

Brown-headed Cowbird parasitism of the Black-throated Sparrow in central Arizona

Matthew J. Johnson¹ and Charles van Riper, III²

USGS Southwest Biological Science Center, Colorado Plateau Research Station, Box 5614, Northern Arizona University, Flagstaff, Arizona 86011 USA

Received 18 August 2003; accepted 19 January 2004

ABSTRACT. From 1994–1996 we investigated effects of Brown-headed Cowbird (*Molothrus ater*) parasitism on Black-throated Sparrow (*Amphispiza bilineata*) nesting success in the Verde Valley of central Arizona. Of 56 Black-throated Sparrow nests, 52% were parasitized. Black-throated Sparrows appear to respond to natural parasitism by accepting the cowbird egg, deserting the nest, or burying the cowbird egg. Removal and damage of host eggs by female cowbirds effectively reduced clutch size from an average of 3.4 to 1.9 eggs. Because of this reduced clutch size, Black-throated Sparrow reproductive success was significantly lower in parasitized nests (0.2 young fledged/nest) as compared to nonparasitized nests (1.6 young fledged/nest). When comparing cowbird parasitism between two habitat types, we found significantly higher parasitism frequencies in crucifixion-thorn (*Canotia holacantha*) versus creosote-bush (*Larrea divaricata*) habitat. We argue that this difference in parasitism is due to the greater number of tall perches (e.g., shrubs >4 m) available in crucifixion-thorn habitat, providing vantage points for female cowbirds to better find Black-throated Sparrow nests.

SINOPSIS. Parasitismo en *Amphispiza bilineata* por parte de *Molothrus ater*

De 1994–1996 investigamos el efecto en el éxito de anidamiento del parasitismo en el gorrión *Amphispiza bilineata* por parte del tordo (*Molothrus ater*). El estudio se llevó a cabo en el Verde Valley, Arizona. De 56 nidos estudiados del gorrión el 52% de estos resultaron estar parasitados. Los gorriónes parecen responder al parasitismo por parte del tordo, ya sea aceptando el huevo, abandonando el nido o enterrando dentro del mismo nido el huevo del tordo. La remoción o daño a los huevos del hospedero por parte de hembras de tordo redujo la camada del gorrión de 3.4 a 1.9 huevos. Debido a esta reducción en la camada, el éxito reproductivo del gorrión resultó significativamente menor en nidos parasitados (0.2 volantones/nido) que en nidos no parasitados (1.6 volantones/nido). Cuando comparamos el parasitismo del tordo entre dos tipos de habitats, encontramos una frecuencia significativamente mayor en el matorral espinoso de *Canotia holacantha* que en el arbustivo de *Larrea divaricata*. Argumentamos que las diferencias en parasitismo se deben al mayor número de perchas altas (ej. arbustos mayores de 4 m) en el matorral espinoso, las cuales proveen de mejores puntos de observación a las hembras de tordo para localizar los nidos de gorrión.

Key words: Arizona, Black-throated Sparrow, Brown-headed Cowbird, cowbird nest searching, nest parasitism, reproductive success

Throughout the arid southwestern United States, parasitism by Brown-headed Cowbirds (*Molothrus ater*) is common in riparian zones (Phillips et al. 1964; Brown 1994; Goguen and Mathews 1996). High levels of nest parasitism in riparian habitat is due in part to the close proximity of cowbird foraging sites (agriculture and urban developments) and the availability of potential hosts (Robinson et al. 1995; Tewksbury et al. 1998). Cowbird parasitism in up-

land habitats in the southwest is less frequent, mainly due to fewer cowbirds and a lower density of potential hosts (Friedmann et al. 1977; Robinson et al. 1995; Curson 1996). The Verde Valley of Arizona is comprised of upland and riparian habitat and has experienced increased agriculture and urban development. Consequently, Brown-headed Cowbirds have recently increased in abundance (Taylor and Jackson 1916; Collins 1951; Philips et al. 1964).

The Black-throated Sparrow (*Amphispiza bilineata*) is locally common and widely distributed in upland habitats throughout the desert southwestern United States (Bent 1968; Naranjo and Raitt 1993; Johnson et al. 2002). Because Black-throated Sparrows breed in desert

¹ Corresponding author. Email: matthew.johnson@nau.edu

² Current address: USGS Southwest Biological Science Center, Sonoran Desert Research Station, 125 Biological Sciences East, University of Arizona, Tucson, Arizona 85721 USA.

uplands, they usually escape cowbird parasitism and have rarely been recorded as a cowbird host (Friedmann 1963; Delesantro 1978; Zimmer 1993; A. Pidgeon, unpubl. data; S. Coe, pers. comm.). Yet, due to the favorable cowbird habitat changes in the Verde Valley, and the fact that Black-throated Sparrow peak breeding period overlaps with cowbird breeding (May–June), this sparrow could be a potential cowbird host (Johnson 1997).

