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MORPHOLOGICAL DIFFERENTIATION OF BROWN-HEADED COWBIRDS IN THE OKANAGAN VALLEY, BRITISH COLUMBIA¹

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Abstract. We investigated morphological variation in Brown-headed Cowbirds *Molothrus ater* in the Okanagan Valley, southern British Columbia, Canada. We found that cowbirds were significantly differentiated in body measurements (wing, tail, tarsus, and culmen lengths) from both western subspecies, *M. a. artemisiae* and *M. a. obscurus*. The pattern of differentiation in body shape suggests Okanagan Valley cowbirds are not hybrids of the two above-mentioned subspecies, *contra* the situation in northern California. Rather, the Okanagan birds appear to have been present and isolated there for sufficient time for morphological differentiation to have occurred. This finding calls into question the hypothesis that many cowbird hosts do not recognize the parasite's eggs because of the recency of arrival of the cowbird in western North America.

Key words: brood parasite, Brown-headed Cowbird, hybridization, *Molothrus ater*, morphology, population differentiation.

INTRODUCTION

There has been much interest in the impact of the brood-parasitic Brown-headed Cowbird *Molothrus ater* on host populations in western North America (Terborgh 1989, Ward and Smith, in press). Attention has focused on the apparent expansion of this species to the West following the introduction of cattle herds by Europeans. It is widely believed that the rapid expansion of this forest-edge species, concomitant with the destruction of forests, has led to the demise of a number of host populations, particularly in the Midwest and eastern North America (Brittingham and Temple 1983, Morse 1989, Terborgh 1989). The reason for this negative impact is purported to be evolutionary lag, that is, the lack of time available for the evolution of appropriate behavioral responses by the hosts to the pres-

ence of cowbird eggs in their nests (Rothstein 1975, Ward et al. 1996).

Recently, however, Rothstein (1994) has stressed that the cowbird may have been in the West for a long time. Indeed, cowbirds have been in western North America long enough for morphological differentiation of two subspecies, the large *M. a. artemisiae* and small *M. a. obscurus*, to have occurred (Grinnell 1909). Until the turn of the twentieth century, *M. a. artemisiae* was considered to be widespread in the area east of the Sierra Nevada and Cascades, while *M. a. obscurus* was restricted to the Colorado River in southern Arizona and California. *M. a. obscurus* started to invade the area west of the Sierra Nevada at about the turn of this century and moved slowly northwards along the Pacific seaboard, reaching Canada in 1955 (Rothstein 1994). There is no evidence to suggest that *M. a. artemisiae* has changed its range over this period.

Early records of *M. ater* in British Columbia (Brooks 1900, Parham 1937) record it as common in the area east of the Cascade range before

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the turn of the twentieth century, but absent from the region west of these mountains. A. J. Brooks shot a single gravid female (*M. a. artemisiae*) near Sumas on the coastal plain on May 26, 1897, but recognized it as a vagrant in his later writings (Brooks 1917).

More recently, *M. a. obscurus* has started to invade the area east of the Sierra Nevada and southern Cascade ranges (Rothstein 1994). This has led to hybridization between *M. a. obscurus* and *M. a. artemisiae*, resulting in a reduction in mean wing length of adult males in the cowbird populations east of these mountains (Fleischer and Rothstein 1988). This hybridization appears to have occurred earlier in the southern part of the range of *M. a. artemisiae*.

An additional change in the cowbird populations east of the Sierra Nevada and Cascades has been in the rictal flange color of the nestlings. *M. a. obscurus* nestlings have yellow rictal flanges, whereas *M. a. artemisiae* nestlings have white flanges (Rothstein 1978). Rictal flanges in the zones of hybridization are mostly yellow, suggesting that the allele for yellow flange color is dominant over white (Stevens 1982). However, Stevens (1982) has established that both yellow and white flanges occur in some hybrid populations in the eastern Sierra Nevada of California.

