AGE STRUCTURE OF ADULT BROWN-HEADED COWBIRDS IN SOUTHWEST COLORADO

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ABSTRACT: We live-trapped and banded Brown-headed Cowbirds (*Molothrus ater*) in La Plata County, southwest Colorado, during the breeding seasons of 1992 to 1999. We captured a total of 1034 adult males and 386 adult females. Although we could not determine the exact ages of newly captured males older than one year (after second year; ASY) and of newly captured adult females, we identified the minimum possible age of each bird captured or recaptured each year. We found that most cowbirds of either sex were 1 or 2 years old, though we recaptured some older individuals. The percentage of recaptured females ≥2 years old increased through the study but appeared to stabilize during the last three years, implying that these older individuals constituted a quarter to a third of the population. The mean estimated minimum age of adult males was significantly greater than that of adult females in 1997 but not in 1998 or 1999. The ratio of yearling to older males varied significantly by year with yearlings becoming more common in the later years of study. Incorporating the age structure of a Brown-headed Cowbird population, especially of females, may increase the utility of various models concerning host populations subjected to cowbird brood parasitism, and this information is relevant to estimating the number of cowbird eggs expected to be laid in an area during a breeding season.

The Brown-headed Cowbird (*Molothrus ater*), an obligate brood parasite, has been reported attempting parasitism on some 248 species (Friedmann 1929, Friedmann and Kiff 1985, Ortega 1998, Lowther 2015). Cowbirds commonly reduce or eliminate the successful rearing of the host's own young (Lowther 1993, 2015, Ortega 1998, Lorenzana and Sealy 1999, Goguen et al. 2009). Many factors, both biological (e.g., timing of potential hosts' breeding season, hosts' incubation period, hosts' diet, hosts' egg-ejection response, etc.) and ecological (e.g., nest height, grazing proximity, forest fragmentation, residential development, etc.), may contribute to the frequency and success of cowbirds' brood parasitism on various hosts (Brittingham and Temple 1983, Ortega 1998, Hahn and Hatfield 2000, Thompson et al. 2000, Tewksbury et al. 2006, Borgmann and Morrison 2010). Indeed, of the 248 species reported parasitized, only 132–172 are known to have successfully raised young cowbirds to fledging (Ortega 1998, Ortega et al. 2005, Lowther 2015).

Few of the many previous studies of the cowbird (see reviews in Lowther 1993, Ortega, 1998, Morrison et al. 1999, and Smith et al. 2000), have examined the species' demography during the breeding season (Darley 1971, Woolfenden et al. 2001, Ortega and Ortega 2009, Anderson et al. 2012), except for the sex ratio (reviewed by Ortega 1998: table 7.2). Especially with respect to the age structure of adult females in a population, this lack of demographic study is surprising since female cowbirds are generally thought to lay typically from 10 to 40 eggs in a breeding season (Walkinshaw 1949, Payne 1965, 1976, Scott and Ankney 1980, Fleischer et al. 1987, Holford and Roby 1993), though Alderson et al. (1999) estimated a mean (± 1 SD) of only 2.8 ± 2.7 eggs laid by a female cowbird in a breeding season. In addition, in both the wild (Fleischer et al. 1987) and in captivity (Holford and Roby 1993), yearling females, lay fewer eggs in a breeding season than do older females. In many species of birds yearling females lay fewer eggs per clutch than do older individuals (Ricklefs 1973, Sæther 1990, Forslund and Pärt 1995), so knowing the age structure of a cowbird population, especially of females, might be useful in predicting the pressure cowbird parasitism exerts on a population of hosts (McGeen 1972, Lowther 2015). Such information could contribute to various models of a host's population responses to cowbird parasitism (for example, see May and Robinson 1985, Pease and Grzybowski 1995, Grzybowski and Pease 1999, Schmidt and Whelan 1999, Powell and Knutson 2006). In addition, the age structure of adult male cowbirds in a population might affect dominance hierarchies and hence mating behaviors and the mating system (see review in Ortega 1998, and references therein). To the best of our knowledge, such a complete description of the age structure of a population of cowbirds has not previously been reported. Therefore, the primary purpose of this paper is to present minimum age estimates and the apparent age structure of adult cowbirds in a population studied over an eight-year period from 1992 to 1999 in southwest Colorado.

