Evolutionary Ecology Research, 2007, **9**: 887–903

The role of weather and migration in assortative pairing within the northern flicker (*Colaptes auratus*) hybrid zone

D.T. Tyler Flockhart and Karen L. Wiebe*

Department of Biology, University of Saskatchewan, 112 Science Place,
Saskatoon, Saskatchewan S7N 5E2, Canada

ABSTRACT

Hypothesis: In the absence of active mate choice, differences in migration patterns lead to assortative pairing between two subspecies of flickers. Large-scale variation in weather may affect migration patterns, which, in turn, may affect the availability of phenotypes during pairing.

Organism: Hybridizing subspecies of the northern flicker (*Colaptes auratus*): yellow-shafted (*C. a. auratus*) and red-shafted flickers (*C. a. cafer*).

Time and place: Between 1998 and 2006 in the hybrid zone at Riske Creek, British Columbia, Canada.

Methods: We captured breeding pairs of flickers, scored their phenotypes to calculate several hybrid indices, and correlated these indices between members of a pair. We used the North American band recovery database to plot migratory routes, and we used systematic surveys to document the arrival of phenotypes to the study area after spring migration. We correlated the annual strength of assortative pairing with regional and large-scale (North Atlantic Oscillation Index) weather patterns.

Results: There was assortative pairing based on individual plumage traits and an overall hybrid index. The subspecies of flickers wintered on opposite sides of the Rocky Mountain Range; hybrids from Riske Creek wintered west of the Rocky Mountains. There were no differences in spring arrival time or nest initiation date between phenotypes. The North Atlantic Oscillation correlated with the annual average phenotype on the study site and correlated weakly with the annual prevalence of assortative mating.

Conclusion: Large-scale weather patterns were associated with the annual prevalence of phenotypes and assortative mating in the northern portion of the hybrid zone, probably as a result of different migration patterns

Keywords: assortative mating, bounded hybrid superiority hypothesis, *Colaptes auratus*, hybridization, migration, North Atlantic Oscillation, northern flicker.

---

* Author to whom all correspondence should be addressed. e-mail: karen.wiebe@usask.ca
Consult the copyright statement on the inside front cover for non-commercial copying policies.

INTRODUCTION

Assortative mating is the pairing of individuals with similar phenotypic traits in a non-random pattern (Burley, 1983). It is of interest to evolutionary biologists because it is one way to enhance pre-mating reproductive isolation between phenotypes in hybrid zones (Dobzhansky, 1937; Mayr, 1942; Coyne and Orr, 2004). Assortative pairing may arise through active mate choice where individuals seek mates that are similar to themselves (like preference), or where a preferred phenotype out-competes others for a mate of the same preferred type (type preference) (Burley, 1983). Alternatively, assortative pairing may arise by passive choice if types are spatially segregated by habitat preference (Craig *et al.*, 1993; Ferrer and Penteriani, 2003) or if phenotype availability is temporally staggered. In plant populations, phenotypes may be temporally staggered as the result of different flowering times (Fox, 2003). In animals, environmental or genetic influences on maturation may similarly lead to temporal isolation between sympatric groups (Hendry and Day, 2005). We are particularly interested in temporal divisions between animal populations that occur when different migration patterns cause different phenotypes to pair at different times (Bearhop *et al.*, 2005).

When two populations have different migration strategies to a single sympatric breeding range, it is known as a 'migratory divide' (Bensch *et al.*, 1999; Bearhop *et al.*, 2005). Differences in arrival times may impose passive constraints on mate choice due to phenotype availability when migratory divides occur within hybrid zones. Different populations may arrive on the breeding grounds at different times because they winter at different locations, because they migrate along different routes or because they migrate at different speeds. For example, blackcaps (*Sylvia atricapilla*) breed in central Europe and winter in two allopatric locations: the British Isles or Iberia (Berthold *et al.*, 1992). Birds that winter in northern areas (Britain and Ireland) react differently to changing photoperiods in spring and arrive at breeding grounds earlier relative to southern populations (Berthold *et al.*, 1992; Bearhop *et al.*, 2005). This leads to assortative pairing between the genetically distinct populations and results in increased reproductive success to early migrants (Bearhop *et al.*, 2005). However, few studies have looked at how migration timing and arrival schedules to sympatric breeding areas can influence assortative mating and hence reproductive isolation in ancient hybrid zones.

