Variation in colour within a population of northern flickers: a new perspective on an old hybrid zone

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Abstract: We used a digital camera to quantify the colour of the tail feathers of 245 northern flickers (*Colaptes auratus*) in central British Columbia and investigate the frequency of colour morphs in the population of hybrids. The colour values generated by the camera corresponded well to the conventional method of ranking colours by eye, but was advantageous because it provided finer discrimination and a continuous colour variable. Rectrix colour varied in a continuum from the yellow of *C. a. auratus* to the red of *C. a. cafer.* By experimentally exposing red and yellow feathers to sunlight we showed that the intermediate orange colours were not a result of secondary fading of the carotenoid pigments. The distribution of colours in the population was bimodal. A paucity of intermediate phenotypes (orange birds) could not be explained by their mortality because return rates of birds to our study area was not associated with colour. New immigrants into the population tended to resemble parental types more often than hybrids. Assortative mating by colour in this population may tend to keep the subspecies separate, contrary to the situation in more southerly areas of the hybrid zone.

Résumé : Nous avons utilisé une caméra digitale pour quantifier la couleur des plumes de la queue chez 245 Pics flamboyants (*Colaptes auratus*) dans le centre de la Colombie-Britannique ainsi que pour déterminer la fréquence des différentes formes au sein de la population d'hybrides. Les valeurs des couleurs générées par la caméra correspondent à celles obtenues par la méthode conventionnelle d'évaluation des couleurs à l'oeil, mais la digitalisation comporte des avantages puisqu'elle permet une discrimination plus raffinée et rend la palette de couleurs continue. La couleur des rectrices varie dans un continuum du jaune de *C. a. auratus* au rouge de *C. a. cafer.* En exposant des plumes jaunes et des plumes rouges à la lumière solaire, nous avons pu démontrer que les colorations orangées intermédiaires ne sont pas le résultat de la décoloration secondaire des pigments caroténoïdes. La distribution des couleurs dans la population est bimodale. Le petit nombre de phénotypes intermédiaires (oiseaux orangés) ne peut être attribuable à la mortalité, puisque les taux de retour à notre site d'étude ne sont pas reliés à la couleur. Les nouveaux immigrants dans la population ont tendance à ressembler davantage aux types parentaux que les hybrides. Le choix d'un partenaire basé sur la couleur dans cette population peut contribuer à maintenir le statut de cette sous-espèce, contrairement à la situation qui prévaut dans les régions plus australes de la zone d'hybridation.

[Traduit par la Rédaction]

> The flicker situation will puzzle all the naturalists in the world.
>
> (Audubon 1843, pp. 71)

Introduction

The northern flicker, *Colaptes auratus*, is a polytypic woodpecker species comprising five subspecies groups differing in plumage colour and body size (Moore 1995). Formerly considered separate species, the red-shafted flicker, *C. a. cafer*, and the yellow-shafted flicker, *C. a. auratus*, hybridize along a zone extending along the Rocky Mountains from Texas to Alaska. This hybrid zone is at least 4000 years old and historical records show that it has been stable in position and width at least since the late nineteenth century (Moore and Buchanan 1985). The subspecies groups (hereafter subspecies) of flickers differ in several plumage traits, the most obvious being the bright colour of the shafts and vanes of the flight feathers. The various plumage traits appear to be inherited independently, so hybrid individuals may show a mosaic of parental types or intermediate phenotypes for single traits (Short 1965; Moore and Price 1993; Wiebe 2000).

What determines the proportion of red or yellow feather colour in flicker populations has been of interest to evolutionary biologists for decades. The bright pigment in flicker flight feathers is a combination of carotenoids that differ in proportions across subspecies (Test 1942; Stradi 1998),and is a product of genetic differences (Test 1969; Moore and Price 1993). Deakin (1936) documented only red or yellow hybrid offspring in two families of mixed parental types and concluded that feather colour resulted from a simple two-allele system, with the gene for yellow dominant over red. Subsequent analyses, however, have recognized intermediate orange phenotypes (Short 1965; Bock 1971; Moore and Price 1993). Deakin (1936) suggested that orange feathers resulted from fading in sunlight, but after exposing one red and one yellow feather to sunlight, Test (1940) found that they did not became orange.