We undertook this study to determine whether cowbird populations in the Okanagan Valley, British Columbia are of hybrid origin, and have undergone similar changes in body size and rictal flange color to populations from California. The Okanagan Valley populations of Brown-headed Cowbirds are of particular interest for two reasons:

(1) This valley contains the most diverse bird populations in Canada (Cannings et al. 1987), and the potential negative impact of cowbird populations is high, due to extremely high levels of parasitism (Ward and Smith, in press). Some species (e.g., Yellow Warbler *Dendroica petechia*, Song Sparrow *Melospiza melodia*, and Warbling Vireo *Vireo gilvus*) suffer more than 50% parasitism, and the Warbling Vireo usually has no surviving young when parasitized. Thus, selection for recognition of cowbird eggs should be extremely strong, yet apparently does not occur. Knowledge of the joint evolutionary history of cowbirds and their hosts in the Okanagan Valley may help us to establish whether the apparent evolutionary lag between cowbirds and their

hosts is a consequence of the short time available for appropriate mutations for cowbird-egg recognition by hosts or due to some other, as yet unproposed, factor.

(2) Birds in this valley have been well studied since the turn of the century, particularly due to the collecting efforts of A. J. Brooks. Brooks recorded the cowbird as common in the Okanagan when he first arrived there in 1898 (Brooks, unpubl. data). Additionally, three nestlings collected by him in the Okanagan Valley (now in the Museum of Vertebrate Zoology, University of California, Berkeley) had whitish yellow gapes (Rothstein 1978), many years before *M. a. obscurus* arrived at that latitude. *M. a. obscurus* was first recorded at the same latitude in Vancouver, 400 km west of the Okanagan Valley, in 1955. Thus, there is some evidence that the Okanagan Valley cowbirds may both have been present there for a long time and have experienced different evolutionary events to those affecting cowbirds elsewhere in western North America.

METHODS

MEASUREMENTS

All birds measured by us were caught at three sites in standard cowbird traps (Robinson et al. 1993) between Okanagan Falls and Oliver in the southern Okanagan Valley, British Columbia in 1994, and measured with vernier calipers. Wing length was measured along the chord. We note that tarsus length may be measured slightly differently by different observers (S. I. Rothstein, pers. comm.) and thus may lead to error. We calculated the repeatability (also known as the intra-class correlation coefficient) of this measure using the procedure outlined by Lessells and Boag (1987) and Krebs (1989). We obtained a repeatability of 0.974. Therefore, we are confident that the measure provided here has minimal interobserver error. Males were aged following Selander and Giller (1960).

Brown-headed Cowbirds shot by A. J. Brooks at Okanagan Landing, British Columbia between 1913 and 1944 were measured at the University of California, Berkeley by S. I. Rothstein. Additionally, we obtained all the birds of the *M. a. obscurus* subspecies in the collection of the University of California, Berkeley measured by Grinnell (1909; all specimens from southern California and Arizona), and Brooks' Okanagan

TABLE 1. Comparison of mean (\pm SE) wing, tail, tarsus, and culmen measurements for male and female Brown-headed Cowbirds shot by Grinnell (1909) and by Brooks (1913–1944) in the Okanagan Valley, and live-trapped in the Okanagan Valley by us. All measurements are in mm and are of adult males and females unless otherwise stated. All *Molothrus ater obscurus* and birds collected by A. J. Brooks were remeasured by one of us (JNMS).

	Wing	Tail	Tarsus	Culmen	n
Males					
<i>M. a. artemisiae</i> (Grinnell)	113.3 \pm 0.83	74.9 \pm 0.90	27.8 \pm 0.33	18.3 \pm 0.34	11
<i>M. a. obscurus</i> (Grinnell)	100.2 \pm 0.83	68.4 \pm 0.90	24.1 \pm 0.33	16.5 \pm 0.34	11
Okanagan Valley (Present study)	111.1 \pm 0.40	77.0 \pm 0.43	23.5 \pm 0.16	16.8 \pm 0.16	48
Okanagan Valley (A. J. Brooks)	111.5 \pm 1.33	78.4 \pm 1.90	24.1 \pm 0.47	16.9 \pm 0.40	8
Okanagan Valley, first year males (Present study)	108.6 \pm 0.47	74.7 \pm 0.18	23.5 \pm 0.18	16.9 \pm 0.17	46
Females					
<i>M. a. obscurus</i> (Grinnell)	91.7 \pm 0.61	64.8 \pm 0.47	20.0 \pm 0.23	14.4 \pm 0.15	26
Okanagan Valley (Brooks)	99.4 \pm 1.04	70.3 \pm 0.81	22.1 \pm 0.39	15.9 \pm 0.26	9
Okanagan Valley (Present study)	99.3 \pm 0.41	68.7 \pm 0.37	22.2 \pm 0.17	15.3 \pm 0.09	69

Valley specimens. All these (male) birds were remeasured by one of us (JNMS) to ensure that differences in body sizes were not due to inter-observer error. Furthermore, JNMS measured all female cowbirds collected by Grinnell and Brooks in this collection. All measurements were log-transformed prior to statistical analysis.