Eastern yellow-shafted flickers (*Colaptes auratus auratus*) and western red-shafted flickers (*C. a. cafer*) have hybridized in a zone that extends from Texas to Alaska at least since the 1800s (Allen, 1892). If hybrids are less fit than pure parental types, natural selection should favour active 'like preference' (Barton and Hewitt, 1985; Liou and Price, 1994). However, hybrid flickers do not seem to have lower fitness than parental types (Moore and Koenig, 1986) and no assortative pairing among the subspecies was found in the southern portions of the hybrid zone (Short, 1965; Bock, 1971; Moore, 1987). In fact, if the bounded hybrid superiority hypothesis for the flicker hybrid zone is true – that is, hybrids have the greatest fitness in the ecotone between parental geographic ranges (Moore, 1977) – there may be selection for random pairing or a preference for hybrid mates in the hybrid zone to increase the likelihood of having superior hybrid offspring.

In contrast to the results from the southern hybrid zone, Wiebe (2000) found assortative pairing in the northern part of the zone where flickers are migratory, and Wiebe and Bortolotti (2001) suggested that different arrival and pairing chronologies between yellow-shafted and red-shafted flickers may be partially responsible. Unfortunately, migration patterns of northern flickers are not well known owing to a paucity of band recoveries and insufficient resolution of stable isotopes (see Hobson, 2005). Nevertheless, local and large-scale climatic systems such as the El Niño/Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) are known to influence migration speed, migration routes or arrival patterns in other birds (Ahola *et al.*, 2004).

We predicted that if the subspecies of flickers winter in different locations or have different migration routes, the phenotypes would show staggered arrival to the breeding grounds. Furthermore, if large-scale weather patterns affect the migration timing of the subspecies differently, this would lead to annual differences in the degree of staggered arrival between phenotypes, which, in turn, would affect the proportion of phenotypes on the breeding grounds during pairing and hence the prevalence of assortative mating. Our objectives were to: (1) test for patterns of assortative mating using a 9-year data set; (2) review information on migration routes based on band recoveries; (3) determine whether the arrival times and breeding phenology of the phenotypes differed in the hybrid zone; and (4) examine the influence of weather on pairing.

MATERIALS AND METHODS

Capturing adults and calculating a hybrid index

The study area near Riske Creek, central British Columbia (51°52′N, 122°21′W) encompasses approximately 100 km^2 of grasslands with scattered trembling aspen (*Populus tremuloides*) and patches of mixed forests of Douglas fir (*Pseudotsuga menziesii*), hybrid spruce (*Picea engelmannii* × *P. glauca*), and lodgepole pine (*Pinus contorta*) (Martin and Eadie, 1999). Here phenotypes range from yellowish to pure red-shafted flickers with most, but not all, individuals displaying hybrid characteristics (Wiebe, 2000; Wiebe and Bortolotti, 2001, 2002). Flickers begin to arrive on site after migration in the latter half of April with territory establishment and nest excavation occurring soon thereafter.

Between 1998 and 2006, approximately 80–140 nests were monitored annually. Nests were discovered by broadcasting flicker territorial calls in early spring to locate active territories and by checking all old sites from previous years. There are no known differences in the territorial ‘long call’ between subspecies (Moore, 1995), so our ability to detect the subspecies should not have been biased. Once a territorial pair responded, cavities in the surrounding trees were checked every few days to determine the onset of egg-laying. During this time we noted if the male and female were already colour-banded or new to the study. Once an active nest was found, it was monitored by cutting a small, replaceable door into the tree trunk to allow access to the eggs and nestlings (Wiebe, 2002). Subsequently, nests were visited approximately every 4 days with a ladder, flashlight, and mirror to determine clutch size, nest fate, and hatching date (Fisher and Wiebe, 2006a).