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Quantifying feather colour in birds is difficult because observers perceive colour differently depending on the context and the degree of illumination (Endler 1990). Previous studies of hybrid flickers have ranked the colour of feathers into 3–5 categories (e.g., Short 1965; Bock 1971), or have named the feather-vane colour according to standardized colour chips (Test 1940). Such conventional methods are being replaced by new methodologies that allow colour to be quantified independently of the human eye (Villafuerte and Negro 1998). In this paper we classify feather colour of flickers according to conventional means and compare it with data provided by a digital camera. Our objective was to examine the frequencies of colour morphs in a population of hybrid flickers and determine whether hybrids showed a discrete intermediate phenotype, or if they exist as a continuum between parental types.

Material and methods

Study site and field methods

The study area near Riske Creek in central British Columbia (51°52′N, 122°21′W) is within the hybrid zone of northern flickers. It encompasses approximately 75 km^2 of grassland with scattered patches of trembling aspen (*Populus tremuloides*) and mixed coniferous forest. More details about the various habitat types in the region are given in Martin and Eadie (1999). We observed flickers in 1998 and 1999 from the time they arrived on territories in late April until the young fledged in late July. Potential territories were searched intensively every 2–3 days in spring using tape-recorded territorial calls, which are the same across subspecies. Because the habitat is fairly open and flickers were responsive to the tapes, we are confident that most adults in our area were detected each year. Even if our detection rates are less than perfect, calculations of return rates to the study area should not be biased by plumage colour. Adult flickers were trapped at the nest (under an animal-care permit) either by stuffing the nest hole during incubation or by pulling a net over the hole during brood-rearing. We trapped ≥94% of adults at the nests we located each year, and there is no reason to believe that trapping success was biased according to plumage colour. We entered six body-size measurements into a principal-component analysis: bill length, bill depth, and the lengths of the wing chord, tarsus, central rectrix and ninth primary. The first component (PC1) was used as a measure of overall body size (Rising and Somers 1989). Because of sexual size dimorphism, we performed separate analyses for each sex.

To the eye, the colour of an individual's wings matched the colour of its tail, so we focused on the latter. A few birds had one or more odd-coloured feathers in the tail (K.L. Wiebe and G.R. Bortolotti, unpublished data), which were not sampled. In the field, K.L.W. scored the colour of the shaft and vane of the third right rectrix using a colour scale of five paint cards ranging from yellow (vane score 1) to orange and red (vane score 5). An intermediate score between two paint cards was given to some feathers, so there were six colour categories in total. According to the standardized colours in Smithe (1975), the extreme yellow on this scale, characteristic of pure *auratus* specimens in museums, is "Orange Yellow," and the extreme red, characteristic of *cafer* specimens is "Flame Scarlet" (reference study skins of pure *cafer* were observed at the McTaggart-Cowan Vertebrate Museum at the University of British Columbia and *auratus* from the Royal Saskatchewan Museum). K.L.W. ranked malar moustache colour in males as follows: 4 = 100% red as in *cafer*, 3 = 0–25% black mixed with red, 2 = 26–50% black, 1 = >50% black (no individuals had 100% black moustaches as in *auratus*). Finally, the red nuchal or nape patch was ranked in five categories: 4 = absent as in *cafer* to 0 = large as in *auratus*.

Photographing feathers

We pulled the third rectrix on the right side from each adult flicker and saved the feather in a paper envelope to be photographed later. In the laboratory we placed feathers in a consistent manner 68 cm from the digital camera (Nikon Coolpix E900s) on a tripod. An external flash unit (Nikon Speedlight SB-28) was suspended 150 cm above the feathers. Feathers were photographed alongside two gray-scale reference cards so that colours could be adjusted to control for differences in illumination (Villafuerte and Negro 1998). We photographed all feathers from both years in November 1999. To minimize bias, one person used Adobe Photoshop software to digitally select the bright area of the medial vane in the distal half of the feather. We also selected a section of the feather shaft to be analysed separately from the vane. To ensure that different photographs could be compared directly, we corrected the raw colour scores for differences in illumination (Villafuerte and Negro 1998).