Host species have been found to respond to cowbird parasitism by either accepting or rejecting the cowbird egg (Rothstein 1975b; Goguen and Mathews 1996; Hosoi and Rothstein 2000). Rejection of parasitism by a host is adaptive, but in many hosts it has not yet become common, possibly because hosts may not have had time to evolve counter defenses to parasitism (Davies and Brooke 1988; Lotem and Rothstein 1995; Rothstein and Robinson 1998). Thus, species that have only recently been exposed to parasitism are in many cases acceptors of parasitic eggs (May and Robinson 1985; Rothstein and Robinson 1998). However, even some hosts with long histories of exposure to parasitism still accept eggs (Rothstein 1975a; Davies and Brooke 1988), even though accepting the cowbird egg can potentially have a negative effect on host reproductive success (Rothstein 1975a; Biermann et al. 1987; Robinson et al. 1995). The response of Black-throated Sparrows to parasitism, in areas recently exposed to Brown-headed Cowbirds, and the effects of parasitism on sparrow reproductive success has not been extensively studied.

Frequency of parasitism and the subsequent impacts of parasitism on reproductive success can also vary according microhabitat features such as nest cover or factors such as proximity and availability of perches (Hauber and Russo 2000). Some studies support the relationship of vegetative cover and the risk of parasitism (Larison et al. 1998; Moskat and Honza 2000), while others have found either no relationship or that the relationship between cover and parasitism varied by study site (Anderson and Storer 1976; Freeman et al. 1990; Clotfelter 1998; Hauber and Russo 2000; Howe and Knopf 2000). It has also been suggested that the ability of cowbirds to locate nests is enhanced when perches are available from which a cowbird can survey for and find nests (Anderson and Storer 1976; Biermann et al. 1987; Freeman et al.

1990; Clotfelter 1998; Hauber and Russo 2000). Throughout the southwestern United States, shrub species in desert upland habitats vary according to geographic location and landscape (i.e., plains vs. hills, slope, aspect, soil type, temperature, precipitation, and elevation; Pase and Brown 1994). Structural height of desert shrub habitats can be dominated by tall stature shrubs, i.e., crucifixion thorn (*Canotia holacantha*) or low-stature shrubs, i.e., creosote bush (*Larrea divaricata*). The tall-stature habitat type in desert uplands may offer vantage points that cowbirds can utilize to find potential host nests, thus resulting in higher parasitism frequencies.

The purpose of this study was to examine effects of Brown-headed Cowbird parasitism on a Black-throated Sparrow population. Specific questions that we addressed were (1) how do Black-throated Sparrows respond to natural Brown-headed Cowbird parasitism; (2) does Brown-headed Cowbird parasitism affect Black-throated Sparrow reproductive success (i.e., clutch size, hatching success, fledging success and nest success); (3) does Brown-headed Cowbird parasitism occur less frequently in nests with increased plant concealment; and (4) do Brown-headed Cowbird parasitism frequencies differ between low- and tall-stature habitat types.

METHODS

Our study was conducted between April 1994 and August 1996 in north central Arizona, approximately 7 km northwest of Camp Verde, at Montezuma Castle National Monument and on adjoining U.S. Forest Service lands. The study area is less than 1 km from Wet Beaver Creek, with an extensive riparian zone, and an upland topography of mixed knolls, slopes and draws (TOPO: GPS UTM NAD 83 422596mE, 3830761mN, elevation 1032 m). The study area was divided into two individual sites based on habitat differences. Study site #1 (total area 42.9 ha), was dominated by low-stature creosote bush, while the adjacent study site #2 (total area 42.2 ha) consisted mainly of the taller crucifixion thorn.

An 8 × 16 m modified Braun-Blanquet 'releve' (Mueller-Dombois and Ellenberg 1974) was used to characterize shrub vegetation at 18 randomly selected locations within each study

site. In each releve' we estimated percent total shrub vegetation coverage using the following cover classes (1, 10–20%; 2, 21–40%; 3, 41–60%; 4, 61–80%; 5, 81–100%). The estimated percent cover of each shrub species, along with elevation, slope, aspect, and slope pitch angle, were also recorded.

To provide an index of cowbird perch availability, we estimated shrub height in each releve' by using the following shrub height categories 1, 0–0.5 m; 2, 0.6–1.0 m; 3, 1.1–2.0 m; 4, 2.1–5.0 m; and 5, >5.0 m. The shrub height in our study areas varied between 0.25 to over 6 m. Based on our observations of cowbird perch use in the two study areas, we determined that relative to the vegetation height within each habitat type, a shrub height of ≥ 4 m was needed for Brown-headed Cowbirds to gain a vantage point to find Black-throated Sparrow nests.

