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Assortative Mating by Color in a Population of Hybrid Northern Flickers

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Yellow-shafted Flickers (*Colaptes auratus auratus*) with black moustache marks and red nape patches, and Red-shafted Flickers (*C. a. cafer*) with red moustaches and no nape patches, formerly were considered separate species (see Moore 1995). Because the two hybridize extensively along a zone that extends along the eastern slope of the Rocky Mountains from Alaska to Texas (Short 1965, Moore 1995), they were classified as a single species, the Northern Flicker (*C. auratus*; AOU 1983). The persistence of hybrids and the apparent stability of the hybrid zone over centuries (Rising 1983, Moore and Buchanan 1985) has been of considerable interest to evolutionary biologists because patterns of mate assortment after secondary contact bear on competing hypotheses for mechanisms of speciation. If genetic incompatibility reduces hybrid fitness, reproductive isolating mechanisms should be favored. However, flickers in the central and southern United States do not appear to mate assortatively (Short 1965, Beck 1971, Moore 1987), and hybrid individuals do not seem to have lower fitness than the parental types (Moore and Koenig 1986).

Little is known about flicker populations in the northern part of the hybrid zone (Rising 1983), where evidence suggests that the distributions of subspecies have shifted over time (McGillivray and Biermann 1987). Using the largest sample of mated

pairs yet obtained from a single location, I examined whether hybrids in a northern population mated assortatively.

Study Area and Methods.—The study area was near Riske Creek, central British Columbia (51°52'N, 122°21'W), and encompassed approximately 71 km² of grassland with scattered clumps of trembling aspen (*Populus tremuloides*) and mixed forest. Flickers of a variety of phenotypes occur at Riske Creek, and many (but not all) display characteristics of hybrids. I observed flickers in 1998 from the time adults arrived on territories in late April until the young left the nest in July. I censused territories about every second day using tape-recorded territorial vocalizations. When a nest with eggs was found, I cut a small "door" into the tree cavity after I determined that the clutch was complete and there was little risk of the pair abandoning.

Adult flickers were trapped at the nest during the incubation or brood-rearing periods. Trapped adults were given a unique combination of colored leg bands and were weighed and measured. Wing chord (flattened) and the lengths of the tail and the 9th primary were measured with a ruler to the nearest mm, and bill length (from the anterior edge of the nostril), bill depth, and tarsus length were measured with digital calipers to the nearest 0.05 mm. Only one parent was trapped at some nests, so sample sizes differed for analyses.

Except where noted, I ranked plumage color following the methods in Short (1965). Malar mous-

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TABLE 1. Morphological measurements of male and female Northern Flickers at Riske Creek, British Columbia. Values are $\bar{x} \pm SD$, with n in parentheses. P -values are from t -tests comparing females with males for each variable.

Variable	Females	Males	P
Wing length (mm)	167.6 \pm 4.3 (71)	170.5 \pm 4.0 (72)	0.002
Bill length (mm)	28.9 \pm 1.5 (67)	30.4 \pm 1.5 (67)	<0.001
Bill depth (mm)	7.7 \pm 0.5 (67)	8.1 \pm 0.6 (67)	<0.001
Tarsus length (mm)	31.2 \pm 1.4 (67)	31.5 \pm 1.0 (69)	0.220
Tail length (mm)	110.7 \pm 4.7 (65)	113.2 \pm 4.4 (66)	<0.002
9th primary length (mm)	98.0 \pm 3.5 (67)	98.8 \pm 4.4 (67)	0.310