To see how the colour of sun-faded feathers might change, six red and five yellow feathers collected in 1998 were photographed in March 1999 and then taped to a piece of cardboard and left exposed in a southerly orientation for 1 month (20 March to 20 April 1999). We photographed the faded feathers again in November 1999, along with all other feathers.

Deriving colour from camera data

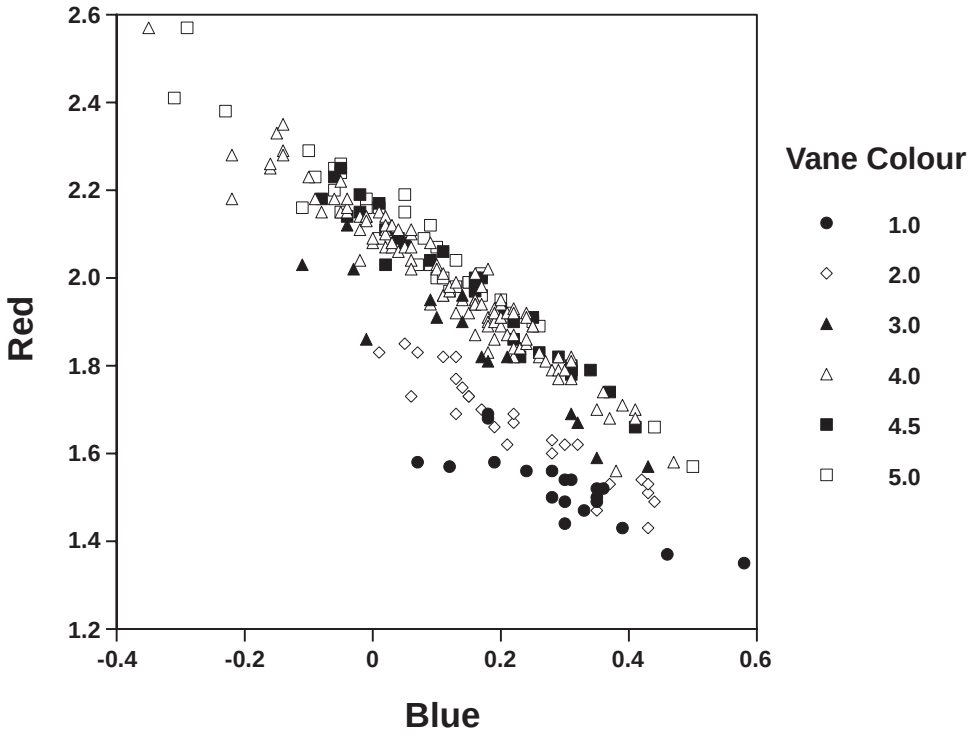
The digital camera provided red, green, and blue brightness values for the shaft and vane, and the three variables each followed a normal distribution. The red and green values were highly correlated with one another for both the vane ($r = -0.98$, $n = 218$, $P < 0.0001$) and the shaft ($r = -0.99$, $n = 218$, $P < 0.001$), making these colours essentially redundant in analyses. Thus, we ignored the green values and plotted feather colours on the red and blue axes. Scatterplots of vane values (Fig. 1) revealed that our six ranked colours were segregated in tight diagonal bands with similar slopes across the two axes. Shaft colours (not shown) had a similar pattern. In other words, neither the total amount of red nor the total amount of blue taken as single variables distinguished the feather colours perceived by us.

To derive a single colour variable we used the reduced major axis technique to fit a regression line through the points for each colour rank separately. We averaged the slopes of each of these lines and fit a new line through the median red and blue values. Residuals were then calculated and used as the new single colour variable. We then tested whether the variation in camera-derived scores could be distinguished by the human eye by asking 18 undergraduate students to rank the colour of feathers from yellow to red and comparing their rankings to residuals. Each student was given three feathers in each of three sets: yellow (within vane colour category 1), orange (vane colour 3), and red (vane colour 5). Each set contained a feather with a statistical mean colour score residual within that category and two feathers that were 1 SD above and below that mean score. Statistical tests were performed using SPSS and all are two-tailed.