Adults were captured by flushing birds into a net placed over the entry hole either as they incubated eggs or brooded chicks, or flew into the cavity to provision young. After capture, adults were banded, weighed, measured, and scored on various plumage attributes (see below). Adults were banded with a Canadian Wildlife Service aluminium band and a unique series of colour bands to allow individual recognition in the field. Previously banded birds were not targeted for recapture in subsequent years, although they were sometimes re-trapped inadvertently when the identity of the individual in the cavity was unknown. Flickers were sexed by plumage because females lack the malar (moustache) stripe and aged up to 4 years based on moult patterns (Pyle, 1997). Both adults were banded at >95% of nests each summer.

Studies of hybridization assume genotypic differences between the two populations but usually analyse phenotypic differences because the ease and cost-effectiveness allow large sample sizes. Recent studies still largely rely on phenotypic hybrid indices, assuming that such indices meaningfully reflect genotypes at least in ordinal rankings (Good *et al.*, 2000; Bronson *et al.*, 2003; Shriver *et al.*, 2005). A recent study confirmed that genetic differences in hybrid sharp-tailed sparrows (*Ammodramus nelsoni subvirgatus* and *A. caudacutus caudacutus*) were correlated with a plumage variation index (Shriver *et al.*, 2005), suggesting that phenotypic hybrid indices are meaningful to test hypotheses of hybridization.

We calculated several types of hybrid index to ensure consistent correlation direction and to ensure our conclusions were robust over a range of methods. Two hybrid indices were based on categorical plumage rank scores. Following Short (1965), we scored throat, ear, nuchal, shaft (mean of tail rachis and vane), and moustache (males only) on a 5-point scale where 0 = pure *auratus* and 4 = pure *cafer*. However, Short's (1965) arbitrary category divisions lumped a large range of hybrids into a single intermediate category between 21 and 79%. We therefore categorized traits (throat, ear, and moustache) using divisions of 0%, 1–33%, 34–66%, 67–99%, and 100%, which provided better resolution to divide individuals among categories. Our general conclusions did not differ between scoring methods.

Since traits vary on a continuum between pure forms, it would be ideal to score each on a continuous scale but only tail feathers provided a large enough area of consistent colour that could easily be collected in the field and later quantified objectively in the laboratory (Hill, 1998). We scanned feathers using a spectrophotometer (Konica Minolta Sensing, Inc., model CM-2600d), which provided reflectance spectra values between 360 and 740 nm at 10-nm intervals. Raw spectral reflectance values between 570 and 700 nm (the portion of the spectral range encompassing yellow, orange, and red) were entered into a principal component analysis (PCA) and extracted using two axes that explain a large proportion of the variation within the sample (Cuthill *et al.*, 1999). The score on the first axis (PC1) differentiated brightness values that are usually independent of colour (Cuthill *et al.*, 1999). The score on the second axis (PC2) differentiated between red, orange, and yellow feathers on a continuum and was consistent with our categorical scores used in the field. Red feathers had a negative PC2 score, while yellow feathers had a positive PC2 score. We rescaled the PC2 scores from 0 (most yellow) to 1 (most red) and incorporated them into some hybrid indices (see below).

We standardized the sum of the categorical plumage traits on a scale of 0 (pure *auratus*) to 1 (pure *cafer*) and then calculated three hybrid indices (HI): HI1 using only the scored plumage traits; HI2 using scored plumage traits but substituting the continuous tail colour for the categorical tail colour score; and HI3, which was exclusively the continuous rectrix score from the spectrophotometer. Sample sizes for HI2 and HI3 were smaller than HI1 because tail feathers were not collected from all flickers in intermediate years of the 9-year study.