To assess predictors of parasitism risk as related to nest concealment (i.e., nest microhabitat features that may either increase or decrease the probability being parasitized), we measured the following Black-throated Sparrow nest microhabitat features: shrub species the nest was built in, shrub height, height of nest above ground, distance from nest rim to top of the shrub, distance from nest rim to the nearest outer shrub edge, and nest azimuth (compass direction of nest placement relative to the main shrub axis). These variables were selected according to previous studies related to nest-site selection (van Riper 1976; Nias 1983; van Riper 1995). However, no studies have been conducted on nest-site selection of Black-throated Sparrows in this habitat type, and therefore variables were also selected according to the vegetative structure that nests were constructed in.

A Black-throated Sparrow nest was defined as active when at least one sparrow egg was laid. Natural parasitism frequency was calculated as the proportion of all nest attempts in an entire breeding season that were parasitized. Because female cowbirds may remove host eggs (Sealy 1992), when a cowbird egg was present, missing Black-throated Sparrow eggs were assumed to have been removed by cowbirds and were counted as losses to parasitism. Damaged eggs observed in parasitized nests could be interpreted as a loss to parasitism, yet these losses could be due to several causes (Blankespoor et al. 1982; Weatherhead 1991), and therefore

damaged sparrow eggs were not counted as losses. Black-throated Sparrow reproductive success was calculated as the number of eggs laid that fledged ≥ 1 young (Van Tyne and Berger 1971). Nesting success was calculated using the Mayfield (1975) method to reduce the error introduced when nests are observed for different lengths of time.

Incidental cowbird observations were conducted while we searched for sparrow nests between 5:00–11:00 and 17:00–19:00 from 15 April–15 August in each year. Nest searching of both study sites was alternated every other day to ensure survey coverage was equal between the two study sites.

Statistical analysis. We used standard parametric statistical tests for all data that were normally distributed. Nonparametric tests were used where sample sizes were small, categorical, or when data were not normally distributed. We used Yates correction for all chi-square tests with one degree of freedom (Yates 1934). Since nest-site data were not normally distributed, all nest-site data were log-transformed.

Rayleigh's test for directionality was used to analyze nest orientation differences between parasitized and nonparasitized nests (Batschelet 1981). Statistical significance was set at $P \leq 0.05$. Mean values ± 1 SE of all statistical measures are reported unless otherwise noted. All statistical tests were two-tailed.

RESULTS

In study site #1, vegetation cover was dominated by creosote-bush (75%), followed by crucifixion-thorn (15%), broom snakeweed (*Gutierrezia sarothrae*, 5%), catclaw acacia (*Acacia greggii*), mahonia (*Berberis haematocarpa*) and one-seeded juniper (*Juniperus monosperma*; all <1%). Vegetation cover in study site #2 was dominated by crucifixion-thorn (55%), followed in decreasing abundance by creosote-bush (35%), catclaw acacia (3%), mahonia, broom snakeweed and one-seeded juniper (<1%).

Over our 3-year study Brown-headed Cowbirds parasitized 52% (29 of 56) of Black-throated Sparrow nests. Parasitism frequencies were higher in 1994 (16/27, 59%) than in 1995 (11/27, 41%), but these differences were not significant ($\chi^2_1 = 2.0$, $P > 0.05$). In 1996, a severe drought occurred throughout Arizona,

Table 1. Mayfield's nesting success calculated for parasitized and nonparasitized Black-throated Sparrow nests during 1994 and 1995 in the Verde Valley, Arizona.

	Probability of survival ^a		
	Egg stage	Nestling stage	Overall
Parasitized	0.37	0.67	0.22
Nonparasitized	0.42	0.98	0.34
Combined	0.38	0.76	0.27

^a Probabilities based on survival of ≥ 1 offspring.

and only two Black-throated Sparrow pairs nested in our study area; cowbirds parasitized both of those nests. Therefore, data were only analyzed from the non-drought period (i.e., 1994 and 1995).

Black-throated Sparrows appear to respond to natural parasitism by either accepting the Brown-headed Cowbird egg (81%, $N = 22$), deserting the nest (15%, $N = 4$), or burying the parasitic egg (4%, $N = 1$). Average sparrow clutch size of parasitized nests at the time of desertion was 0.9 ± 0.18 ($N = 4$). Average sparrow clutch size of nests prior to parasitism was 3.3 ± 0.33 , ($N = 3$).