Results

In total, 245 flicker tail feathers were collected, 111 in 1998 and 134 in 1999. To ensure the independence of data points, we discarded the 27 feathers from flickers that returned the second year from analyses of colour frequencies in the population. The proportion of feathers in the six colour categories did not differ between years ($\chi^2_{[5]} = 2.56$, $n = 218$, $P = 0.76$). The modal colour in the population was 4.0

Fig. 1. Scatterplots of vane colour of 218 flicker feathers. Rankings on the red and blue axes were determined using a digital camera. The different symbols represent the colour categories as ranked by the human eye.



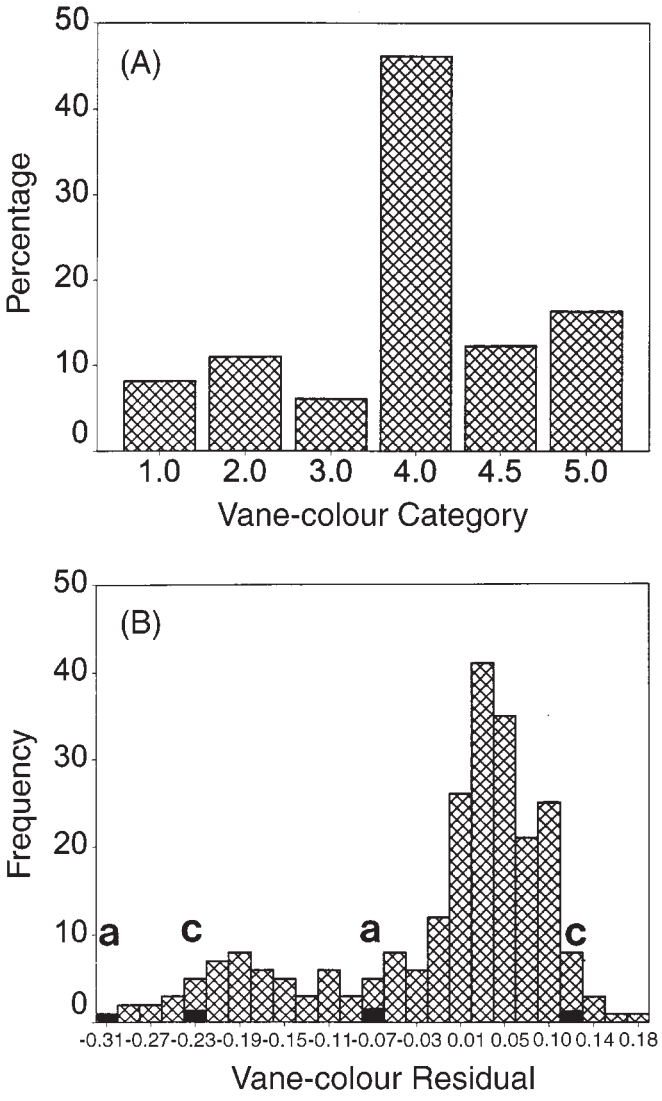
on the scale, a dark orangish red (approximately "Chrome Orange"; Smithe 1975), accounting for 46% of individuals (Fig. 2A). At either extreme, 8% of individuals ranked as 1.0 (pure *auratus*-like yellow) and 15% as 5.0 (intense *cafer*-like red). The colour rankings of the shaft and vane of a feather were strongly correlated (r_S = 0.88, n = 218, P < 0.001), but in 30% of cases were qualitatively different within a feather. The same pattern appeared with the shaft and vane colour residuals. Where the two rankings differed, in all cases except one the shaft was more reddish than the vane. The shaft and vane colours were most similar for feathers at the red end of the spectrum, while feathers with yellow vanes often had darker orange shafts.

The camera-derived residuals corresponded to the six ranked colour categories perceived by us, although, as would be expected, residuals in the intermediate category of 4.5 overlapped with categories 4.0 and 5.0 (Fig. 3). To us, more subtle variation was apparent within each category, so we tested the ability of 18 students to discriminate the mean ± SD in the yellow, orange, and red sets of feathers. A high proportion of students correctly ranked the two extreme feathers (2 SD apart) in each colour category (100, 100, and 94% correct, respectively). The correct ranking for all three feathers (at intervals of 1 SD) was still high for yellow and orange (both 94%) but less accurate for red (55% correct). However, the SD was smaller for the red category than for the other categories ($\bar{x}$ – SD = 0.08 for yellow and orange and 0.03 for red; Fig. 4). Overall, the human eye was able to corroborate the finer variation of colour residuals within each category to a resolution of at least 0.08.