METHODS

Study Area

From 1992 to 1999, we live-trapped cowbirds at the San Juan Basin Research Center (then run by Colorado State University; 37° 14′ N, 108° 3′ W; 2316 m elevation) in southwest Colorado. The center covers 2541 ha and consists primarily of three habitats. One, a riparian corridor where Narrowleaf Cottonwood (*Populus angustifolia*) dominates, followed by River Birch (*Betula fontinalis*), Thinleaf Alder (*Alnus tenuifolia*), and various willows (*Salix* spp.). Two, in uplands, woodland dominated by Gambel Oak (*Quercus gambelii*) with a few junipers (*Juniperus* spp.), Quaking Aspens (*Populus tremuloides*), and Ponderosa Pines (*Pinus ponderosa*). Because of past overgrazing, both the density and height of the understory in these two habitats was low. Three, alfalfa and hay fields, but cowbirds made little use of this habitat.

Trapping Cowbirds

Each year, we trapped cowbirds from mid-May (as early as 9 May 1995) to late July or early August (as late as 13 August 1994) in a cage measuring 130.2 × 121.3 × 186.4 cm and stocked with decoy cowbirds. In 1998, however, because of an outbreak of Sin Nombre hantavirus and because rodents that may spread the virus were attracted to seeds with which the traps were baited, we trapped cowbirds only from 20 May to 12 June. We placed the decoy trap on the western side of the primary stockyard and barn centrally located at our study site. In addition, we trapped cowbirds in two to four two-cell Potter traps set next to the decoy trap. Typically, the decoy trap contained at least two adult male cowbirds and one adult female cowbird. We provided wild bird feed, along with water from a standard poultry-watering bottle, for cowbirds caught in the decoy trap; Potter traps were baited with this same wild bird feed. The decoy trap contained a platform measuring 40.3 × 120.3 cm to provide shade and a perch, and in some years bare branches as additional perches. Except the decoy cowbirds, which were typically held for only a single day of trapping, all cowbirds were released immediately after they were handled (see below).

Marking and Aging Cowbirds

We banded all cowbirds with uniquely numbered aluminum bands supplied by the U.S. Fish and Wildlife Service. We sexed and estimated the minimum age of newly captured individuals by plumage characteristics (Selander and Giller 1960, Ortega et al. 1996). Adult males could be yearlings (1 year old; SY) or older (≥2 years old; ASY; Selander and Giller 1960, Ortega et al. 1996). When we recaptured ASY males originally captured in their year of hatching (HY, $n = 22$) or in their second year ($n = 101$), we recorded their actual age. We could not, however, determine the exact age of newly captured ASY males. At the time that this study was completed, we could not distinguish adult females as SY or ASY by plumage or body measurements (Selander and Giller 1960, Ortega et al. 1996). Five recaptured females could be identified as yearlings because they had been banded as juveniles the previous year. But we could not categorize an adult female an ASY female until it was recaptured in a following year. For both adult males and adult females, we emphasize that the resulting apparent age structure represents minimum ages. As individuals were retrapped in later years, we then added the appropriate number of years to the initial estimates of their minimum age, so assessing the apparent age structure (based upon minimum age) of our population of cowbirds on an annual basis.

Statistical Analyses

Because the proportion of known ASY females appeared to have stabilized during the last three years of our study (1997–1999), we tested for differences in average estimated minimum ages of adult males and females within each of these years by a two-tailed Mann–Whitney *U* test (Zar 1996). We used the nonparametric Mann–Whitney *U* test for these comparisons because our data were not normally distributed (Zar 1996). To examine potential differences in the frequencies of yearling and older males from year to year, we used the appropriate *G* test with Williams' correction factor (Sokal and Rohlf 1981). To examine potential differences in the frequencies of newly captured adult females and known ASY females from year to year, we used the same procedure but did not include data from 1992 because in this initial year of the study, all adult females were newly captured. For all statistical tests, we considered a value of $P \leq 0.05$ statistically significant.

