept and slope parameters are given in addition to Pearson correlation coefficients (r). Axes extend below zero to illustrate points that would have otherwise lain on axis lines



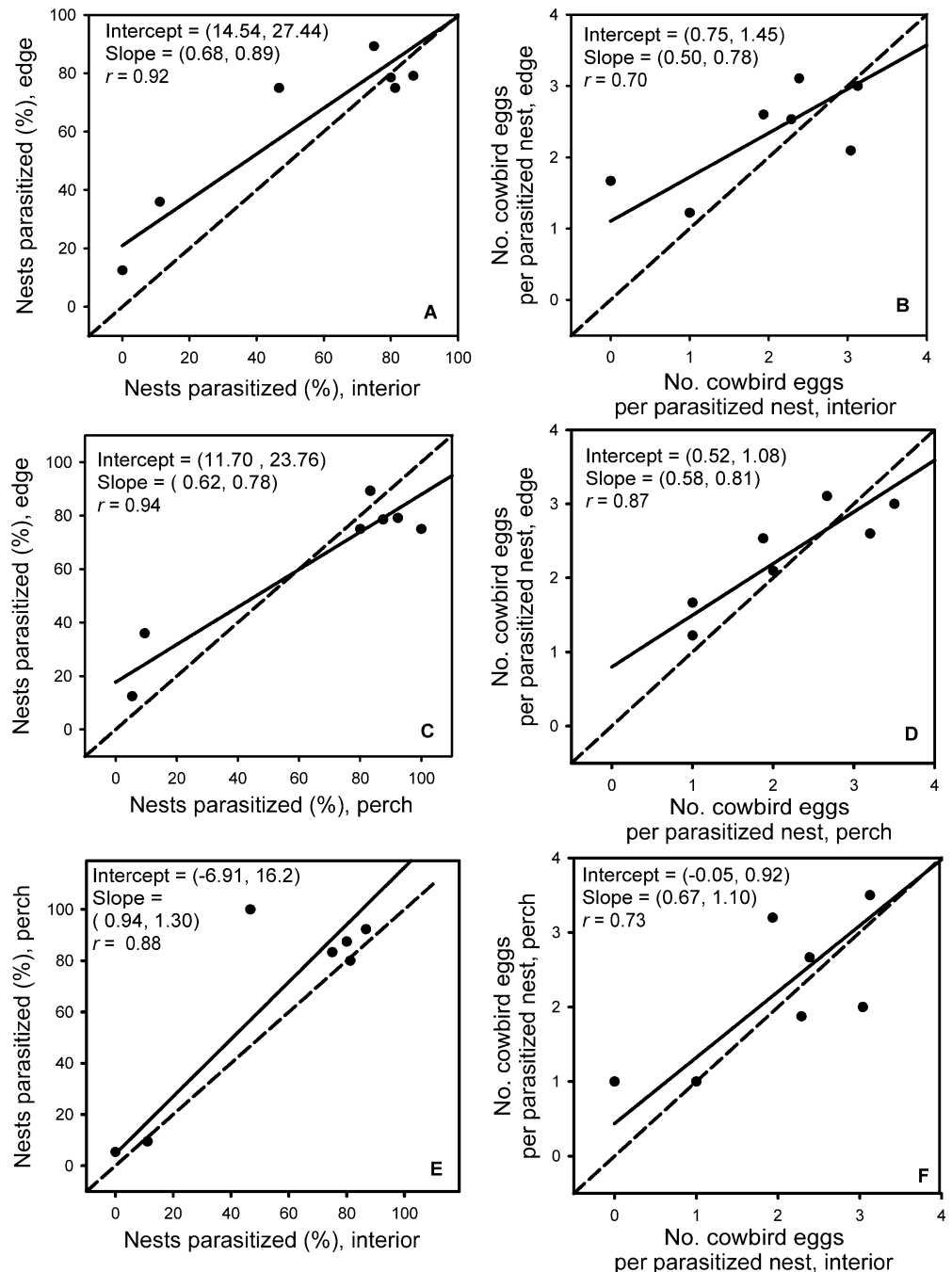
slope of cowbird:host ratios among the experimental perch and prairie interior habitats did not differ from one (Fig. 3f); thus, this measure changed at an equal rate among the two habitats along the geographical cowbird:host ratio gradient. However, isodar y -intercepts did not significantly differ from the origin when parasitism frequency and intensity (Figs. 4e, f) were regressed between the experimental perch and prairie interior habitats, and the slopes of these regressions did not differ significantly from one (Fig. 4). Therefore, levels of cowbird parasitism of dickcissel nests were not significantly different among the experimental perch and prairie