To see whether the various hybrid traits were inherited independently, we also examined correlations between feather colour and other phenotypic traits. The bill, wing, tail, and tarsus are longer in red-shafted than in yellow-shafted flickers (Moore 1995; Wiebe 2000), but we found no correlation between colour residuals and body size (PC1) (males: r_S = 0.03, n = 107, P = 0.75; females: r_S = –0.03, n = 111, P = 0.79). There was no association between tail colour and the four categories of nape-patch size (Kruskal–Wallis test, $\chi^2_{[4]}$ = 1.2, P = 0.87). For males with four categories of mustache colour, there was no relationship with the flight-feather colour (Kruskal–Wallis test, $\chi^2_{[3]}$ = 4.0, P = 0.26). Although hybrids showed a wide mix of phenotypes, there were individuals appearing as "pure" parental types when colours of the tail and mustache and nape patch were considered together (see Fig. 2B).

The distribution of the colour residuals showed a large peak on the *cafer* side of the spectrum similar to the distribution of the six colour categories (Fig. 2). Both the camera and the human eye detected a range of intermediate orange phenotypes, but the distribution was more distinctly bimodal using the finer discrimination provided by the camera. This bimodal pattern was consistent in both years, and for both sexes plotted separately. Intermediate orange could not be explained by fading red or yellow feathers. After they were exposed to sunlight, the colour of both red and yellow feathers appeared washed out, but none had an orange hue. When matched to a Munsell (1976) colour chart, faded feathers seemed to be both lighter in colour (less value) and grayer (less saturated or intense), but the hue did not change. The camera detected less red colour and more blue in faded than in fresh feathers (Fig. 4). Fading had the effect of shifting colour values along the regression line characteristic of a given hue (compare Figs. 1 and 4); consequently, the colour residuals did not change after fading (paired t test, t = –0.75, n = 11, P = 0.46). The shifts with fading did not occur

Fig. 2. Colour distribution in a population of hybrid flickers as determined by two methods. (A) Individuals are grouped into six vane-colour categories determined by comparing feathers with paint chips. High numbers on the *x* axis indicate increasingly red feathers. (B) Colour residuals from digital camera data. The total sample consisted of 218 feathers from different flickers collected in British Columbia over 2 years. Black bars indicate the colour range for males with "pure" parental characters for mustache and nape (a, *auratus*; c, *cafer*).



perpendicular to the regression as one would expect if the hue changed from red to orange.

One explanation for the relative paucity of intermediate orange phenotypes between the two modes in Fig. 2 is that hybrid individuals suffered higher mortality or dispersed more. Therefore, we compared the colour of individuals that returned in the subsequent year to breed with the colour of those that did not. Of 110 adults in 1998, 34 (31%) returned, but their colour did not differ from birds that did not return (Mann–Whitney test, $U = 1300$, $n = 111$, $P = 0.85$). We also divided the vane-colour scores into three categories: yellow as in *auratus* (category 1), orange (categories 2–4), and red (category 5) to see whether obvious hybrids may have had greater mortality than parental types. In the three categories

Fig. 3. Means and 95% confidence intervals for vane-colour residuals calculated on the basis of camera data compared with colours ranked according to eye.