RESULTS

We captured a total of 1420 adult cowbirds, 386 females and 1034 males, of which 669 were SY and 365 were ASY at the time of their initial capture

(Ortega and Ortega 2009). After 1992, when all were newly captured, the percentage of adult males recaptured each year, both age categories combined, averaged 31.2% (± 2.0, standard error). Among ASY males, an average of 33.4 ± 5.9% were newly captured each year. For adult females, the annual averages were 83.7 ± 4.6% newly captured and 16.3 ± 4.6% recaptured. Within any one year, the estimated average minimum age of adult males ranged from 1.55 ± 0.08 years (n = 208 individuals) in 1996 to 2.14 ± 0.08 years (n = 191 individuals) in 1994 (Table 1). For adult females, the estimated average minimum age increased steadily through the study to a peak of 1.63 ± 0.27 years (n = 19) in 1999 (Table 1). During the last three years of the study, the average minimum age of adult males was significantly greater than that of adult females only in 1997 (Table 1).

The proportion of SY to ASY males differed significantly by year ($G_{adj.}$ = 148.149, df = 7, $P << 0.001$), being greater later in the study (Figure 1). The proportion of newly captured adult females to recaptured females known to be ≥2 years old also differed significantly from year to year ($G_{adj.}$ = 151.278, df = 6, $P << 0.001$). However, in contrast to the pattern in adult males, known ASY females were more common during the later years of the study (Figure 2).

DISCUSSION

Age Structure

We recaptured few cowbirds (male or female) older than two years, but occasional recaptured individuals were much older: two adult males at least 8 years old and one adult female at least 5 years old when last trapped (Table 1). With data from the Bird Banding Laboratory, Fankhauser (1971) found a maximum age at death of 9 years for an adult male and 6 years for an adult female. Similarly, in southern Manitoba, Woolfenden et al. (2001) observed six males that lived to at least 7 years, and three females lived to at least 5 years. Our observation that the majority of cowbirds in southwest Colorado apparently live for no more than two years is corroborated by our previous findings concerning probability of adults' survival in this population (Ortega and Ortega 2009: table 2). That is, in the first year after their initial capture and banding the average (± 1 SE) survival probability (ϕ) of adult females was 0.092 ± 0.025, but in any following year, it was 0.358 ± 0.082. In comparison, in the first year after their initial capture, SY and ASY males had average survival probability values of 0.184 ± 0.050 and 0.197 ± 0.068, respectively. Males' probability of survival also increased in the following years (for SY males, ϕ = 0.447 ± 0.048; for ASY males, ϕ = 0.461 ± 0.043). Even though the cowbird is a brood parasite, the typical observed life span of adults, two years or less, is consistent with that of many other species of temperate-zone passeriform birds, whose annual survivorship (which is not the same as survival probability) is 40–60% (see review in Ricklefs 1973). It is important to note that our estimates based on minimum apparent age are the result of randomly capturing cowbirds primarily in our decoy trap. Therefore, if cowbirds become better at obtaining natural food sources with age, if they become more reluctant to enter

Table 1 Apparent Age Structure, by Sex, of Adult Brown-headed Cowbirds Captured at the San Juan Basin Research Center, La Plata County, Colorado, 1992–1999, Expressed as Mean Estimated Minimum Age by Year

				Age (years)								
Year	Sex[a]	Mean	SE	1	2	3	4	5	6	7	8	P[b]
1992	Male	1.57	0.03	113	151							
	Female	1.00	0.00	35								
1993	Male	1.98	0.05	38	94	35						
	Female	1.05	0.04	21	1							
1994	Male	2.14	0.08	64	69	26	32					
	Female	1.03	0.03	67		1						
1995	Male	1.78	0.07	164	49	22	14	18				
	Female	1.07	0.03	95	5	1						
1996	Male	1.55	0.08	150	31	10	9	3	5			
	Female	1.13	0.04	75	9	1						
1997	Male	1.81	0.09	72	52	11	3	6	1	1		0.000
	Female	1.35	0.07	64	14	8						
1998	Male	1.89	0.18	38	7	9	5	2			1	0.434
	Female	1.57	0.17	20	5	3	2					
1999	Male	1.83	0.17	53	8	4	7	4	1		1	0.625
	Female	1.63	0.27	14		4		1				

[a]Exact ages of males first banded as yearlings (second year; SY) and of males (n = 22) and females (n = 5) originally banded as juveniles (year of hatching; HY) are known. However, for males first captured at an age ≥2 years (after second year; ASY) and for adult females, their ages are estimated as the minimum possible.