Data on reproductive success came from non-depredated nests in 1994 and 1995. We observed 1.5 fewer Black-throated Sparrow eggs remaining in the nest at the time of hatching in parasitized nests (1.9 ± 0.2 , $N = 16$) than in nonparasitized nests (3.4 ± 0.1 , $N = 14$; $t_{28} = 5.5$, $P = 0.06$). This contributed to a significantly lower number of host chicks hatching in parasitized nests (0.4 ± 0.2 , $N = 16$), compared to nonparasitized nests (1.6 ± 0.4 , $N = 14$, $t_{28} = 2.8$, $P = 0.01$). The high occurrence of Black-throated Sparrow hatching failure was due principally to egg damage. In 26% of parasitized nests ($N = 16$), small puncture marks

or cracks were detected in host eggs compared to 0% in nonparasitized nests ($N = 14$). Among non-depredated nests, the number of young that successfully fledged from parasitized nests (0.3 ± 0.1 , $N = 16$) was significantly less than for nonparasitized nests (0.6 ± 0.3 , $N = 14$; $t_{28} = 1.2$, $P = 0.01$).

Overall nest success using Mayfield (1975) estimates was not significantly different between 1994 and 1995; therefore, these data were combined ($\chi^2_1 = 1.60$, $P > 0.05$). The probability of a Black-throated Sparrow surviving 21 d to fledge at least one young was 0.27, with nestling success greater than egg success among parasitized and nonparasitized nests (Table 1). Furthermore, parasitized nests had lower probability of success than nonparasitized nests.

All nest concealment variables from the two study sites were pooled because there were no significant differences between the study sites. There were no significant differences between parasitized and nonparasitized nests in the shrub species that nests were built in (creosote-bush vs. crucifixion-thorn; $\chi^2_1 = 0.09$, $P > 0.05$). There also were no significant differences between parasitism frequencies and the four nest microhabitat features used as an index of nest concealment (Table 2). For orientation of the nest relative to the center of the shrub, we found no significant differences between parasitized (mean angle = 69°) and nonparasitized nests (mean angle 154° ; $\chi^2_1 = 1.0$, $P > 0.05$). Nests nearer to the outside of the shrub were not parasitized significantly more frequently than nests near the center of the shrub (Table 2).

During 1994 and 1995 parasitism frequencies were significantly greater in study site #2 (crucifixion-thorn habitat; 70%) than in study site #1 (creosote-bush habitat; 30%; $\chi^2_1 = 8.8$, $P < 0.05$; Table 3). The average number of

Table 2. Nest substrate characteristics measured for nonparasitized ($N = 24$) and parasitized ($N = 22$) Black-throated Sparrow nests during 1994 and 1995 in the Verde Valley, Arizona.

Variable	Nonparasitized Mean \pm SE	Parasitized Mean \pm SE	z	P^a
Shrub height (cm)	187.6 \pm 8.8	192.1 \pm 9.9	-0.15	0.88
Nearest edge (cm)	54.3 \pm 4.0	46.9 \pm 4.8	-1.31	0.19
Nest to top (cm)	153.1 \pm 7.5	155.6 \pm 8.1	-0.18	0.86
Nest height (cm)	34.5 \pm 5.0	35.9 \pm 7.8	-0.12	0.26

^a Mann-Whitney U -test on log-transformed data.

Table 3. Differences in cowbird parasitism rates of Black-throated Sparrow nests by habitat type, number of perches available, and shrub height during 1994 and 1995 in the Verde Valley, Arizona.

	Habitat		<i>P</i> ^a
	Creosote-bush (study site #1)	Crucifixion-thorn (study site #2)	
Brood parasitism (%)	30% (8/27)	70% (19/27)	<0.05
Perches available (mean ± SE)	3.5 ± 1.3 (<i>N</i> = 18)	12.2 ± 3.0 (<i>N</i> = 18)	0.001
Shrub height (mean ± SE)	3.6 ± 0.3 (<i>N</i> = 30)	7.4 ± 0.53 (<i>N</i> = 90)	0.001

^a Comparing habitat types; $\chi^2_1 = 8.8$ for brood parasitism, $Z = -3.2$ and $Z = -3.3$ for perch availability and shrub height (Mann-Whitney *U*-test), respectively.

shrubs ≥ 4 m in height (available cowbird perches) was significantly greater in study site #2 than in site #1 (Mann-Whitney *U*-test, $z = -3.2$, $P = 0.001$; Table 3). The average shrub height was two times taller in study site #2 than in site #1 (Mann-Whitney *U*-test, $z = -3.3$, $P = 0.001$).

DISCUSSION

The incidence of Brown-headed Cowbird parasitism of the Black-throated Sparrow population in the Verde Valley was much higher (52%) than had been reported in previous studies (Friedmann 1963; Delesantro 1978; Zimmer 1993; A. Pidgeon pers. comm.; S. Coe, pers. comm.). This higher frequency of parasitism could be due to the fact that cowbirds have become more common in the Verde Valley as agriculture and urban development has increased (Taylor and Jackson 1916; Collins 1951; Robinson et al. 1995). The increasing number of cowbirds has led to high parasitism frequency in Black-throated Sparrows, a species not usually parasitized in desert upland habitats throughout the western United States (Friedmann 1963; Robinson et al. 1995).