Our plumage scoring was repeatable: of seven birds trapped and scored twice in the same season, no plumage trait was ranked differently except for a single case of tail colour shifting by one category (paired *t*-test: $t_7 = -0.24$, $P = 0.81$). Individuals trapped and scored in different years also maintained the same phenotype (paired *t*-test: $t_{182} = -0.06$, $P = 0.96$). Therefore, in cases when a previously banded bird was not recaptured in a given year, we used its HI from its last capture.

Measuring assortative mating

Flicker pairs sometimes remained together over multiple seasons but we only included the first year to avoid pseudoreplication in the correlations. When an individual obtained a new mate, we did include it. We also excluded pairs that formed after their first nest was depredated, since the pool of available mates may be very restricted late in the season and probably would not reflect arrival of phenotypes in spring.

The hybrid index in flickers is based on plumage traits that seem to assort independently (Erskine, 1962; Moore, 1987) and so individuals may show different combinations of 'yellow-shafted' and 'red-shafted' plumage traits. Since it is unknown whether mate choice could be strongly based on one particular trait as opposed to an overall degree of 'hybridness' reflected in a composite index, we calculated correlations between the sexes for all possible combinations of plumage attributes and for the three different hybrid indices. We used non-parametric Spearman correlations for the ranked scores of the plumage traits and hybrid indices, except for HI3, which was a continuous measure and could be analysed with Pearson correlations. We corrected for multiple comparisons among plumage trait comparisons using the binomial likelihood ratio test (e.g. Kinnison *et al.*, 2002). Correlations were done for all years pooled and also for individual years to determine annual variability in the prevalence of assortative mating in relation to weather (see below).

Linking wintering and breeding locations of northern flickers

We obtained band-recovery records from the Canadian Wildlife Service and sightings from individuals originally marked at Riske Creek between 1998 and 2006. We plotted movements of flickers throughout Canada and the United States west of longitude 90°W (Mississippi River) on a continental scale using records of individuals that were both on a breeding area (20 April to 15 July) and a wintering area (15 November to 15 February). Distances of less than 200 km, which may represent local dispersal rather than migration, were excluded. For hybrids at Riske Creek, we used a more generous cut-off period from 1 October to 28 February to increase sample size. Distance from the study area was not dependent on date of recovery in this sample ($F_{1,13} = 0.06$, $P = 0.80$), suggesting that these individuals were at or near their wintering grounds when the bands were reported.

Arrival of phenotypes

We monitored arrival dates of yellow and red flickers to Riske Creek in 2006 using taped playbacks of flicker territorial calls. It took 3–4 days to complete one sweep of the entire study area and we made several 'rounds' between 17 and 30 April as detections of new individuals dropped considerably after that time. Flickers here nest in discrete clumps of trees separated by open grassland. Repeated censusing of previously banded adults in spring showed that they did not change their defended tree clump once they occupied it. However, most of the birds arriving to breed were unbanded due to low annual survival (Fisher and Wiebe, 2006b). Therefore, to avoid double-counting the arrival times of unbanded individuals, we only recorded the first sighting of a territorial individual in a certain tree clump and assumed it was the same individual thereafter if its phenotype was the same, classifying its colour as red, orange or yellow. We used observations per hour because sampling effort varied on different days, and conducted a two-sample Kolmogorov-Smirnov test (Siegel and Castellan, 1988) to establish whether the distribution of red and yellow phenotypes differed over time.

We did not observe arrival dates directly in other years but if arrival correlates with nest initiation date, indirect information on arrival times may be obtained by examining the nest initiation dates between phenotypes. We tested this assumption by correlating the known arrival times of banded birds in 2006 with the day they initiated laying. There was a significant correlation for both males ($r = 0.45$, $P = 0.011$, $n = 31$) and females ($r = 0.50$, $P = 0.028$, $n = 19$) and the interval between arrival and laying date was not associated with the HI1 for either males ($F = 0.15$, $P = 0.70$) or females ($F = 0.20$, $P = 0.66$). Therefore, we also analysed annual variation in laying dates between the phenotypes with analysis of variance (ANOVA) as a measure reflecting differences in arrival.