RECTAL FLANGE COLOR

We recorded rectal flange color in nestlings in the Okanagan Valley in 1994 and 1995. To ensure that rectal flange color was correctly identified, we induced the begging response in nestlings.

RESULTS

POPULATION DIFFERENTIATION

Males. Fleischer and Rothstein (1988) have shown that first-year males have shorter wings than older males. Hence, we first performed our analyses on adult males only. There were significant differences among Grinnell's two subspecies, *M. a. artemisiae* (collected in northern Nevada) and *M. a. obscurus* (collected in southern California and Arizona), and our Okanagan birds in wing ($F_{2,67} = 82.5$, $P < 0.001$), tail ($F_{2,67} = 37.0$, $P < 0.001$), tarsus ($F_{2,67} = 67.9$, $P < 0.001$), and culmen length ($F_{2,67} = 8.8$, $P < 0.001$). Birds in this study were more similar to *M. a. artemisiae* than to *M. a. obscurus* in wing and tail length, whereas the reverse was true for tarsus and culmen length (Table 1).

In a discriminant function analysis (using wing, tail, tarsus, and culmen lengths as variables), we found that all three groups (*M. a. artemisiae* and *M. a. obscurus* measured by Grinnell and our Okanagan birds) could be significantly discriminated (Wilks $\lambda = 0.086$, $F_{8,128} = 38.6$, $P < 0.001$) (Fig. 1). This overall significance value only indicates that at least one group differs from the rest (Neter et al. 1990). To determine whether the Okanagan birds were significantly differentiable from *M. a. artemisiae* and *M. a. obscurus*, we performed a cross-validation procedure (as outlined in the statistical program SYSTAT, Wilkinson 1992). The predicted values were first computed for all cases and the success of the classification determined by classifying the "new" cases (i.e., the Okanagan birds) according to the groups. Ninety Okanagan birds were correctly classified, two were mis-classified as *M. a. artemisiae* and a further two birds as *M. a. obscurus*. Hence, the discriminant function analysis was successfully cross-validated in 96% (90/94) of cases.

As a further check on our analyses, we performed a principal component analysis on all the above-mentioned (adult male) specimens, and then identified individuals of each group. Principal components analysis attempts to maximize the variance within the sample, assuming all observations are from the same group. Hence, plotting individuals in principal component space should show any hybrids occurring between the

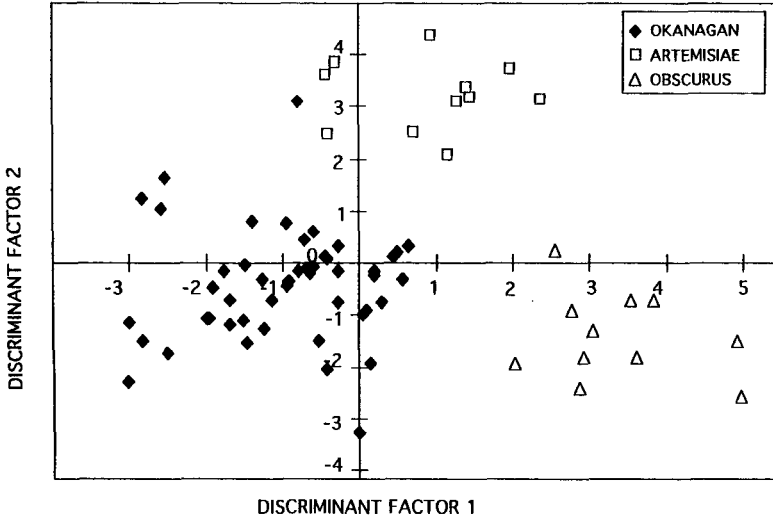


FIGURE 1. Discriminant function plot of the first and second discriminant factors. All measurements of *M. a. artemisiae* and *M. a. obscurus* were made by Grinnell (1909) when he classified these subspecies; Okanagan Valley cowbirds were measured in 1994. If the Okanagan Valley birds were hybrids of the two subspecies, we would expect them to lie between the two subspecies in discriminant space, and not to one side as they do in this figure.

