EVIDENCE OF BROOD PARASITISM AND QUANTIFICATION OF RANGEWIDE OVERLAP BETWEEN THE OLIVE WARBLER AND BROWN-HEADED COWBIRD

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ABSTRACT: Brood parasitism is a fascinating natural history phenomenon that provides a window into the coevolution of antagonistic interactions. Many ecological and evolutionary aspects of brood parasitism remain unknown, and new hosts of brood parasites are still being discovered. We document the second instance of brood parasitism of the Olive Warbler (*Peucedramus taeniatus*) by the Brown-headed Cowbird (*Molothrus ater*). Apparent lack of habitat and elevation overlap across the ranges of these two species prompted us to examine how frequently they come into contact. We analyzed >3 million Olive Warbler and Brown-headed Cowbird occurrence records from two open-source repositories, eBird and GBIF, to examine both synchronous and asynchronous locality overlap during the breeding season. We found that the two species were documented together simultaneously in only 3.1% of analyzed instances, but that they co-occurred in similar habitat types and/or at similar elevations at 11.8% of localities analyzed across the Olive Warbler's range. Additional research on aspects of ecology and evolution, such as host selection, the cowbird's diurnal patterns of movement, and the dynamics of intracellular pathogens infecting brood parasites and their hosts, may shed light more broadly on the ecological interactions and mechanisms underlying brood parasitism.

Obligate avian brood parasites lay their eggs in the nests of heterospecific hosts and rely on hosts to raise young. All five cowbird species in the genus *Molothrus* (family: Icteridae) parasitize avian hosts, and their selection of hosts varies from specialized to generalized (Lanyon 1992, Lowther 2018). The most widespread and generalist cowbird is the Brown-headed Cowbird (*Molothrus ater*), which lays its eggs in the nests of >220 host species (Brown 1994). It has been suggested that Brown-headed Cowbirds may prefer smaller-bodied hosts, that they may avoid large or aggressive hosts with strong defensive capabilities (Strausberger and Ashley 1997), and that they may select for host nests with a certain number of eggs and/or eggs of a certain size (White et al. 2007, 2009). Cowbirds' host selection remains challenging to study, and field observations of brood parasitism are a valuable way through which this type of ecological interaction is documented.

On the morning of 2 August 2020, we encountered an adult female Olive Warbler (*Peucedramus taeniatus*) feeding a Brown-headed Cowbird fledgling near Burro Peak, southwestern New Mexico (32.5930° N, 108.4302° W, ~2370 m elevation; photo on this issue's inside back cover) in ponderosa pine (*Pinus ponderosa*) and oak (*Quercus* sp.) forest. The cowbird fledgling was first seen perched on an exposed oak branch and was located by its persistent, high-pitched begging calls. To our surprise, the cowbird fledgling was fed twice by the adult Olive Warbler over the course of ~3 minutes. Each feeding lasted

a few seconds before the Olive Warbler resumed foraging. After the second feeding, the cowbird moved from its perch and was seen again approximately 30 minutes later in the same general area, where it was easily relocated by its begging calls. The female Olive Warbler was not seen during the second brief sighting of the cowbird fledgling.

The literature suggests that parasitism of the Olive Warbler by the Brown-headed Cowbird is rare (Lowther and Nocedal 2012, Lowther 2018), and only one instance has been previously documented (Corman and Wise-Gervais 2005). Additionally, this combination seems unlikely given apparent differences in breeding habitat and elevation. This evidence prompted us to ask: How often do these two species co-occur synchronously and/or asynchronously in habitat and/or elevation? We sought to assess the potential for the Brown-headed Cowbird to parasitize the Olive Warbler by assessing their range-wide overlap during the breeding season and by considering aspects of life history that might inhibit or facilitate their interaction.