The relatively recent increase in cowbird parasitism in Verde Valley upland habitats may explain the pattern of Black-throated Sparrow response to parasitism. During our study, the most common response of Black-throated Sparrows to natural parasitism was acceptance (81%), followed by deserting the nest (15%) or burying the cowbird egg in the nest (4%). Our results were similar to a study in New Mexico where Black-throated Sparrows responded to parasitism by acceptance (74%), nest desertion (22%) or egg burial (4%; Delesantro 1978). However, studies may underestimate the fre-

quency of parasitism of rarely used hosts, if these hosts are rejecters, because cowbird eggs may be ejected before being observed. Therefore, status of hosts such as Black-throated Sparrows can only be classified correctly (as acceptors or rejecters) through experimentation. Yet, we suggest that Black-throated Sparrows appear to be acceptors to cowbird parasitism because of the relatively high frequency of parasitism (52%) recorded in this study. Freidmann et al. (1977) has suggested that a species can be assumed to be an acceptor if parasitism is noted in more than 20% of its nests.

During this study, nest desertion by Black-throated Sparrows was also a response to parasitism, but this only occurred when one host egg remained. This was the case in all four parasitized nests that were deserted. We found that if the host clutch was not reduced below two eggs, female sparrows completed incubation, which seems to suggest that Black-throated Sparrows may be sensitive to a clutch-size threshold. This type of nest desertion among other parasitized hosts has been considered a response to partial clutch reduction rather than to the act of parasitism (Rothstein 1986; Hill and Sealy 1994).

A third response was burying the cowbird egg with nest material, an effective adaptation to cowbird parasitism used particularly by Yellow Warblers (*Dendroica petechia*; Burgham and Picman 1989; Sealy 1995). This could be an effective anti-parasite strategy for Black-throated Sparrows, but we detected it in only one of 29 parasitized nests. In this instance it is unknown if this cowbird egg was laid before host clutch initiation. It has been suggested that if the cowbird mis-timed laying the egg (i.e., before nest building was complete), this may not be a response to the cowbird egg, but just a

continuation of nest building (Clark and Robertson 1981).

It appears that no single response to counter parasitism has yet developed in the Verde Valley Black-throated Sparrow population. The apparent lack of adaptive responses (e.g., rejection) to cowbird parasitism by Black-throated Sparrows appears to support the evolutionary lag hypothesis (Rothstein 1990; Hosoi and Rothstein 2000). Black-throated Sparrows' acceptance of the cowbird egg, and occasionally nest desertion or egg burial, probably does not reflect a direct response to parasitism because the birds may not recognize the cowbird egg as a foreign egg (Ward et al. 1996). Rejection of parasitism by a host is adaptive, but in many hosts it has not yet become common because it takes time for new genetic variants to appear and increase as a result of selection (Davies and Brooke 1988; Lotem and Rothstein 1995). It has only been in the last 150 yrs that western North American populations of songbirds have been exposed to parasitism, and this may be insufficient time for counter adaptations to have evolved in many of these hosts (Terborgh 1992; Lotem and Rothstein 1995; Robinson et al. 1995). This may be especially true among Black-throated Sparrows since Brown-headed Cowbirds have only become common in recent years in Arizona (Phillips et al. 1964), and this host has probably only been exposed to extensive cowbird parasitism for less than 100 yrs (Taylor and Jackson 1916; Collins 1951).

Because Black-throated Sparrows have not developed effective strategies toward parasitism, parasitism affects sparrow reproductive success. Parasitized Black-throated Sparrow clutches averaged 1.5 fewer eggs than nonparasitized clutches, presumably because of egg removal. These results coincide with those of Sealy (1992), where female cowbirds removed at least one host egg from 33%–90% of all parasitized Yellow Warbler nests. Another negative influence on reproductive success was host egg damage. There was a significantly greater number of Black-throated Sparrow eggs cracked in parasitized (26%) than in nonparasitized (0%) sparrow nests. Although damaged eggs in parasitized nests could be the result of several causes (Blankespoor et al. 1982; Weatherhead 1991), the fact that we found none in nonparasitized nests suggests that these losses are likely attributable to parasitism. Damage to host

eggs may occur while the cowbird is attempting to remove host eggs from the nest, while laying her egg, or during incubation when the parasitic egg knocks against the host eggs (Spaw and Rohwer 1987; Røskaft et al. 1990; Weatherhead 1991).

We also found that nest success was lower in 1994, when the parasitism frequency was higher (57%) than in 1995 (41%). These differences in parasitism frequencies from year to year may be explained by differences in the arrival date of the parasite on the breeding grounds (Trail 1992; Robinson et al. 1995). Cowbirds arrived relatively late (mid May) in 1995; in contrast, they arrived as early as mid April in 1994 (M. Johnson, unpubl. data). Because cowbirds may time parasitism to coincide with the period of maximum host nest availability, early nesting species such as Black-throated Sparrows and late nesting hosts may experience lower rates of parasitism (Robinson et al. 1995).