Influence of weather patterns

To understand how spring weather can affect annual pairing patterns and breeding phenology, we correlated regional and continental (ENSO and NAO) weather variables with nest initiation date, correlation coefficients of assortative mating (using HI1), the proportion of yellow individuals, and the average phenotype (mean HI1) in the population. For 'regional' weather effects, we calculated mean March and April temperatures from the Seattle-Tacoma Airport, Washington, a location that seems to be along the migration route of many individuals in our population (see Fig. 1).

For the continental-scale climate variables we used ENSO and NAO indices, which are linked to large-scale patterns of temperature and precipitation that can vary annually (Hurrell, 1995) and can influence migration and arrival time of birds to their breeding grounds in the northern hemisphere (Hüppop and Hüppop, 2003; Vähätalo *et al.*, 2004). Positive phases of ENSO generally lead to La Niña conditions that produce colder and wetter conditions across western North America, whereas positive phases of NAO lead to warmer winter temperatures in eastern North America. During negative phases, these temperature anomalies are reversed between locations (Wallace and Gutzler, 1981). The indices we used were the Pacific-North American (PNA) pattern influenced by ENSO and the NAO proper (Horel and Wallace, 1981; Wallace and Gutzler, 1981). We examined both the PNA and NAO indices because their centres of action occur over the continental regions where pure parental forms of flickers overwinter. Variation in the PNA or NAO may thus affect migration and arrival patterns of one phenotype more than the other. The exact timing of migration in our population is unknown, but if flickers arrive in April, it is reasonable to expect that conditions about 2 months earlier (February) may be those that influence migration timing. Monthly indices for NAO and PNA are standardized for 3-month periods (i.e. February patterns are calculated based on January through March mean monthly standardized anomaly fields; http://www.cpc.ncep.noaa.gov/).

RESULTS

Assortative mating patterns

The direction of most correlations between the individual plumage traits for 613 nesting pairs was positive but only three positive and one negative correlation were statistically significant (Table 1). By the binomial likelihood method at $\alpha = 0.05$, the probability of three