METHODS

We used specimen records from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and observation data from eBird (www.eBird.org) to quantify breeding season overlap. To obtain GBIF records, we used the package "rgbif" (Chamberlain et al. 2019) to download all Olive Warbler records (doi: https://www.gbif.org/occurrence/download/0033584-200613084148143). To limit our analysis more closely to the Olive Warbler's range, we limited our selection of Brown-headed Cowbird records to latitudes south of 37° N and longitudes between 85.5° and 114° W (doi: https://doi.org/10.15468/dl.hzxwyz). We excluded observations missing coordinates, with coordinate uncertainty >3 km, observations with unknown "basis of record," and duplicate records. We obtained all eBird data for the Olive Warbler and Brown-headed Cowbird (downloaded on 21 October 2020), and subset the latter to the same latitude and longitude limits as the GBIF data. We eliminated duplicate records, and, to limit observations resulting from extreme sampling effort, we excluded records covering >3.2 km in distance, areas of >1.0 hectares, and durations >5 hours, generally following best practices for using eBird data recommended by Strimas-Mackey et al. (2020). We then selected data corresponding to the May–July breeding period, merged GBIF and eBird data, standardized latitude and longitude coordinates to a resolution of ~100 m (3 decimal places), and calculated localities where the two species overlap. We mapped overlapping localities onto elevation rasters downloaded with the package "raster" (Hijmans et al. 2020), cropped to study areas of Mexico and the southwestern USA.

All analyses were conducted in R, version 4.0.2, with the RStudio interface (R Core Team 2019). Analysis code is available on GitHub: https://github.com/jlwilliamson/OLWA-BHCO. We emphasize that instances of locality overlap may be affected by quality of input data, filtering criteria, and data-processing choices, and that there are likely many more localities where these species co-occur.

RESULTS

We analyzed a total of 1241 filtered of 44,134 raw Olive Warbler records and 38,638 filtered of 3,005,800 raw Brown-headed Cowbird records from GBIF and eBird. Olive Warblers and Brown-headed Cowbirds co-occurred synchronously in 3.1% of instances, or on 26 of 827 eBird checklists reporting the Olive Warbler. Additionally, we found 1959 total instances of asynchronous overlap at 81 localities during both species' breeding seasons from at least 1969 to 2020 (Figure 1), representing 11.8% asynchronous locality overlap (81 of 687 distinct Olive Warbler localities). Together, this suggests that Olive Warblers and Brown-headed Cowbirds are rarely reported together but may co-occur infrequently across parts of the Olive Warbler's range. Localities of synchronous and asynchronous overlap extend from the northernmost to nearly the southernmost limits of the Olive Warbler's range