interior habitats at any point along the geographical gradient in cowbird parasitism.

The regression coefficients (r) for cowbird:host ratios among habitats were generally lower than those for cowbird relative abundances (Fig. 3). Thus, there was less variability in cowbird relative abundance among habitats than cowbird:host ratio among habitats as local cowbird abundance increased.

We now address cowbird parasitism intensity as a density-dependent effect on cowbird reproductive success. Neither the habitat treatment variable nor its interaction with parasitism intensity of nests across plots within habitats explained significant variation in models of

Fig. 4 Isodar plots of cowbird parasitism frequency (percentage of nests parasitized) and parasitism intensity (number of cowbird eggs per parasitized nest) of dickcissel nests between locally-adjacent habitat pairs of **a, b** edge and interior, **c, d** edge and perch, and **e, f** perch and interior. *Edge* is prairie ≤ 100 m of a wooded edge. *Interior* is prairie >100 m from a wooded edge. *Perch* is an experimental perch plot containing artificial perches for cowbirds. Each point is a parasitism level coordinate between adjacent habitats on a particular site, averaged across years. *Solid lines* are geometric mean regressions correlating these measures among habitat pairs, where *dashed lines* passing through the origin with a slope of one reference isodar slopes equal to one (i.e., hypothetical density-independent habitat selection). The 95% confidence limits for regression intercept and slope parameters are given in addition to Pearson correlation coefficients (r). Axes extend below zero to illustrate points that would have otherwise lain on axis lines



cowbird egg hatchability or nest mortality rates (i.e., all had ΔAIC values <2 compared to the model including parasitism intensity only). Using these best fit models including parasitism intensity as the sole explanatory variable, neither cowbird egg hatchability nor daily nest predation during incubation were significantly related to multiple parasitism intensity (Table 2). However, daily nest predation during the nestling stage was positively related to parasitism intensity (Table 2). Thus, cowbird nestlings experienced increased levels of nest predation in dickcissel nests during the nestling stage as multiple parasitism intensity increased across all parasitized nests, but this effect was independent of habitat type. As there

was no significant trend of cowbird egg hatchability in relation to parasitism intensity, the number of cowbird eggs per nest corresponded to the number of cowbird nestlings present.

The distributions of cowbird eggs across dickcissel nests approximated a random Poisson distribution on five of seven sites ($P > 0.05$) (Table 3). Deviations of cowbird egg distribution from randomness on two sites were apparently due to greater numbers of nests with multiple cowbird eggs than expected by chance.

Table 2 Logistic regression model results of cowbird egg hatchability (proportion of incubated eggs that hatched) and daily nest mortality rates during incubation and nestling stages and in relation to cowbird parasitism intensity within dickcissel nests (1 to ≥ 6 cowbird eggs per nest). Losses (unhatched eggs or depredated nests), sample sizes (n) (number of cowbird eggs for hatchability model, nest exposure days for nest mortality models), and wald χ^2 statistics and P -values for slope parameters (β) are given. Positive or negative slopes indicate trends in the response variable as parasitism intensity increased. Sample sizes of nests per level of parasitism intensity are given in Table 3