The probability that a nest will be parasitized may also be influenced by the degree of concealment of the host nest (Hauber and Russo 2000). However, none of the structural features (i.e., height of the shrub, distance of nest to the nearest edge of the shrub, distance of nest to the top of the shrub, nest height from the ground, and nest orientation) that we measured appear to be related to the probability of parasitism (Table 2). Creosote-bush and crucifixion-thorn, the primary shrubs used for nesting by Black-throated Sparrows, are relatively open desert shrubs and lack the dense vegetative cover to conceal a nest. Thus, perhaps nests in these shrubs are relatively visible to Brown-headed Cowbirds. Alternatively, our results may only reflect the variables we chose as an index of concealment, and perhaps other measures more accurately reflect nest conspicuousness. However, Saunders et al. (2003) used similar variables and found that well concealed Song Sparrow (*Melospiza melodia*) nests were parasitized less often. Our findings may have also been influenced by the vegetation cover at different scales (Larison et al. 1998), such as the proximity of perches surrounding the nest shrub (Saunders et al. 2003). Our study does suggest that the relationship between vegetative cover and parasitism varies by site and structure (i.e., shrub species) that the nest is built in (Clotfel-

ter 1998; Hauber and Russo 2000; Howe and Knopf 2000).

While nest concealment strategies appear to have little effect on the frequency of cowbird parasitism of Black-throated Sparrow nests, the proximity and availability of perches and host behavioral cues may have an effect on parasitism (Hauber and Russo 2000; Banks and Martin 2001; Robinson and Robinson 2001). We found significantly higher parasitism frequencies in the taller crucifixion-thorn habitat than in creosote-bush habitat (Table 3). Therefore, we suggest that at these two study sites the higher parasitism rate in the former habitat may be influenced by the availability of significantly higher natural perches.

There are a few other studies that support the relationship between perch height availability and parasitism. In Alberta, sagebrush sites with parasitized Brewer's Sparrow (*Spizella breweri*) nests had perches up to 4 m in height, situated in a nearby riparian strip, whereas sites without parasitism had no perches (Biermann et al. 1987). Anderson and Storer (1976) observed that in an open jack-pine (*Pinus banksiana*) habitat, parasitism of Kirtland's Warblers (*Dendroica kirtlandii*) was more likely when a dead snag was near the nest than in areas without dead snags. Cowbirds were also more efficient at finding active Red-wing Blackbird (*Agelaius phoeniceus*) nests where there were a higher number of perches (i.e., trees) available in close proximity to the nest (Freeman et al. 1990; Clotfelter 1998). Finally, Strausberger and Burhans (2001) suggested that trees provide vantage points from which cowbirds can observe nests undetected and thereby avoid aggressive host nest defense.

Because of its extensive geographic breeding range, the Black-throated Sparrow may be less vulnerable at the population level to the negative effects of cowbird parasitism than other species that are more geographically restricted, (e.g., the Black-capped Vireo (*Vireo atricapillus*), and the Golden-cheeked Warbler (*Dendroica chrysoparia*). The heavily parasitized Black-throated Sparrows in the Verde Valley may represent a metapopulation sink that can be maintained and supplemented by immigrants produced in more xeric areas where parasitism levels are lower (Hassel and May 1974; May and Robinson 1985). However, we suggest that as anthropogenic activities continue to ex-

pand into arid regions of the southwestern United States and Mexico, Brown-headed Cowbird populations will follow and may ultimately have a dramatic negative impact on arid-land passerine bird productivity.

ACKNOWLEDGMENTS

This study was funded by the National Park Service, a grant from the Southwest Parks and Monuments Association, and the United States Geological Survey. We thank Beth Bardwell, Mark Smedick, Randy Miller, and Dena Greenwood for assistance in the field. Mark Sogge, Charles Drost, Jennifer Holmes, Sandy van Riper, Maureen Stuart, and anonymous reviewers provided insightful comments on an earlier draft of the manuscript. This paper is contribution # 23-98 of the Colorado Plateau Field Station Technical Report Series.