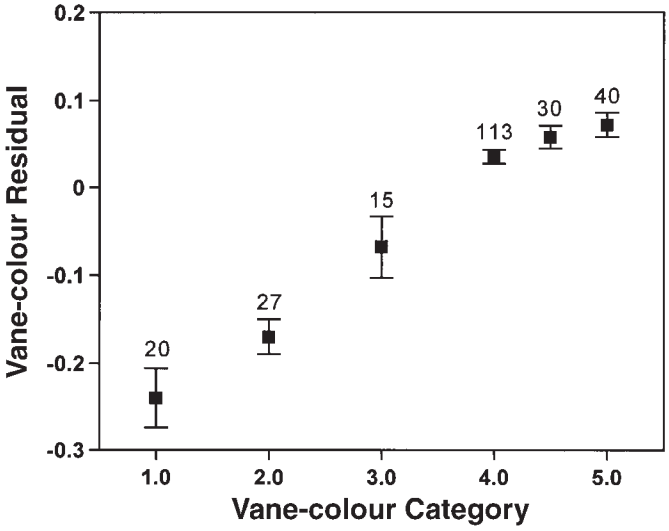
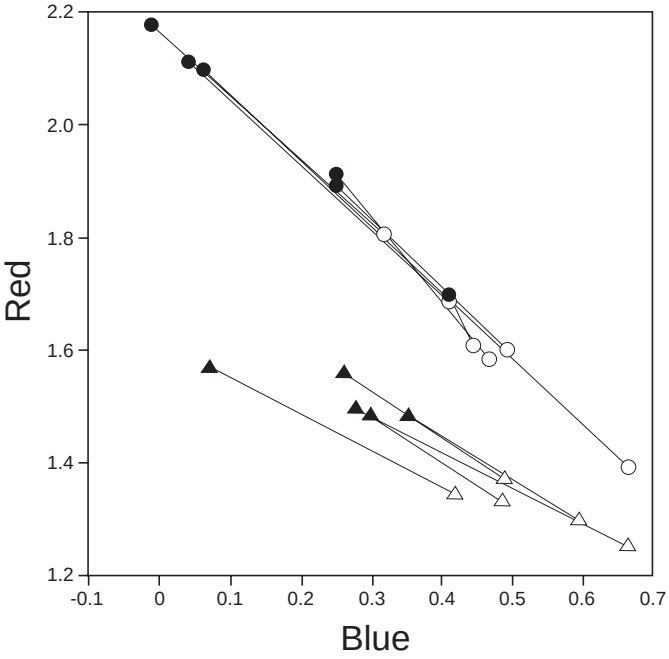
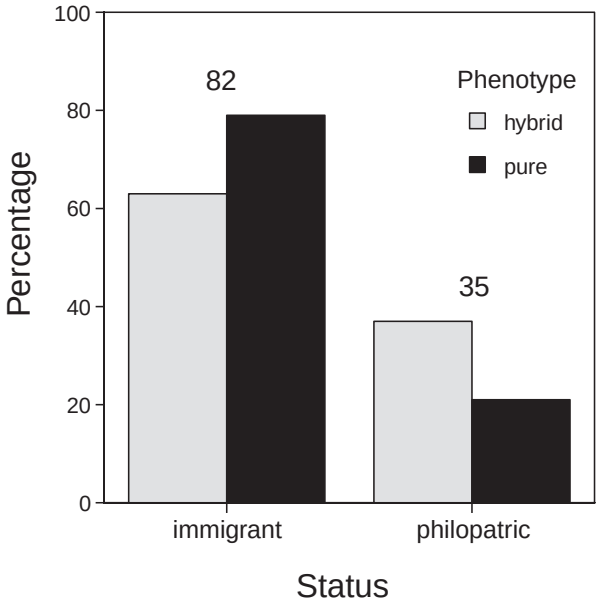


Fig. 4. A comparison of flicker tail feather colours before and after exposure to sunlight for 1 month. The sample consisted of six red feathers (circles) and five yellow feathers (triangles), and straight lines on the graph link the values before (solid symbols) and after (open symbols) exposure for each feather. The red and blue axes were determined using a digital camera.



40, 26, and 31% of birds, respectively, returned but the numbers did not vary among categories ($\chi^2_{[2]} = 0.76$, $P = 0.68$). If the mode of yellow individuals were new immigrants into the population, one would expect more yellow among new, unbanded birds on the study area in 1999 than among returning birds from the previous year. Only 5 of 313 chicks (1.6%) banded in 1998 returned to the study area in 1999 to

Fig. 5. Percentages of parental-type colour (vane categories of extreme yellow or red) versus hybrid (intermediate) colour in immigrant flickers and returning adults philopatric to the study area at Riske Creek, British Columbia.



breed as yearlings, therefore most yearlings in our population were new immigrants. There was a trend towards the colour of yearlings (pooled sample over both years) being more of a pure parental type (extreme yellow or red; colour categories 1 or 5) than that of returning breeders, which were more intermediate in colour ($\chi^2_{[1]} = 3.01$, $P = 0.08$; Fig. 5).