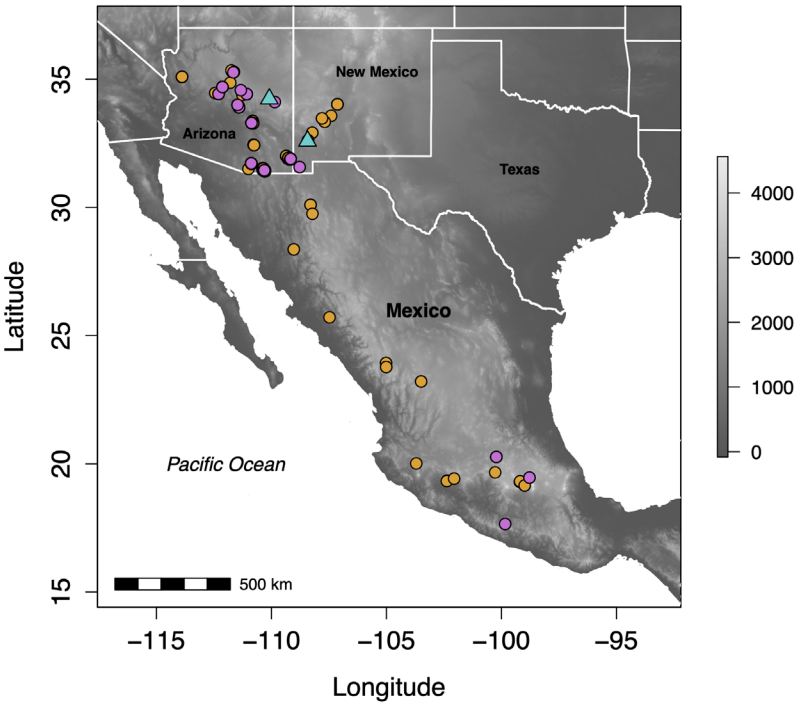

FIGURE 1. Localities of overlap during the breeding season, ~1969–2020, of the Olive Warbler and Brown-headed Cowbird, calculated with data from GBIF and eBird. Lighter shading represents higher elevations. Pink points indicate localities of simultaneous overlap (n = 26); orange points indicate localities of non-simultaneous overlap (n = 81). Not all points are visible, as some overlay others, and multiple instances of overlap at the same locality are not shown. Turquoise triangles indicate localities of the two documented observations of Olive Warbler brood parasitism by the Brown-headed Cowbird.

(Figure 1), suggesting that the potential for overlap exists range wide and is not limited to specific regions.

DISCUSSION

Our observation from southwestern New Mexico is the second documented case of parasitism of an Olive Warbler by a Brown-headed Cowbird. The first was reported on 14 July 2000 along the Mogollon Rim west of Show Low, Arizona, on a survey for the breeding bird atlas (Corman and Wise-Gervais 2005). Both brood-parasitism observations suggest that the Olive Warbler may be a true host, or species that rears cowbird young, rather than simply a victim, or species that receives a brood parasite's eggs in the nest (Lowther 2018). Alternatively, because fledgling Brown-headed Cowbirds may beg to individuals that are not their foster parents (Ficken 1967, Sealy and Lorenzana 1997), it is possible that the Olive Warbler we observed was not a Brown-headed Cowbird host at all and that it was simply feeding a begging fledgling. Although this explanation is not the most parsimonious, the scarcity of parasitism records in light of overlap at >10% of breeding season localities does raise questions about why the Olive Warbler is infrequently documented as a Brown-headed Cowbird host.

Lowther and Nocedal (2012) hypothesized that Olive Warbler parasitism by the Brown-headed Cowbird is unlikely because of habitat separation despite range overlap. The Olive Warbler favors mid- to high-elevation pine–oak forest (Lowther and Nocedal 2012), while the Brown-headed Cowbird is generally found in lower-elevation riparian areas and disturbed habitats (Lowther 1993, Barnagaud et al. 2015). In some parts of its range, such as the Sierra Nevada of California, the Brown-headed Cowbird has expanded to mixed pine and ponderosa forest with introduction of pack animals and expansion of human settlement (Rothstein et al. 1980, Purcell and Verner 1999, Borgmann and Morrison 2010). In northern New Mexico, the Brown-headed Cowbird occurs across a range of elevations and habitats, including disturbed shortgrass prairie (Goguen and Mathews 2001, Goguen et al. 2005), pinyon–juniper woodland (Goguen and Mathews 2001, Goguen et al. 2009), and mixed conifer forest (Curson et al. 2000). Our findings support that the Olive Warbler and Brown-headed Cowbird do co-occur, or have the potential to co-occur, in habitat and/or elevation more frequently than previously documented (Figure 1).

Despite evidence of habitat and elevation overlap, previous censuses in Olive Warbler habitat in Arizona and New Mexico have not documented cowbirds (Balda 1969, Nocedal 1984). It is possible that previous census efforts simply failed to account for the presence of Brown-headed Cowbirds in Olive Warbler habitat, or that the Brown-headed Cowbird may overlap in habitat and elevation with the Olive Warbler in such low numbers that it is rarely detected. Lack of regular census or birding effort in many regions and more remote areas of the Olive Warbler's range may also limit simultaneous detections of these two species.

An alternative hypothesis is that the Brown-headed Cowbird is rarely detected in mixed conifer forest because of its unique daily pattern of spatial and temporal habitat use. During the breeding season, female cowbirds may