two "parent" types. In this analysis, the first two principal components explained 81% of the variance in the data. Component loadings for the first principal component axis were (0.848-wing length + 0.716-tail length + 0.595-tarsus length + 0.663-culmen length) and for the second principal component axis were (-0.348-wing length - 0.619-tail length + 0.672-tarsus length + 0.511-culmen length). In a multiple analysis of variance (MANOVA) using these two principal component axes as dependent variables, there was a significant difference among the three groups, viz. *M. a. artemisiae*, *M. a. obscurus*, and Okanagan birds (Wilks $\lambda = 0.3$, $F_{4,224} = 50.8$, $P < 0.001$).

We then performed analyses of variance on these two variables separately. For Principal Component 1, there was a significant difference among the groups ($F_{2,113} = 50.1$, $P < 0.001$). We performed a *post hoc* test to determine differences between pairs of groups, using a Bonferroni adjustment of α to protect the comparisonwise error rate. Each group was significantly different from each of the other groups ($P < 0.001$). A similar result was obtained for Principal Component 2 ($F_{2,113} = 49.4$, $P < 0.001$; *post hoc* tests: $P < 0.003$). Hence, the three groups are differentiable from one another on both principal component axes.

Regarding the possibility that Okanagan birds are hybrids of *M. a. artemisiae* and *M. a. obscurus*, the mean \pm SE value for Okanagan birds was intermediate between those of the two recognized subspecies on the first axis (172.7 ± 0.5 vs. 178.5 ± 1.4 [*artemisiae*] and 159.2 ± 1.4 [*obscurus*]), but larger than both subspecies on the second axis (-60.8 ± 0.3 vs. -57.9 ± 0.8 [*artemisiae*] and -52.6 ± 0.8 [*obscurus*]). These results indicate, as do the results from the discriminant function analysis, that the Okanagan birds are not a simple intermediate form between the two recognized subspecies.

Some of Grinnell's *M. a. artemisiae* specimens not measured by us may have been first-year birds; therefore, we repeated our analysis using all male cowbirds we caught, regardless of age. The three groups still were significantly differentiable (Wilks $\lambda = 0.4$, $F_{8,434} = 30.0$, $P < 0.001$). Sixteen of the 201 cowbirds (8%) from our study fell within the group comprising the smaller *M. a. obscurus*. This partial overlap is not surprising, because first-year males have shorter wings ($F_{1,94} = 16.2$, $P < 0.001$) and tails ($F_{1,92} = 13.6$, $P < 0.001$) than adults in our population (as well as in other populations, Fleischer and Rothstein 1988), although they did not differ significantly in tarsus ($F_{1,93} = 0.02$, $P =$

TABLE 2. Rictal flange color in Okanagan Valley cowbirds. Numbers indicate the number of cowbird nestlings (one per nest) with that rictal flange color.

Host	Host flange	Cowbird nestlings with	
		White flange	Yellow flange
Song Sparrow <i>Melospiza melodia</i>	White	4	0
Chipping Sparrow <i>Spizella passerina</i>	White	1	0
Warbling Vireo <i>Vireo gilvus</i>	White	6	2
Yellow Warbler <i>Dendroica petechia</i>	Yellow	0	4
Western Wood-Pewee <i>Contopus sordidulus</i>	Yellow	2	0

0.9) or culmen length ($F_{1,93} = 0.07$, $P = 0.79$) from older birds (Table 1).

Females. Our female birds differed significantly in wing, tail, tarsus, and culmen length from Grinnell's *M. a. obscurus* birds (MANOVA; Wilks $\lambda = 0.06$, $F_{8,196} = 76.63$, $P < 0.001$, Table 1). All univariate F -tests were significant for the four measurements, with the *M. a. obscurus* birds being smaller than ours on all variables (all F s > 17.0 , all P s < 0.001).

CHANGES IN MORPHOLOGY OVER TIME

There was no significant difference in body size (wing, tail, tarsus, and culmen lengths) of cowbirds shot by A. J. Brooks and our birds (MANOVA; males: Wilks $\lambda = 1.0$, $F_{4,212} = 1.17$, $P = 0.3$; females: Wilks $\lambda = 0.9$, $F_{4,73} = 1.91$, $P = 0.1$). These results are inconsistent with the hypothesis that hybridization with a smaller subspecies has occurred.