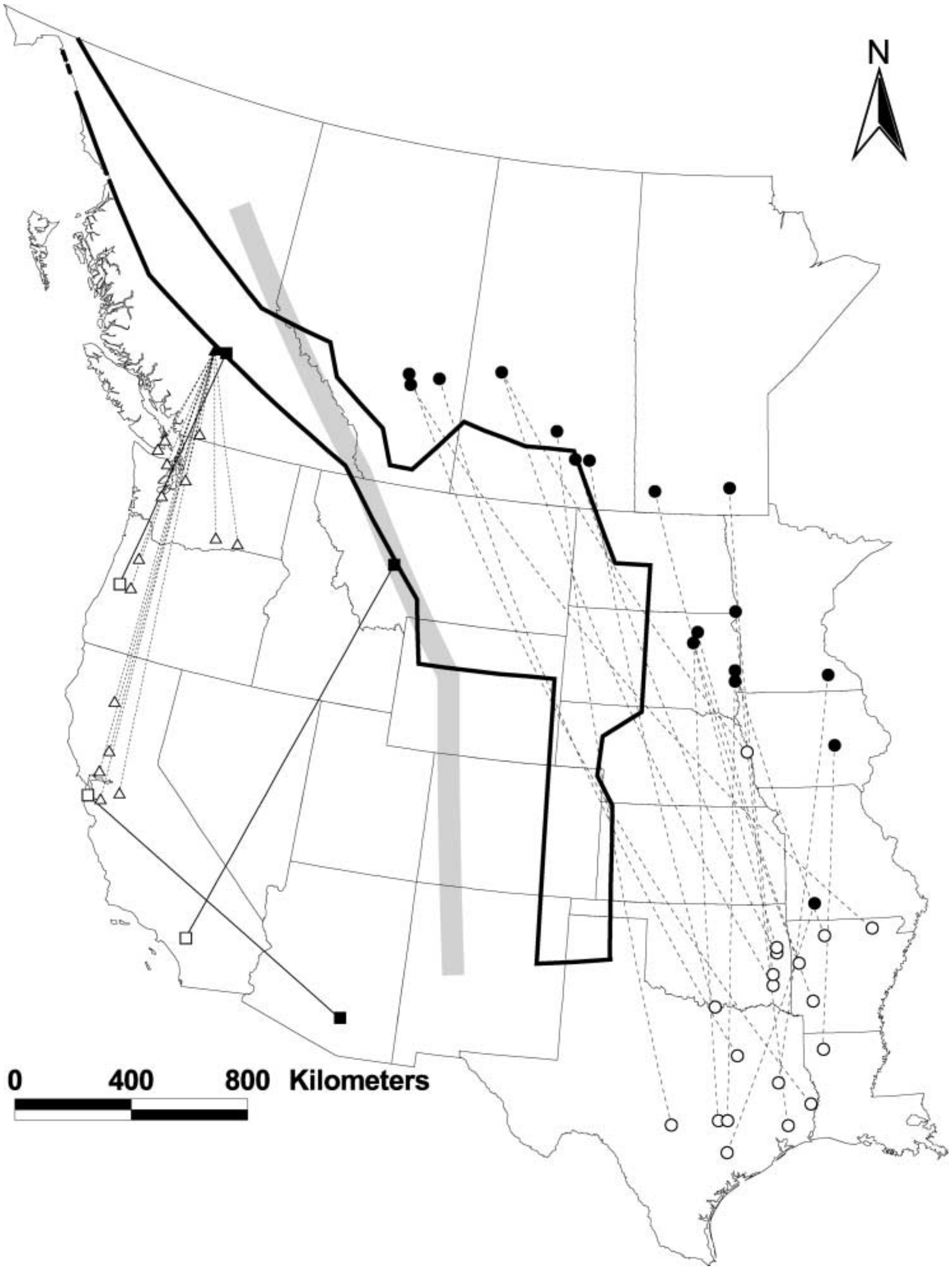

Fig. 1. Breeding (solid symbols) and wintering (open symbols) locations for migratory yellow-shafted (circles), hybrid (triangles), and red-shafted flickers (squares) in western North America. The hybrid zone, outlined in black, is the estimated 20% and 80% transition contours (Moore, 1995) for eastern yellow-shafted flickers and western red-shafted flickers. The grey line running northwest–southeast is the rocky mountain belt.

Table 1. Spearman rank correlations between plumage traits of males and females within mated pairs of flickers at Riske Creek

		Males				
Females		Throat	Ear	Nuchal	Shaft	Moustache
Throat	r_s	**0.164**	−0.040	**−0.107**	0.033	−0.011
	P	**0.002**	0.629	**0.033**	0.507	0.828
	n	**360**	146	**397**	395	393
Ear	r_s	0.025	0.002	−0.109	−0.026	−0.018
	P	0.751	0.980	0.153	0.734	0.817
	n	161	144	173	173	172
Nuchal	r_s	**0.106**	0.138	0.025	0.016	0.036
	P	**0.036**	0.088	0.535	0.703	0.376
	n	**391**	154	596	596	595
Shaft	r_s	0.069	**0.253**	0.076	0.041	0.058
	P	0.178	**0.002**	0.064	0.317	0.153
	n	388	**150**	604	605	604

Note: Data are for 1998–2006 but sample sizes differ because not all traits were measured in all years. The four significant correlations at $\alpha = 0.05$ are shown in bold.