seek nests asocially in mixed conifer forest at higher elevations and spend only mornings in these host-rich habitats, during which time they are largely silent. Each afternoon, they may commute to disturbed areas at lower elevations (i.e., near human settlements, pastures, and horse stables) where they spend the remainder of the day foraging in large social groups (Rothstein et al. 1984, Goguen and Mathews 2001). In New Mexico, individual female cowbirds have been recorded to commute >18 km one way between breeding and feeding sites (Curson et al. 2000). In the evening, cowbirds may roost communally in groups as large as 1000 individuals, together with other blackbird and grackle species, and roosts may be distant from both breeding and foraging areas (Curson et al. 2000). Although Brown-headed Cowbird abundance and probability of parasitism decrease with increased distance from livestock grazing (Goguen and Mathews 2000), cowbirds' ability to travel long distances each day between breeding, foraging, and roosting sites suggests high behavioral flexibility for responding to widely dispersed resources necessary for survival and reproduction. It also suggests that cowbirds may be rarely detected in Olive Warbler habitat during certain periods of the day.

Brood parasites tend to lay their eggs in the nests of relatively smaller hosts because larger brood-parasitic young have a competitive advantage over the host's smaller nestlings (Strausberger and Ashley 1997). It has also been shown that Brown-headed Cowbirds parasitize small (<100 g) species significantly more often than large (>100 g) species (Strausberger and Ashley 1997). Additionally, other small passerines, such as parulid warblers, gnatcatchers, and passerellid sparrows, are common Brown-headed Cowbird hosts (Brown 1994, Lichtenstein and Sealy 1998, Lowther 2018). In this regard, the Olive Warbler (mean body mass 11.0 g) appears to be a suitable host for the Brown-headed Cowbird (mean body mass of females 38.1 g, of males 48.7 g; Dunning 2007). Yet, despite the cowbird's apparent preference for smaller hosts, its nestlings may grow and survive better in the nests of medium-sized hosts, which provide young with more resources than can smaller hosts (Lorenzana and Sealy 2001, Kilner 2003, Kilner et al. 2004). Cowbirds have been observed to parasitize the nests of species across a range of body sizes that do not result in successful fledging (Hatch 1967, 1971), suggesting that nest parasitism may not always be an adaptive behavior. Taken together, the evidence suggests that host choice involves many factors beyond size.

Novel interactions between brood hosts and parasites, such as the Olive Warbler and Brown-headed Cowbird, have the potential to inform our understanding of a different host–parasite relationship: the coevolutionary "arms race" between hosts and pathogens (Valen 1973). Brood parasites may avoid the burden of host-specific ectoparasites and endoparasites, such as malaria-causing haemosporidian blood parasites, by laying their eggs in the nests of species that have different specialized endoparasite fauna (e.g., Soler et al. 1999). Thus host-specific pathogens may be more abundant in *hosts* than in brood parasites reared in the same environment. Communities of some endoparasites, such as haemosporidians, turn over at finer spatial scales than their hosts, suggesting that bird hosts may encounter diverse pathogens across their ranges, resulting in spatially varying selection on hosts' immune systems (Williamson et al. 2019, McNew et al. 2021). Could the Brown-headed Cowbird's parasitism of novel or rare hosts such as the

Olive Warbler, and possible increased use of habitats where it has not been documented in high numbers previously, such as ponderosa pine forest, represent a mechanism for pathogen-pressure avoidance? It is not possible to rule out upslope range expansion or increased use of forested habitat by the Brown-headed Cowbird as a result of changing temperature regimes, landscape modification, and human influence, which we did not test. However, it is plausible that environmental and anthropogenic factors could be coupled with mechanisms of parasite avoidance, which in turn may be linked to environmental and anthropogenic change. Studying intracellular parasite communities of brood parasites and their interspecific brood parasite hosts represent one lens through which we can approach the evolutionary dynamics of ecological interactions, species distributions, and how both will be affected by future climate change.

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LITERATURE CITED

Balda, R. P. 1969. Foliage use by birds of the oak–juniper woodland and ponderosa pine forest in southeastern Arizona. Condor 71:399–412; doi.org/10.2307/1365738.

Barnagaud, J. Y., Papaïx, J., Gimenez, O., and Svenning, J. C. 2015. Dynamic spatial interactions between the native invader Brown-headed Cowbird and its hosts. Divers. Distrib. 21:511–522; doi.org/10.1111/ddi.12275.