tache color (only in males) varied on a five-point scale from 0 = 100% black to 4 = 100% red. The nuchal patch, or nape, was ranked from 0 = large as in *auratus* to 4 = absent. The color of the underside of the rectrix varied from 0 = yellow as *auratus* to 4 = red as *cafer*; however, I used a series of five color cards to rank rectrices in the field, and if the color of the rachis was different than the color of the vane, the feather was given a score midway between the two colors. Thus, my color scale for the rectrices had more gradations than the one used by Short (1965). A rank of 0 on this scale is equivalent to Orange Yellow, 2 is Spectrum Orange, and 4 is Flame Scarlet in the color scheme of Smithe (1975). I calculated a hybrid index as in Short (1965) by summing the ranks for each plumage character, so *auratus*-like hybrids had low index scores and *cafer*-like individuals had high scores. For reference, I measured study skins of pure *cafer* at the McTaggart-Cowan Vertebrate Museum at the University of British Columbia and skins of *auratus* at the Royal Saskatchewan Museum. These samples were collected at about the same latitude as Riske Creek and should help control for the latitudinal gradient in body size of flickers (Short 1965).

Statistics were performed using SPSS, and all tests were two-tailed. I used Spearman rank correlations for plumage variables; previous studies have used Pearson correlations for color, but this is incorrect because colors are ranked and cannot be assumed to be based on a linear scale. Tests were performed using the hybrid index and also with the three plumage variables considered separately, but to save space, I have not reported all of the nonsignificant statistical results.

Results.—I trapped 72 male and 71 female flickers. Means for morphometric variables from these flickers were calculated separately for each sex and compared with the museum specimens to determine the place of the Riske Creek population along the east-west hybrid gradient. Within this population containing hybrids, males were larger than females for all morphometric variables except tarsus length and 9th primary length (Table 1).

To compare subspecies, I used a two-way ANOVA with sex and subspecies as factors. Scheffé post-hoc contrasts showed that wing length of flickers from

Riske Creek did not differ from that of *cafer* but was longer than that of *auratus* ($F = 37.5$, $df = 2$ and 192 , $P < 0.001$). Bill length ($F = 35.8$, $df = 2$ and 197 , $P < 0.001$) and bill depth ($F = 7.5$, $df = 2$ and 194 , $P = 0.001$) of the hybrids differed from those of *cafer* and *auratus* (Fig. 1), whereas tarsus length of hybrids was longer than that of *auratus* ($F = 8.0$, $df = 2$ and 182 , $P < 0.001$) but did not differ from that of *cafer*. Hybrid males had larger red nape patches than did females. Moreover, only 23% ($n = 66$) of the hybrid females, versus 65% ($n = 64$) of the males, had a nape patch, and the distribution of nape scores differed between the sexes ($\chi^2 = 27.5$, $df = 4$, $P < 0.001$). The mean rectrix color was 2.8 and was shifted toward the *cafer* end of the spectrum; rectrix color did not differ between the sexes (Mann-Whitney U -test, $P = 0.88$). No male from Riske Creek had a completely black moustache, whereas 74% had completely red moustaches. Although the red-shafted subspecies averages larger than the yellow-shafted, within the hybrid population there were no significant correlations between the plumage-color variables and the six body-size variables for males ($n = 65$, all $P > 0.12$). For females ($n = 66$), bill width was negatively correlated with color ($r = -0.29$, $P = 0.018$) and with the hybrid index score ($r = -0.30$, $P = 0.015$), i.e. red females had thinner bills than did yellowish females.

I trapped both members of the pair at 58 nests. I examined Pearson correlations between pair members for the six body-size variables, but none was significant (all $P > 0.09$). Among plumage variables, female color was positively correlated with the male hybrid index and with components of that index: color and nape (Table 2, Fig. 2). Assortative mating may arise "passively" if two groups have different breeding chronologies. Using only first nests, I examined the relationship between laying date and phenotype and found a significant positive correlation between date and the hybrid index for females ($r_s = 0.32$, $n = 66$, $P < 0.001$) and for males ($r_s = 0.32$, $n = 65$, $P = 0.018$; Fig. 3). On average, *cafer*-like birds had later laying dates than *auratus*-like birds. Nevertheless, when I controlled for laying date in a partial correlation, the positive relationship between male and female color within pairs persisted ($r = 0.26$, $n = 58$, $P = 0.046$), suggesting that breeding chronology is