Reproductive response variable	Losses	n	β	χ^2	P
Cowbird egg hatchability	115	232	-0.02	0.05	0.83
Daily nest mortality rates					
During incubation	99	1,447	-0.04	0.22	0.64
During nestling stage	41	422.5	0.22	4.04	0.04

Discussion

As indicated from multiple indices of density and host use among habitats, brown-headed cowbirds exhibited a pattern of density-dependent selection of tallgrass prairie edge versus interior habitats across a geographical gradient in cowbird abundance. Cowbird density was highest near wooded edges on study sites where local cowbird density was low. Moreover, female cowbirds and their eggs were only found near wooded edges on the study site where cowbird density was lowest. This resembles previously documented edge effects on cowbird parasitism of grassland birds (Johnson and Temple 1990), and provides further evidence that wooded edges are a primary cowbird habitat in grassland landscapes. However, as local cowbird density increased geographically, cowbird density increased at a higher rate in prairie interior and experimental perch habitats, presumably secondary cowbird habitats.

Results of cowbird use of the experimental perch habitat were mixed. At sites of low cowbird abundance, cowbird relative abundance and cowbird:host ratios were signifi-

cantly higher in the experimental perch habitat than in prairie interior. Cowbird relative abundance increased at a slightly higher rate in prairie interior as local cowbird abundance increased, whereas cowbird:host ratios increased at equal rates in both habitats. However, the experimental perches had no effect on parasitism levels of dickcissel nests at all levels of local cowbird parasitism. Thus, the experimental perch and prairie interior habitats were functionally similar with regard to actual cowbird use of hosts in the habitats.

The index of host quantity (host relative abundance) was greatest at the wooded edge (Fig. 2). In accordance with isodar theory, cowbird density measures had positive intercepts along the wooded edge axis, which might reflect cowbird perception of edges being host rich. In urban landscapes in Spain, Fernández-Juric (2001) similarly found isodar intercepts of avian densities to be positive in park habitats containing what were claimed to be quantitatively superior resources (measures of vegetation structure). A similar isodar pattern was found for migrant frugivorous warblers in Israel, where warbler densities were initially highest in habitats with greater fruit densities (Shochat et al. 2002). However, the isodar regression coefficients for cowbird:host ratios among habitats were lower than those for cowbird relative abundances (Fig. 3). Like the observed geographic variation in cowbird to host abundance, this indicates that cowbird abundance does not closely parallel host abundance among habitats as cowbird density changes across the study sites. Thus, the positive isodar intercepts along the edge axis suggests that cowbirds might also be cuing into host accessibility at edges, due to the presence of survey perches, in their perception of host quantity. The lack of a consistent experimental perch effect on cowbird abundance or parasitism suggests a possible synergy between perch presence and host abundance being important to cowbird habitat selection.

Table 3 Distribution of the observed and expected number of cowbird eggs per dickcissel nest across eight study sites in tallgrass prairie. Expected Poisson distributions of eggs across nests determined using the method of Mayfield (1965)

Study site	No. of nests	Number of cowbird eggs/nest									No. of cowbird	
		0	1	2	3	4	5	6	7	No. of nests ^a	Eggs P^b	
Chase County SFL	Observed	7	8	12	10	3	5	1	0			
	Expected	4.7	10.7	12.2	9.3	5.3	2.4	0.9	-	46	105	0.34
El Dorado SP	Observed	11	8	11	6	4	0	1	0			
	Expected	7.4	12.7	10.8	6.1	2.6	0.9	0.3	-	41	70	0.20
Fall River Area	Observed	0	0	0	0	0	0	0	0			
	Expected	-	-	-	-	-	-	-	-	13	0	-
Jeffrey WA	Observed	8	8	18	7	5	1	2	0			
	Expected	6.1	12.7	13.2	9.2	4.7	2.0	0.7	-	49	102	0.18
Konza Prairie, 2001	Observed	6	2	5	16	7	2	3	1			
	Expected	2.2	6.6	9.6	9.4	6.9	4.0	2.0	0.8	42	123	0.006
Konza Prairie, 2002	Observed	15	15	22	8	7	3	1	1			
	Expected	10.4	20.2	19.4	12.5	6.1	2.3	0.8	0.2	72	139	0.19
Tallgrass Preserve	Observed	83	3	2	0	0	0	0	0			
	Expected	81.3	6.5	0.26	-	-	-	-	-	88	7	<0.01
Woodson WA	Observed	43	10	1	0	0	0	0	0			
	Expected	43.2	9.6	1.1	-	-	-	-	-	54	12	0.99