LITERATURE CITED

- ANDERSON, W. L., AND R. W. STORER. 1976. Factors influencing Kirtland's Warbler nesting success. *Jack-Pine Warbler* 54: 105-115.
- BATSCHULET, E. 1981. Circular statistics in biology. Academic Press, London, UK.
- BANKS, A. J., AND T. E. MARTIN. 2001. Host activity and the risk of nest parasitism by Brown-headed Cowbirds. *Behavioral Ecology* 12: 31-40.
- BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part 3. United States National Museum Bulletin 237, Washington, D.C.
- BIERMANN, G. C., W. B. MCGILLIVRAY, AND K. E. NORDIN. 1987. The effect of cowbird parasitism on Brewer's Sparrow productivity in Alberta. *Journal of Field Ornithology* 58: 350-354.
- BLANKESPOOR, G. W., J. OOLMAN, AND C. UTHE. 1982. Eggshell strength and cowbird parasitism of Red-winged Blackbirds. *Auk* 99: 363-365.
- BROWN, B. T. 1994. Rates of brood parasitism by Brown-headed Cowbirds on riparian passerines in Arizona. *Journal of Field Ornithology* 65: 160-168.
- BURGHAM, M. C., AND J. PICMAN. 1989. Effect of Brown-headed Cowbirds on the evolution of Yellow Warbler anti-parasite strategies. *Animal Behaviour* 38: 298-308.
- CLARK, K. L., AND R. J. ROBERTSON. 1981. Parasitism and evolution of anti-parasite strategies in the Yellow Warbler. *Wilson Bulletin* 93: 249-258.
- CLOTFELTER, E. D. 1998. What cues do Brown-headed Cowbirds use to locate Red-winged Blackbird host nests? *Animal Behaviour* 55: 1181-1189.
- COLLINS, H. H. 1951. Birds of Montezuma Castle and Tuzigoot National Monument. Southwest Monuments Association, Tucson, AZ.
- CURSON, D. R. 1996. Nest predation and brood parasitism of passerine birds in pinyon-juniper woodland in northeast New Mexico. M.S. thesis. University of Wisconsin, Madison, WI.
- DAVIES, N. B., AND M. DE L. BROOKE. 1988. Cuckoos versus Reed Warblers: adaptations and counter adaptations. *Animal Behaviour* 36: 262-284.

- DELESANTRO, M. C. 1978. The breeding ecology of the Black-throated Sparrow in southern New Mexico. M.S. thesis. New Mexico State University, Las Cruces, NM.
- FREEMAN, S., D. F. GORI, AND S. ROHWER. 1990. Red-winged Blackbirds and Brown-headed Cowbirds: some aspects of a host-parasite relationship. *Condor* 92: 336–340.
- FRIEDMANN, H. 1963. Host relations of the parasitic cowbirds. United States National Museum Bulletin 233, Washington, DC.
- , L. F. KIFF, AND S. I. ROTHSTEIN. 1977. A further contribution to knowledge the host relations of the parasitic cowbirds. *Smithsonian Contributions to Zoology* 235: 1–75.
- GOGUEN, C. B., AND N. E. MATHEWS. 1996. Nest desertion by Blue-gray Gnatcatchers in association with Brown-headed Cowbird parasitism. *Animal Behaviour* 52: 613–619.
- HASSEL, M. P., AND R. M. MAY. 1974. Aggregation of predators and insect parasites and its effects on stability. *Journal of Animal Ecology* 43: 567–594.
- HAUBER, M. E., AND S. A. RUSSO. 2000. Perch proximity correlates with higher rates of cowbird parasitism of ground nesting Song Sparrows. *Wilson Bulletin* 112: 150–153.
- HILL, D. P., AND S. G. SEALY. 1994. Desertion of nests parasitized by cowbirds: have Clay-colored Sparrows evolved an anti-parasite defense? *Animal Behaviour* 48: 1063–1070.
- HOSOI, S. A., AND S. I. ROTHSTEIN. 2000. Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. *Animal Behaviour* 59: 823–840.
- HOWE, W. H., AND F. L. KNOPF. 2000. The role of vegetation in cowbird parasitism of Yellow Warblers. In: *Ecology and management of cowbirds and their hosts* (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, eds.), pp. 200–203. University of Texas Press, Austin, TX.
- JOHNSON, M. J. 1997. Cowbird parasitism of the Black-throated Sparrow in the Verde Valley of central Arizona. M.S. thesis. Northern Arizona University, Flagstaff, AZ.
- , C. VAN RIPER III, AND K. PEARSON. 2002. Black-throated Sparrow (*Amphispiza bilineata*). In: *The birds of North America* (A. Poole, and F. Gill, eds.), no. 637. The Birds of North America, Inc., Philadelphia, PA.
- LARISON, B., S. A. LAYMON, P. L. WILLIAMS, AND T. B. SMITH. 1998. Song Sparrows vs. cowbird brood parasites: impacts of forest structure and nest-site selection. *Condor* 100: 93–101.
- LOTEM, A., AND S. I. ROTHSTEIN. 1995. Cuckoo-host coevolution: from snapshots of an arms race to the documentation of microevolution. *Trends in Ecology and Evolution* 10: 436–437.
- MAY, R. M., AND S. K. ROBINSON. 1985. Population dynamics of avian brood parasitism. *American Naturalist* 126: 475–494.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87: 456–466.
- MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. Wiley, New York, NY.
- MOSKAT, C., AND M. HONZA. 2000. Effect of nest and nest site characteristics on the Cuckoo (*Cuculus canorus*) parasitism in the Great Reed Warbler (*Acrocephalus arundinaceus*). *Ecography* 23: 335–341.
- NARANJO, L. G., AND R. J. RAITT. 1993. Breeding bird distribution in Chihuahuan Desert habitat. *Southwestern Naturalist* 38: 43–51.
- NIAS, R. C. 1983. Nest-site characteristics and reproductive success in Superb Fairy-wrens. *Emu* 86: 139–144.
- PASE, C. P., AND D. E. BROWN. 1994. Warm-temperature scrublands. In: *Biotic communities: southwestern United States and northwestern Mexico* (D. E. Brown, ed.), pp. 85–99. University of Utah Press, Salt Lake City, UT.
- PHILLIPS, A., A. J. MARSHALL, AND G. MONSON. 1964. *The birds of Arizona*. University of Arizona Press, Tucson, AZ.
- ROBINSON, S. K., S. I. ROTHSTEIN, M. C. BRITTINGHAM, L. J. PETTIT, AND J. A. GRZYBOWSKI. 1995. Ecology and behavior of cowbirds and their impact on host populations. In: *Ecology and management of Neotropical migratory birds* (T. E. Martin, and D. M. Finch, eds.), pp. 428–460. Oxford University Press, New York, NY.
- ROBINSON, W. D., AND T. R. ROBINSON. 2001. Is host activity necessary to elicit brood parasitism by cowbirds? *Ethology, Ecology and Evolution* 13: 161–171.
- RØSKAFT, E., G. H. ORIANS, AND L. D. BELETSKY. 1990. Why do Red-wing Blackbirds accept eggs of Brown-headed Cowbirds? *Evolutionary Ecology* 4: 35–42.
- ROTHSTEIN, S. I. 1975a. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77: 250–271.
- . 1975b. Evolutionary rates and host defenses against avian brood parasitism. *American Naturalist* 109: 161–176.
- . 1986. A test of optimality: egg recognition in the Eastern Phoebe. *Animal Behaviour* 34: 1109–1119.
- . 1990. A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics* 21: 481–508.
- , AND S. K. ROBINSON. 1998. The evolution and ecology of avian brood parasitism: an overview. In: *Avian brood parasitism* (S. I. Rothstein, and S. K. Robinson, eds.), pp. 3–56. Oxford University Press, New York, NY.
- SAUNDERS, C. A., P. ARCESE, AND K. D. O'CONNOR. 2003. Nest site characteristics in the Song Sparrow and parasitism by Brown-headed Cowbirds. *Wilson Bulletin* 115: 24–28.
- SEALY, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. *Condor* 94: 40–54.
- . 1995. Burial of cowbird eggs by parasitized Yellow Warblers: an empirical and experimental study. *Animal Behaviour* 49: 877–889.
- SPAW, C. D., AND S. ROHWER. 1987. A comparative