[b]From 1997 to 1999, the mean estimated minimum age of adult males and adult females is compared with a two-tailed Mann–Whitney U test (Zar 1996).

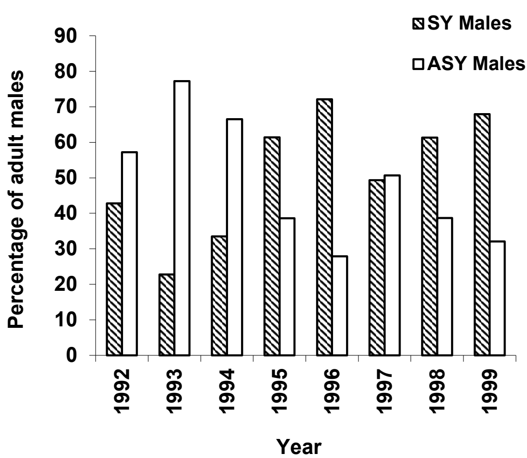

Figure 1. Percentages of yearling (second-year; SY) and older (after-second-year; ASY) male Brown-headed Cowbirds captured each year from 1992 to 1999 at the San Juan Basin Research Center, La Plata County, Colorado. Number of adult males captured annually varied from 62 (1998) to 268 (1995).

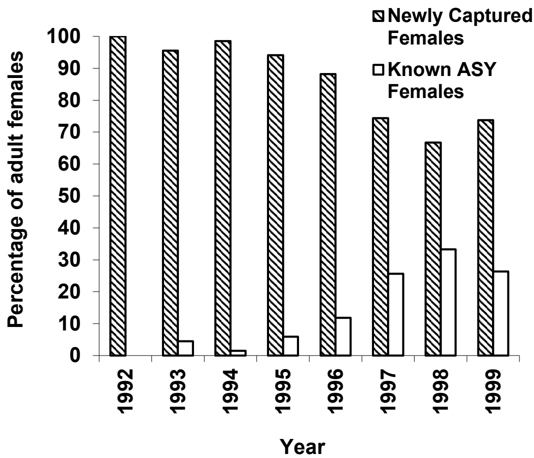

Figure 2. Percentages of newly captured female Brown-headed Cowbirds and recaptured banded females at least two years old (after-second-year; ASY) from 1992 to 1999 at the San Juan Basin Research Center, La Plata County, Colorado. Number of adult females captured annually varied from 19 (1999) to 101 (1995).

traps with age, and/or if they become busier with breeding activities with age, then the likelihood of recapturing individuals might decrease as their age increases, lowering the minimum age estimate.

Of the three years (1997–1999) whose results we compared statistically, only in 1997 did the average minimum age of adult males differ significantly from (being greater than) that of adult females (Table 1). Nevertheless, our minimum age estimates and our previous survival-probability estimates (Ortega and Ortega 2009) suggest that adult males often live longer than adult females. In southern Manitoba, from 1993 to 1998, Woolfenden et al. (2001: table 6) also found the survival probability of adult males greater than that of adult females. Contrasting with our results, and those of Woolfenden et al. (2001), in the eastern Sierra Nevada from 1982 to 1988, Anderson et al. (2012: figure 3A) estimated the probability of adults' survival to be highest in ASY males (63.4%), lower in females (56.1%) and lowest in SY males (32.9%). Adult female cowbirds may often have shorter lives than adult males because, laying so many eggs in a breeding season, adult females may have difficulty obtaining enough resources to survive this large reproductive effort (Darley 1971). Also, many hosts attack adult female cowbirds, decreasing their survival probability (Ortega 1998).

Second-Year Versus Older Cowbirds

We observed different patterns of capture ratios in adult cowbirds. First, over the later years of the study, SY males were typically caught more than ASY males. Second, although newly captured adult females outnumbered recaptured females within any year, the frequency of capture of known ASY females generally increased as the study progressed.

Since mate acquisition, at least for male cowbirds, is a function of dominance and age (see Ortega 1998 and references therein), this apparent increase in the proportion of SY males may have allowed a greater proportion of them to obtain mates during the later years of study. We are not sure why SY males became more numerous during most of the later years of the 1990s (Figure 1). Two potential explanations are cowbird control elsewhere and production of cowbirds in preceding years.