RICTAL FLANGE COLOR

Although our data are scanty, there appear to be as many yellow-flanged as white-flanged nestlings (Table 2). There is a tantalizing suggestion that matching of rictal flange color may occur, especially in Yellow Warbler and Song Sparrow hosts. In our study, more yellow-flanged cowbirds were found in Yellow Warbler nests, whereas white-flanged cowbirds were found in Song Sparrow nests. These two host species also are the hosts whose eggs are best matched by cowbird eggs (pers. observ.). Across host species, there was a significant matching of cowbird rictal flange color with that of the host ($\chi^2_4 = 10.0$, $P < 0.05$).

DISCUSSION

MORPHOLOGICAL DIFFERENTIATION

The similarity of Okanagan cowbirds to *M. a. artemisiae* in some features (wing and tail length) and to *M. a. obscurus* in others (tarsus and culmen length), rather than an overall difference in body size, suggests a distinct evolutionary history for the Okanagan birds. Indeed, when delineating the subspecies of *Molothrus ater*, Grinnell (1909, p. 279) wrote that "A survey of relevant cases among birds leads me to argue that as a rule mere uniform increase or decrease in size signifies less of phylogenetic separation than do changes in proportion of parts." A similar argument has been made by Grant (1986) with regard to the evolution of bill size and shape in Darwin's finches in the Galapagos.

The degree of morphological differentiation of Okanagan Valley cowbirds from the specimens used by Grinnell (1909) to define the subspecies *M. a. artemisiae* and *M. a. obscurus* suggests that these birds: (1) have been present in the Okanagan Valley for a long enough time for morphological differentiation to have occurred, or (2) there is great clinal variation in cowbirds, resulting in differentiation of Okanagan birds from cowbirds in Nevada (*M. a. artemisiae*).

The first possibility is substantiated by older records of this species' presence, indicating that cowbirds have long been common in the Okanagan Valley. The absence of change in body size of adult Brown-headed Cowbirds in the Okanagan Valley since the turn of the twentieth century is inconsistent with the expectation that hybridization has occurred between an original population of large *M. a. artemisiae* and the invasive population of smaller *M. a. obscurus*. We can not discount possibility 2, namely that there is sufficient clinal variation in the species. Further measurement of birds between northern Nevada (Grinnell's specimens) and the Okanagan Valley will be necessary to establish this possibility. Nonetheless, clinal variation, like allopatric differentiation, requires time for selection to occur. Thus, regardless of whether this morphological differentiation of Okanagan and other groups is allopatrically or clinally induced, we consider it necessary to reconsider statements about evolutionary lag in cowbird hosts being due to the recent arrival of cowbirds in the West. If cowbirds have been in the Okanagan Valley

long enough for morphological differentiation to occur, natural selection is presumably acting more quickly on cowbird body size than on the evolution of counter-adaptations in the hosts.

The long wings and tails, and short tarsi and culmens of Okanagan birds are consistent with Bergmann's and Allen's rules, namely that populations of animals at higher latitudes tend to be larger (Bergmann's rule) but have shorter extremities to reduce heat loss (Allen's rule) (James 1970). It will be necessary to measure these morphological features along a north-south gradient to determine whether there is any support for this hypothesis. If these geographic rules underlie the morphological patterns we have detected, more northern populations of cowbirds should have even longer wings and shorter tarsi and culmens than the Okanagan Valley birds.

RICTAL FLANGE COLOR

Fleischer and Rothstein (1988) found a unique pattern of yellow flange color in populations east of the Sierra Nevadas in California as a result of hybridization of endemic *M. a. artemisiae* with invasive *M. a. obscurus*. In contrast, the presence of cowbird nestlings in the Okanagan Valley with yellow rictal flanges 50 years before *M. a. obscurus* arrived at the 49th parallel indicates that the Okanagan population may always have been polymorphic for this trait. Our admittedly small data set for Okanagan nestlings suggests that there may be matching of mouth color of cowbirds with those of their hosts, much like the processes that led to the differentiation of the parasitic widowfinches (*Vidua*) of Africa (Nicolai 1974). That is, selection for mouth color recognition in the host led to selection for matching mouth color in the parasite. Further work is needed to establish whether this has led to differentiation of Okanagan cowbird demes with different host preferences.

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