^aNumber of nests found during laying or incubation only

^bDeviations from Poisson distributions determined from χ^2 goodness of fit tests. Egg distributions with P -values >0.05 are considered to be randomly distributed across nests

The isodar slopes of cowbird distribution observed in this study might indicate how cowbirds perceived habitat quality with increasing cowbird density (Morris 1988). The isodar functions of cowbird density approached from the wooded edge axis and tended toward the experimental perch and prairie interior axes (Figs. 3 and 4), reflecting the increase in cowbird density in prairie interior as local cowbird density increased geographically. From these graphs (Figs. 3 and 4), it appears that cowbirds became more abundant and parasitized more nests in prairie interior at sites of highest cowbird abundance and parasitism. This resembles *crossover regulation* illustrated in Morris (1988) where perceived fitness in the primary habitat is predicted to decline with increasing density at a steeper rate than in the secondary habitat. Our data on cowbird success in dickcissel nests alone do not match this prediction. We did detect a density-dependent effect on cowbird reproductive success in dickcissel nests: as multiple parasitism intensity increased across nests, daily nest predation rates increased during the nestling stage. This density-dependent effect could provide incentive for cowbirds to exploit hosts in otherwise unoccupied secondary habitats as their conspecific density increases within primary edge habitat. The density effect on cowbirds, however, was statistically similar among dickcissel nests in all habitats. Based on examination of cowbird success in dickcissel nests alone, we would predict *parallel regulation* (Morris 1988) of cowbird distribution, where settlement should occur at equal rates in both habitats due to similar density-fitness functions. This mismatch in isodar slope versus density-reproductive success functions may be due to our inability to fully assess cowbird fitness perceptions among habitats. Density-dependent effects on cowbird reproductive success may have been more severe for cowbirds at wooded edges than was detected, possibly due to losses of cowbird eggs to rejection or desertion of parasitized nests by other host species (McGeen 1972), or conspecific egg removal by cowbirds. On Konza Prairie (Kansas), Bell's vireos (*Vireo bellii*) nest in wooded edges and desert multiply parasitized nests with much greater frequency than singly parasitized nests (K. Kosciuch, unpublished data). Cowbird territoriality (Rothstein et al. 1986) and variation in competitive abilities (Sutherland and Parker 1985) among cowbirds could have provided a despotic mechanism underlying the observed patterns of cowbird distribution. Although actual fitness-density functions may have been similar among the habitats, despotic cowbirds dwelling at edges may have affected perceived fitness (Morris 2003) at edge habitats. The elevated perches and host densities at wooded edges might afford cowbirds in that habitat the opportunity to be despotic through facilitating defense of host resources within a relatively smaller area (Rothstein et al. 1986; Elliott 1980). However, we have no data on habitat-specific dominance in cowbirds.

Alternatively, cowbirds may violate the 'ideal' assumption of the ideal free distribution and not be optimally distributed among available habitats (Robinson et al. 1999). In Illinois, cowbirds did not occur more frequently

in host communities with fewer rejecter species and lower nest predation (Robinson et al. 1999). However, host community composition—and likely nest predation (Chalfoun et al. 2002)—are quite variable across the geographic range of cowbirds, so cowbird density should present the most consistent indicator of host habitat suitability across the cowbird's range. Mechanisms regulating density-dependent habitat selection in cowbirds need further study.