Discussion

Camera-derived colour

Although the colour variable generated from the camera data matched well with the colour categories distinguished by eye (Fig. 3), the relationship between the camera data and the colour perceived by us was not as simple. Villafuerte and Negro (1998) found that Munsell (1976) colour chips with different hues of red gave distinctly different brightness readings on the camera's red axis. In contrast, we found that red and yellow flicker feathers that appeared very different to the human eye overlapped on the camera's red axis, although, on average, red feathers did have higher scores than yellow feathers (Fig. 1). The feather colours only became distinct when the blue axis was added. The carotenoid-based colour of flicker flight feathers is only visible on the underside of the vane, as the dorsal side of the feather is all black. Therefore, different amounts of black show through the feather depending on the angle of the vane relative to the eye (personal observation). Variation in the amount of black may account for some of the variation along the blue axis recorded by the camera. The sun-faded feathers, which appeared lighter and greyer but no different in hue, were shifted downwards, parallel to the regression line in the scatterplot (Fig. 4). This suggests that some of the natural scatter of points that formed diagonal bands for a certain colour (hue) was also due to differences in the value and intensity (brightness) of feathers. Our belief that colour residuals indicated different hues of colour was corroborated by the large proportion of undergraduate students who could rank the "redness" of feathers in the same manner that the camera did.

The hybrid spectrum

The colour residuals confirmed our impression from scoring the colour of flickers in the field; there was a continuous gradation of colour from the extreme yellow (*auratus*) type to the red (*cafer*) type (Fig. 2). Orange phenotypes could not be explained by secondary exposure of either red or yellow feathers to the environment. Pedigree data suggest that feather colour in flickers is a polygenic trait (unpublished data cited in Moore 1995), in contrast to the two-allele system proposed by Deakin (1936). The exact nature of the genes controlling colour is unknown, but our data also seem to rule out a simple two-allele system. The fact that 42% of birds at Riske Creek showed hybridization with respect to another plumage trait, the nape patch, means that, on average, at least 42% of individuals should have had *auratus* alleles and should have been pure yellow if that allele were dominant as in Deakin's (1936) model. A lack of correlations between colour of the flight feathers and other hybrid traits confirms that they are not genetically linked (Moore 1995), and that alleles have mixed independently during introgression.

Frequencies of colour in the hybrid zone

Further study is needed to determine the precise relationship between genotype and colour in flickers; however, for a polygenic trait such as colour, mean phenotypes in the population shift from one parental type to the other across the hybrid zone, usually following a sigmoid cline (Barton and Gale 1993). In flickers, orangish-red individuals should predominate in hybrid populations on the west side of the hybrid zone and orange-yellow birds on the eastern side. A classic sigmoid cline for feather colour was described by Short (1965), who sampled a series of flicker populations across an area about 200 km wide in the hybrid zone in Colorado and Nebraska. Comparing our colour scores with the results of other studies is difficult because most have not reported variation in colour directly, but rather have given a single hybrid index score based on several phenotypic traits. An exception is Bock (1971), who, using a spotting scope, reported 24% red, 35% orange, and 41% yellow flickers in a population in eastern Colorado, a location nearer to the centre of the hybrid zone than our site at Riske Creek. If orange phenotypes are relatively abundant at the centre of the hybrid zone, a large mode in the orange–red part of the spectrum (Fig. 2) seems to be consistent with polygenic inheritance and the close proximity of Riske Creek to the western red-shafted flicker parental type. However, the second mode of yellowish *auratus*-type birds in our population cannot be explained by a sigmoid cline and simple diffusion of alleles across a hybrid zone.