Table 2. Individuals in mated pairs of flickers at Riske Creek showed positive assortative mating for HI1 but not for the other indices (see text for definitions)

	HI1	HI2	HI3
r_s/r	0.084	0.091	0.038
P	0.038	0.132	0.527
n	613	274	274

Note: HI3 was tested with Pearson correlations, the other two indices with Spearman rank correlations.

or more tests being significant by chance is 6.3%, while the likelihood of four or more tests being significant is 1.4%. Therefore, there is some support for assortative mating according to plumage traits. Positive assortative mating was found for HI1 but was not significant for HI2 or HI3, perhaps because of the smaller sample size for the latter two indices. However, the small r^2 in all cases suggested that assortative mating was not particularly strong (Table 2, Fig. 2). We limit the following results to HI1 because of the larger sample size.

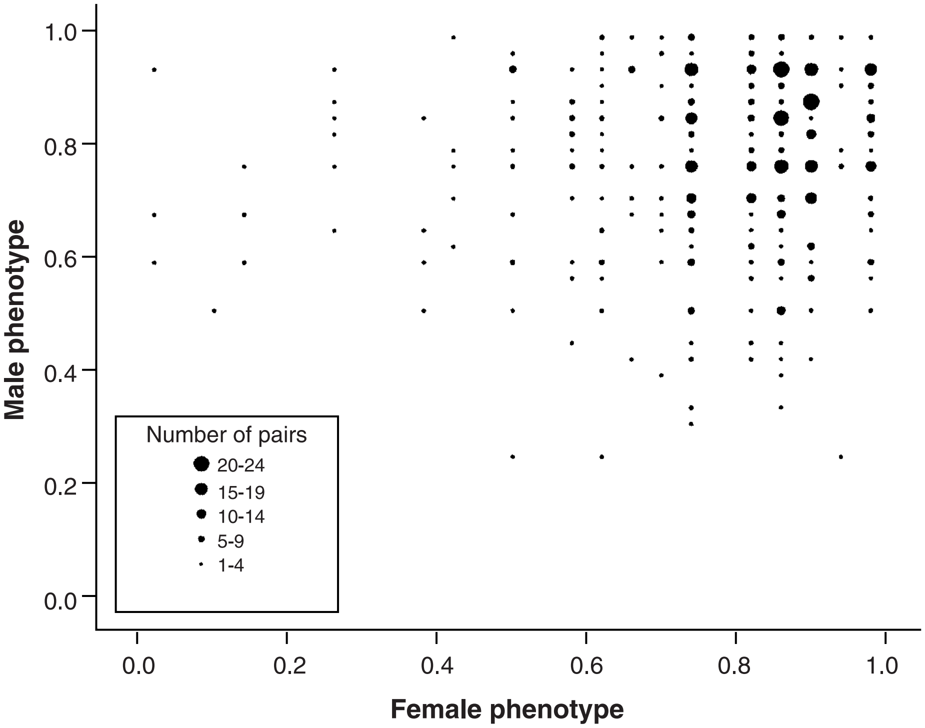

Fig. 2. Males and females of mated pairs at Riske Creek showed positive assortative mating for phenotype (HI1) with 9 years of pooled data. A phenotype of 0 is a pure yellow-shafted flicker, while 1 is a pure red-shafted flicker.

Migration patterns based on band recovery data

Only 34 of over 1000 records provided by the bird banding office and three records from observations of banded flickers away from Riske Creek fit our criteria. Yellow-shafted flickers in the northern and central prairies typically migrated east of the Rocky Mountains to the southern United States west of the Mississippi River. Red-shafted flickers typically migrated west of the Rocky Mountains (Fig. 1), suggesting that pure parental forms have segregated winter ranges. All 15 migratory records of hybrid flickers come from birds banded at Riske Creek (Fig. 1). There was no relationship between hybrid index and migration distance in this sample ($F_{1,11} = 3.54$, $P = 0.087$), but all recovered individuals were ‘red to orange’ with a hybrid index between 0.56 and 0.88.