Borgmann, K. L., and Morrison, M. L. 2010. Factors influencing the frequency of nest parasitism by Brown-headed Cowbirds in the northern Sierra Nevada. W. N. Am. Nat. 70: 137–143; doi.org/10.3398/064.070.0201.

Brown, B. T. 1994. Rates of brood parasitism by Brown-headed Cowbirds on riparian passerines in Arizona. J. Field Ornithol. 65:160–168.

Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., L, G., K, R., 2019. rgbif: Interface to the Global Biodiversity Information Facility API, R package version 1.4.0; https://cran.r-project.org/web/packages/rgbif/index.html.

Corman, T., and Wise-Gervais, C. (eds.). 2005. Arizona Breeding Bird Atlas. Univ. of New Mexico Press, Albuquerque.

Curson, D. R., Goguen, C. B., and Mathews, N. E. 2000. Long-distance commuting by Brown-headed Cowbirds in New Mexico. Auk 117:795–799; doi.org/10.2307/4089606.

Dunning, J. B. 2007. Handbook of Avian Body Masses, 2nd. ed. CRC Press, Boca Raton, FL; doi.org/10.1201/9781420064452.

Ficken, M.S. 1967. Interactions of a crow and a fledgling cowbird. Auk 84:601–602; doi.org/10.1086/128466.

Goguen, C. B., and Mathews, N. E. 2000. Local gradients of cowbird abundance and parasitism relative to livestock grazing in a western landscape. Cons. Biol. 14:1862–1869; doi.org/10.1046/j.1523-1739.2000.99313.x.

Goguen, C. B., and Mathews, N. E. 2001. Brown-headed Cowbird behavior and movements in relation to livestock grazing. Ecol. Appl. 11:1533–1544; doi.org/10.1890/1051-0761(2001)011[1533:BHCBAM]2.0.CO;2.

Goguen, C. B., Curson, D. R., and Matthews, N. E. 2005. Behavioral ecology of the

Brown-headed Cowbird (*Molothrus ater*) in a bison-grazed landscape in New Mexico. Ornithol. Monogr. 57:71–83; doi.org/10.2307/40166815.
Goguen, C. B., Curson, D. R., and Mathews, N. E. 2009. Effects of parasitism by Brown-headed Cowbirds (*Molothrus ater*) on reproductive success of three frequent hosts in New Mexico. Southwest. Nat. 54:58–67; doi.org/10.1894/MH-44.1.
Hatch, D. R. M. 1967. Cowbird egg in crow nest. Blue Jay 25:863; doi.org/https://doi.org/10.29173/bluejay3005.
Hatch, D. R. M. 1971. Brown-headed Cowbird parasitism on Spotted Sandpiper and Wilson's Phalarope. Blue Jay 29:17–18; doi.org/10.29173/bluejay3655.
Hijmans, R. J., van Etten, J., Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R. Busetto, L., Canty, M., Fasoli, B., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J. A., Hiemstra, P., and Kassel Hinge, R W. 2020. Raster: Geographic data analysis and modeling; https://cran.r-project.org/web/packages/raster/index.html.
Kilner, R. M. 2003. How selfish is a cowbird nestling? Anim. Behav. 66:569–576; doi.org/10.1006/anbe.2003.2204.
Kilner, R. M., Madden, J. R., and Hauber, M. E. 2004. Brood parasitic cowbird nestlings use host young to procure resources. Science 305:877–879; doi.org/10.1126/science.1098487.
Lanyon, S. M. 1992. Interspecific brood parasitism in blackbirds (Icterinae): A phylogenetic perspective. Science 255:77–79; doi.org/10.1126/science.1553533.
Lichtenstein, G., and Sealy, S. G. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic Brown-headed Cowbird chicks in Yellow Warbler nests. Proc. R. Soc. B Biol. Sci. 265:249–254; doi.org/10.1098/rspb.1998.0289.
Lorenzana, J. C., and Sealy, S. G. 2001. Fitness costs and benefits of cowbird egg ejection by Gray Catbirds. Behav. Ecol. 12:325–329; doi.org/10.1093/beheco/12.3.325.
Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*), in The Birds of North America, (A. Poole and F. Gill, eds.), no. 47. Acad. Nat. Sci., Philadelphia; doi.org/10.2173/bow.bnhcow.01.
Lowther, P. E., 2018. Lists of victims and hosts of the parasitic cowbirds (*Molothrus*), version 5 September 2018; https://www.fieldmuseum.org/sites/default/files/cowbird-hosts-05sep2018.pdf.
Lowther, P. E., and Nocedal, J. 2012. Olive Warbler (*Peucedramus taeniatus*), in The Birds of North America (A. F. Poole, ed.), no. 310, version 2.0. Cornell Lab Ornithol., Ithaca, NY; doi.org/10.2173/bow.oliwar.01.
McNew, S. M., Barrow, L. N., Williamson, J. L., Galen, S. C., Skeen, H., DuBay, S. G., Gaffney, A. M., Johnson, A. B., Bautista-Obispo, E., Ordoñez, P., Schmitt, C. J., Smiley, A., Valqui, T., Bates, J. M., Hackett, S. J., and Witt, C. C. 2021. Contrasting drivers of diversity in hosts and parasites across the tropical Andes. Proc. Natl. Acad. Sci., in press.
Nocedal, J., 1984. Estructura y utilización del follaje de las comunidades de pájaros en bosques templados del Valle de México. Acta Zool. Mex 6:1–45.
Purcell, K. L., and Verner, J. 1999. Abundance and rates of brood parasitism by Brown-headed Cowbirds over an elevational gradient in the southern Sierra Nevada. Studies Avian Biol. 18:97–103.
R Core Team, 2019. R: A language and environment for statistical computing. R Found. Stat. Comput. Vienna, Austria.
Rothstein, S. I., Verner, J., and Stevens, E. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97:253–267.