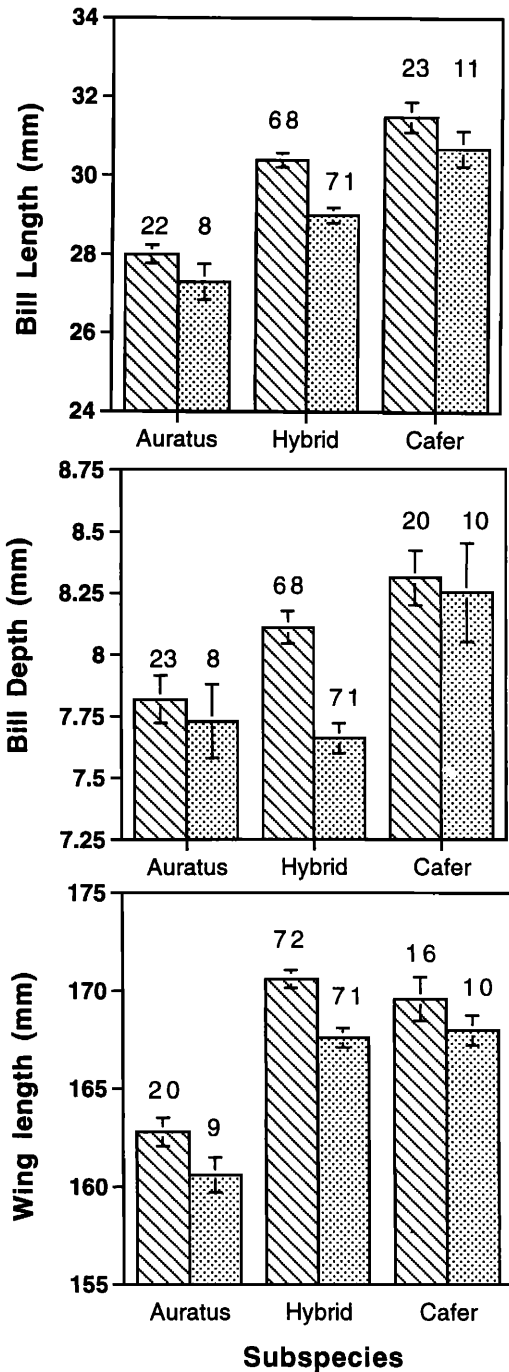


FIG. 1. Comparison of three morphometric variables between the sexes and among the subspecies of Northern Flickers. Bars are \bar{x} with SE, with sample sizes above. Hybrids are live individuals from Riske Creek, British Columbia. Crosshatching = males; stippling = females.

TABLE 2. Spearman correlation coefficients between plumage characteristics of 58 mated pairs of Northern Flickers at Riske Creek, British Columbia. The hybrid index is the sum of the individual plumage characters (see Methods).

	Female color	Female nape	Female index
Male color	0.35**	0.18	0.31
Male nape	0.27*	-0.08	0.14
Moustache color	0.08	0.001	0.06
Male index	0.33*	-0.03	0.22

*, $P < 0.05$; **, $P < 0.01$.

largely, although not completely, responsible for assortative mating.

Discussion.—In this first study to document assortative mating in Northern Flickers, nonrandom pairing was detected with respect to rectrix color, and with female color and the male hybrid index (Table 2). Interestingly, the correlation between indices (including the female's nape score) was weak ($P = 0.09$). The size of the red nape is a sex-linked trait (see Erskine 1962) and thus may not reflect the degree of hybridization in females. Because the subspecies differ both in color and in size (Fig. 1), it was necessary to control for body size when examining mating patterns. Body size may confer advantages in intrasexual competition, or it may be important in mate choice (see Bortolotti and Iko 1991). Previous studies of flickers have not analyzed the body size of mated pairs, but I found no significant correlations. Thus, it appears that flickers at Riske Creek mated according