Although there was some previous evidence that brood parasitism can increase the incidence of nest depredation (e.g., Dearborn 1999), this is the first documentation, of which we are aware, of an increase in nest depredation during the nestling stage with increasing multiple parasitism intensity. We assume the increases in multiple parasitism were due to increasing overlap among female cowbird laying ranges, as supported by previous molecular maternity studies (Fleischer 1985; Hahn et al. 1999; Strausberger and Ashley 2003). Zimmerman (1983) found no effect of parasitism on nest depredation in dickcissels, but he did not consider this possible effect during separate nest stages (i.e., incubation vs nestling). Activity associated with many cowbird young in nests (parental feeding trips, noises made by begging cowbird young, etc.) might be especially attractive to nest predators (Martin et al. 2000; Dearborn 1999). In another study, cowbirds from multiply parasitized dickcissel nests had lower mass at fledging than cowbirds from nests with fewer cowbird eggs (Hatch 1983), which presents another cost of multiple parasitism. Although not found in the present study, cowbirds experienced reduced egg hatchability in relation to parasitism intensity in wood thrush (*Hylocichla mustelina*) nests (Trine 2000). Thus, density-dependent effects of multiple parasitism on cowbird reproductive success are apparent in dickcissels and other hosts.

If the depressive effect of multiple parasitism on cowbird fitness influences cowbird habitat selection, what might be the signal to cowbirds that threshold densities have been reached within host habitats? One possibility is that cowbirds might avoid laying in already parasitized nests (Ortega et al. 1994), which might result in more of an ideal preemptive distribution (Pulliam and Danielson 1991). This is doubtful in the Flint Hills study area due to the commonly observed random distribution of cowbird eggs among already parasitized nests (Table 3, Elliott 1977; see also Johnsgard 1997; Trine 2000). A proximate density cue for female cowbirds in selecting habitats might simply be the presence of conspecifics. Negative effects of multiple parasitism on reproductive success or despotism might then ultimately reinforce this density cue.

This study examined density-dependent cowbird selection of a single host species among habitats along a naturally-occurring geographical gradient in cowbird abundance. As local cowbird abundance was not experimentally manipulated across this wide geographic area, the observed patterns may have covaried with other factors that could affect cowbird selection of hosts in edge versus interior habitats. Incorporation of such covariates into geometric mean regressions has not been described.

However, the local availability of hosts across the region was not associated with the geographic trend in cowbird abundance, as described above. In other analyses (Jensen 2003), this trend in cowbird abundance was also found not to correlate with woodland:grassland habitat ratios in surrounding landscapes or variation in prairie vegetation structure among study sites. Only the local density of female cowbirds was correlated with parasitism levels (Jensen 2003). Others have found parasitism rates of forest and grassland birds in the continental United States to correlate more strongly with regional variation in cowbird abundance than variables of landscape configuration or habitat availability (Thompson et al. 2000; Herkert et al. 2003). Existing cowbird removal programs (Rothstein and Cook 2000) could be used to test experimentally the effect of cowbird density on cowbird host selection within and among habitats.

Density-dependent habitat selection has relevance to the research and management of brood parasites of conservation concern. For example, where local cowbird abundance is high, habitat preferences of cowbirds may not be evident due to density dependence in their habitat selection. Thus, it would be incorrect to conclude that cowbird host use is independent of habitat type if studied when or where cowbirds are especially abundant (e.g., Zimmerman 1993). Furthermore, direct or indirect management of brood parasite abundance as a method to reduce parasitism levels on hosts of conservation concern may only significantly affect parasitism levels in secondary cowbird habitats (e.g., habitat interior), or on secondarily-preferred host species (Woolfenden et al. 2003). In theory, less of a reduction in parasite population size would be required to reduce or eliminate parasitism from secondarily-preferred cowbird habitats or host species.

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