Rothstein, S. I., Verner, J., and Stevens, E. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65:77–88; doi.org/10.2307/1939460.

Sealy, S. G., and Lorenzana, J. C. 1997. Feeding of nestling and fledgling brood parasites by individuals other than the foster parents: A review. Can. J. Zool. 75:1739–1752: doi.org/10.1139/z97-804.

Soler, J. J., Møller, A. P., Soler, M., and Martínez, J. G. 1999. Interactions between a brood parasite and its host in relation to parasitism and immune defence. Evol. Ecol. Res. 1:189–210.

Strausberger, B. M., and Ashley, M. V. 1997. Community-wide patterns of parasitism of a host "generalist" brood-parasitic cowbird. Oecologia 112:254–262; doi.org/10.1007/s004420050308.

Strimas-Mackey, M., Hochachka, W. M., Ruiz-Gutierrez, V., Robinson, O. J., Miller, E. T., Auer, T., Kelling, S., Fink, D., and Johnston, A. 2020. Best Practices for Using eBird Data. Cornell Lab Ornithol., Ithaca, NY; doi.org/10.5281/zenodo.3620739.

Van Valen, L. 1973. A new evolutionary law. Evol. Theory 1:1–30.

White, D. J., Ho, L., de los Santos, G., and Godoy, I. 2007. An experimental test of preferences for nest contents in an obligate brood parasite, *Molothrus ater*. Behav. Ecol. 18:922–928; doi.org/10.1093/beheco/arm062.

White, D. J., Ho, L., and Freed-Brown, G., 2009. Counting chicks before they hatch. Psychol. Sci. 20:1140–1145; doi.org/10.1111/j.1467-9280.2009.02418.x.

Williamson, J. L., Wolf, C. J., Barrow, L. N., Baumann, M. J., Galen, S. C., Schmitt, C. J., Schmitt, D. C., Winter, A. S., and Witt, C. C., 2019. Ecology, not distance, explains community composition in parasites of sky-island Audubon's Warblers. Int. J. Parasitol. 49:437–448; doi.org/10.1016/j.ijpara.2018.11.012.

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A female Olive Warbler (*Peucedramus taeniatus*) feeding a recently fledged Brown-headed Cowbird (*Molothrus ater*) in the Burro Mountains of southwestern New Mexico, representing only the second known instance of this combination of brood parasite and host.

Photo by Matthew J. Baumann