In the early to mid-1990s, some large-scale efforts at cowbird trapping were underway in both California (from 15 March to 15 July each year [Griffith and Griffith 2000]) and Texas (from March to June each year [Kostecke et al. 2005]). Such cowbird-removal programs have helped decrease the frequencies of brood parasitism on several endangered species, or subspecies, of cowbird hosts, and in some cases, targeted host populations increased as a result of cowbird removal (Decapita 2000, Griffith and Griffith 2000, Hayden et al. 2000, Whitfield 2000, Kostecke et al. 2005). Also, we do not know to where our population of cowbirds migrated for the winter. On the basis of trapping, however, most juvenile cowbirds left our study site in mid to late July and early August, after most adults had already left to begin their southward migration. Therefore, if juvenile and older males migrated to different locations, perhaps one age class would not have been trapped as readily in any large-scale cowbird-removal efforts.

A second possible explanation for the increased proportion of SY males during most of the later years of our study (Figure 1) is that in the years preceding the peaks, production of cowbirds (including males) was exceptionally high. For comparison, in southern Manitoba, during some of the same years from 1993 to 1998, Woolfenden et al. (2001) found an increased ratio of ASY males to SY males in the resident population, and, except in 1993 and 1997, they also found that ASY males outnumbered SY males in the nonresident population (Woolfenden et al. 2001: table 3). In the Sierra Nevada of California from 1978 to 1991, however, Anderson et al. (2005) caught more SY males than ASY males.

In our study, the increase in captures of known ASY females as the study progressed was the result of the accumulation of recaptures, allowing us to identify more females as being older. By the later years of our study (1997–1999), however, the frequency of captures of known ASY females appeared to have approached a plateau of about 26–33% of captures of all adult females within a year (Figure 2).

Age Structure of Female Brood Parasites and Host-Population Models

We suggest that knowledge of the age structure of a population of cowbirds, especially of adult females, might allow for better modeling of such attributes of a host's population as population dynamics (May and Robinson 1985), seasonal fecundity (Pease and Grzybowski 1995, Schmidt and Whelan 1999), and productivity (Powell and Knutson 2006). However, none of these proposed, and/or modified, models for describing host populations, both with and without cowbird parasitism, incorporated the age structure of the brood-parasitic females. For example, in their model of a population of adult female hosts, May and Robinson (1985: equation 2) incorporated, "parasitism probability," p. The "simple" and "more complex" models of Pease and Grzybowski (1995) included the parameter of brood-parasitism rate, ρ. Grzybowski and Pease (1999: table 1 and equations 1a and 1b) incorporated into their suggested models cowbird abundance, C, and a cowbird auto-interference coefficient, m (representing a decrease in cowbirds' success in nests parasitized more than once). In other models, Schmidt and Whelan (1999: equation 1) included the probability of parasitism, N, and Powell and Knutson (2006: figure 1) included a "randomly selected" probability of parasitism, θ (evaluated on the basis of data recorded in the field and/or available in the literature). Because younger (one-year-old) females lay on average fewer eggs than do older females in many species of birds (Ricklefs 1973, Sæther 1990, Forslund and Pärt 1995), including the cowbird (Fleischer et al. 1987, Holford and Roby 1993), it could be useful to include the parameter of age structure of the population of brood-parasitic females into these various models.

SUMMARY

The importance of the age structure of the cowbird population, especially of females, will clearly vary with the host population targeted for modeling or management. Although the apparent age structure of a population of cowbirds, both males and females, can vary through time, we suggest that developing models for describing host populations that incorporate an age-structure parameter for the parasite can only increase our understanding of avian host–parasite interactions. However, we make this suggestion recognizing that incorporating into these models the parameter of age structure within a population of female cowbirds, which affects the cowbirds' egg production, will be difficult to accomplish until the discovery of criteria—plumage or other morphological differences—for distinguishing yearling and older female cowbirds in the field. Better estimates of the maximum lifespan of females will result in more accurate population models and better management decisions.

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Brewer's Blackbirds chasing a female Brown-headed Cowbird from their nest

Sketch by Tim Manolis