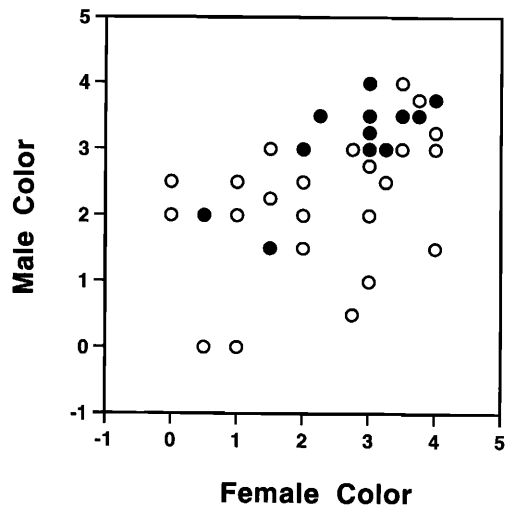


FIG. 2. Relationship between the color of females and that of males for 58 mated pairs of Northern Flickers in central British Columbia. Solid dots represent more than one data point.

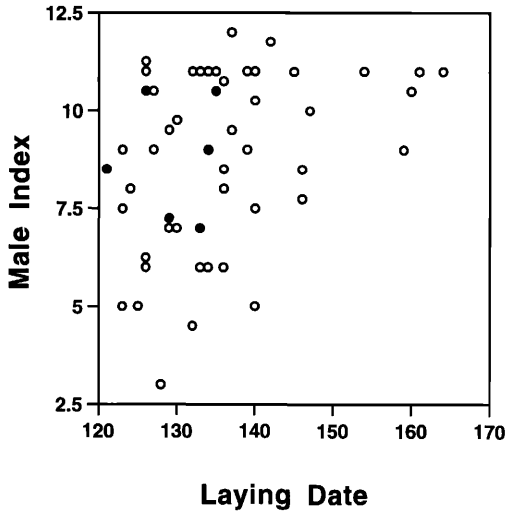


FIG. 3. Relationship between the color of male Northern Flickers and the Julian date of the initiation of egg laying at Riske Creek, British Columbia. Solid dots represent more than one data point.

to color per se, and not body size. Males were larger than females for most measures, contrary to the information in Moore (1995), which suggests that body size in flickers is partly the result of sexual selection.

Assortative mating may arise from active mate choice by one or both sexes, or it may result from patterns of passive contact between phenotypes (Burley 1983). I did not attempt to test hypotheses for assortative mating, but I showed that color was associated with laying date for males and females. If laying dates reflect arrival times on the study area, then yellowish individuals may pair earlier, on average, than redder birds. If so, assortative mating in the Riske Creek population may partly be a consequence of different migration schedules of the phenotypes. Red-breasted Sapsuckers (*Sphyrapicus ruber*) and Red-naped Sapsuckers (*S. nuchalis*), which also hybridize in central British Columbia and at Riske Creek, have a temporal separation in breeding that minimizes contact (Johnson and Johnson 1985, Campbell et al. 1990). Previous studies (Beck 1971, Rising 1983) may not have detected assortative mating in flickers because of smaller sample sizes. Moore (1987) analyzed 123 pairs of living and dead birds from 13 locations by transforming the index scores to percentiles, but such percentiles may have been biased because they were based on small original samples. It is possible, but perhaps unlikely, that mate choice is stronger in the north because the eastern and western populations came into contact more recently after the withdrawal of glaciers and thus had more time to diverge prior to secondary contact. Alternatively, mate choice may be more important in

the north if a reduction in hybrid viability only is apparent in harsher or more extreme environmental gradients. Perhaps the most parsimonious explanation is that in a northern migratory population, the phenotypes have different schedules of movement and breeding, and this results in nonrandom pairing. To date, most evidence favors the "bounded hybrid superiority" hypothesis for the flicker hybrid zone in the south (Moore and Buchanan 1985), suggesting that hybrids have higher fitness where the subspecies meet and that assortative mating is not advantageous. Clearly, more information on reproductive success and dispersal and migration patterns of the different subspecies is needed to fully explain mate choice in flickers.

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