- study of eggshell thickness in cowbirds and other passerines. *Condor* 89: 307–318.
- STRAUSBERGER, B. M., AND D. E. BURHANS. 2001. Nest desertion by Field Sparrows and its possible influence on the evolution of cowbird behavior. *Auk* 118: 770–776.
- TAYLOR, W. P., AND H. T. JACKSON. 1916. Biological survey report: the birds of the Verde Valley. Montezuma Castle National Monument, AZ.
- TERBORGH, J. 1992. Why American songbirds are vanishing. *Scientific American* 266: 56–62.
- TEWKSBURY, J. J., S. J. HEJL, AND T. E. MARTIN. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79: 2890–2903.
- TRAIL, P. 1992. Nest invaders. Pacific Discovery Spring: 32–37.
- VAN RIPER III, C. 1976. Aspects of House Finch breeding biology in Hawaii. *Condor* 78: 224–229.
- . 1995. Ecology and breeding biology of the Hawaii Elepaio (*Chasiempis sandwichensis bryani*). *Condor* 97: 512–527.
- VAN TYNE, J., AND A. J. BERGER. 1971. Fundamentals of ornithology, 1st ed. Wiley, New York, NY.
- WARD, D., A. K. LINDHOLM, AND J. N. M. SMITH. 1996. Multiple parasitism of the Red-winged Blackbird: further experimental evidence of evolutionary-lag in a common host of the Brown-headed Cowbird. *Auk* 113: 408–413.
- WEATHERHEAD, P. J. 1991. The adaptive value of thick-shelled eggs for Brown-headed Cowbirds. *Auk* 108: 196–198.
- YATES, F. 1934. Contingency tables involving small numbers and the χ^2 test. *Journal of the Royal Statistical Society, Supplement 1*: 217–235.
- ZIMMER, K. J. 1993. Spatial and temporal variation in the breeding and foraging ecology of Black-throated Sparrows. Ph.D. dissertation. New Mexico State University, Las Cruces NM.