There are three explanations for a bimodal phenotypic distribution in a hybrid zone (Barton and Gale 1993). Relative scarcity of intermediates could result from selection against orange flickers; however, return rates to our area were not associated with colour. Another explanation is that intermediate phenotypes are rarely hatched because parental types mate assortatively. Studies of flickers in more south-

erly locations have shown no preferential mating according to colour (Bock 1971; Rising 1983; Moore 1987), but significant assortative mating did occur at Riske Creek (Wiebe 2000). For southern populations of flickers, it is believed that natural selection for assortative mating is weak because mixed pairs were found to have the same numbers of eggs and young nestlings as matched parental types (Moore and Koenig 1986). However, the conclusion that reproduction rates are equal across phenotypes may be premature because survival and recruitment rates of of fledglings are unknown. Much of the assortative mating at Riske Creek seemed to be a result of different phenologies, and possibly different patterns of migration, of yellow versus red birds (Wiebe 2000). Similarly, red-breasted sapsuckers (*Sphyrapicus ruber*) and red-naped sapsuckers (*S. nuchalis*), which also hybridize in central British Columbia and at Riske Creek, exhibit temporal separation in breeding that minimizes contact (Johnson and Johnson 1985). The fitness of hybrid flickers and mixed pairs needs further study, but regardless of the cause, assortative mating would tend to maintain two distinct phenotypes in the population at Riske Creek.

A third explanation for our observed distribution of phenotypes is the influx of parental-type immigrants into the population (Barton and Gale 1993). The ability of flickers to disperse long distances is supported by the lack of genetic differentiation within northern flickers continentwide (Grudzein et al. 1986) and band recoveries of yearlings 100 km and more from their natal site (Moore and Buchanan 1985). Dispersing *auratus* types would appear quite distinct in this western population, where *cafer* alleles seem to predominate. Immigrants tended to be more like either parental type than like hybrids (Fig. 5). A flow of immigrant *auratus* alleles into the hybrid population and a tendency to mate assortatively might delay the incorporation of yellow plumage traits into the hybrid population at Riske Creek.

Implications for theories about the hybrid zone

In this paper we did not test theories of hybridization directly, but colour morphs of flickers in central British Columbia do not seem follow the straightforward patterns and explanations offered for the hybrid zone farther south on the Great Plains of the United States (Moore and Price 1993). According to Short (1965), there should have been ample time during the approximately 8000 years since glaciers receded in British Columbia for the two types of flickers to interbreed. Given the expansive forests in British Columbia, which further enhance dispersal ability, we should have seen by now the complete mixing of genomes and the breakdown of distinct parental types if mating was random. Presuming a reasonably high rate of gene flow, the most plausible hypothesis for the long-term persistence of the flicker hybrid zone in the south is that it is due to "bounded hybrid superiority" (Moore and Price 1993); a given flicker phenotype is the best adapted to certain local environmental conditions, which vary across the hybrid zone, and hybrids have the highest fitness in intermediate habitats. Exogenous selection maintains each phenotype in its geographic range so that red and yellow-shafted individuals cannot invade each other's areas of distribution (Moore and Price 1993).

If exogenous selection is the underlying force maintaining the flicker hybrid zone, how can red- and yellow-shafted flickers in British Columbia breed side by side in territories separated by 100 m or less? First, environmental gradients may be less distinct and on a much smaller spatial scale in the mountainous topography of British Columbia, where climate and vegetation are greatly influenced by altitude. Second, population densities of flickers as estimated by breeding bird surveys are greater in the north than in the southern plains hybrid zone (see Figs. 8–2 in Moore and Price 1993). Finally, flickers do not overwinter at Riske Creek, in contrast to populations farther south. It may be that migrating individuals are less philopatric to breeding territories, and with the high population density, dispersal occurs on a larger scale in the north than in the south. An environment that is patchy on a smaller scale than dispersal distance would mean that neither parental phenotype (or hybrid type) would become established as a pure population in a local area. The introgression of alleles and phenotypic gradients would not be smooth.

In the north, contact and interbreeding of the two flicker subspecies may depend on migration routes and timing of migration. If the two routes differ, patterns of territory settlement in central British Columbia may represent a rather chaotic fallout from a clash of two migration waves. There is some indication that the northern flicker hybrid zone is not stable and movement over the Rocky Mountains is increasing. Based on museum specimens, McGillivray and Biermann (1987) showed that the hybrid zone in north-central Alberta, at the same latitude but east of Riske Creek, had expanded since 1960 (*cafer*-like birds were invading the *auratus* range). They hypothesized that large-scale clearing of forests in the foothills and Rocky Mountains had facilitated contact between the subspecies. If so, the genotype and phenotype frequencies of flickers in central British Columbia are not from a closed population, and are not at equilibrium.

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