Arrival of phenotypes

More red-shafted than yellow-shafted individuals were observed on the study area but there was no significant difference in the pattern of arrival between the two colour forms in 2006 ($Z = 0.45$, $P = 0.99$; Fig. 3). Date of first egg was correlated with year (males: $F_{8,722} = 8.56$, $P < 0.001$; females: $F_{8,719} = 9.57$, $P < 0.001$) and parental age (males: $F_{2,722} = 29.45$, $P < 0.001$; females: $F_{2,719} = 25.54$, $P < 0.001$), but not HI1 (males: $F_{2,722} = 0.91$, $P = 0.40$; females: $F_{2,719} = 1.21$, $P = 0.30$), and there were no interactions between the factors.

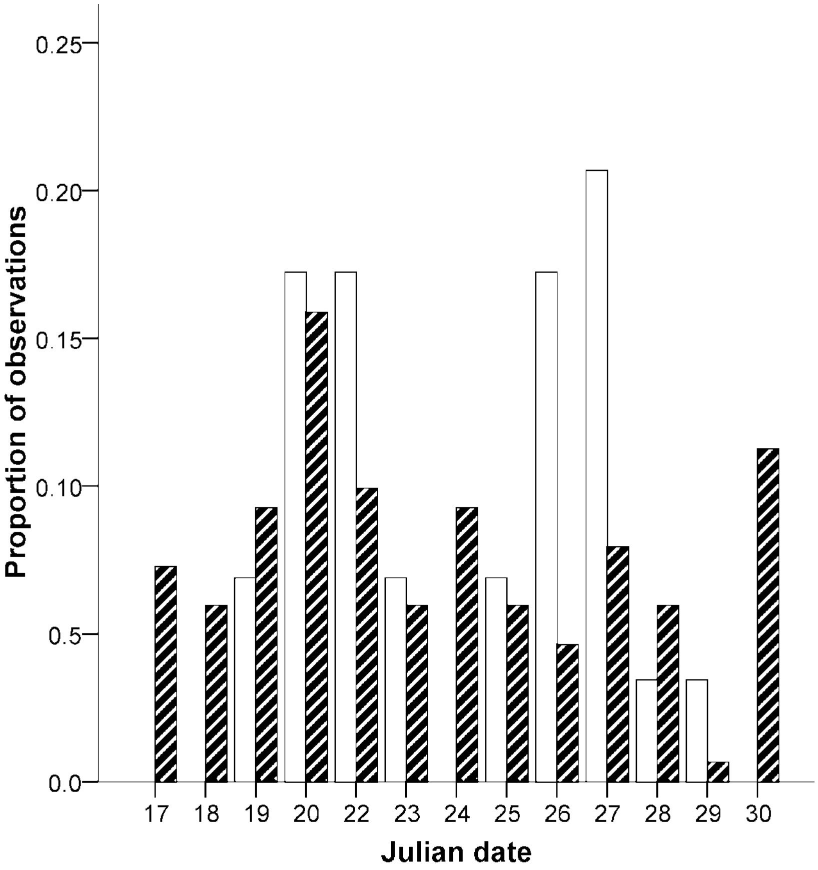

Fig. 3. Proportional observations of newly arrived individuals to Riske Creek in 2006. For clarity, individuals that were hybrid were excluded and only extreme red (hatched bars) and yellow (open bars) phenotypes were plotted. Julian date 17 is 17 April.

Annual variation in patterns of assortative mating and weather

While assortative pairing according to HI1 was significant and positive with years pooled (see above), there were no significant relationships with the 9 years considered individually. Furthermore, the direction of the correlations varied from positive in some years to negative in others. Cold regional April temperatures from Seattle resulted in later mean nest initiation date on our study area, suggesting that weather did influence breeding phenology ($r = -0.79$, $P = 0.011$). The proportion of yellow flickers on our study area was positively correlated with April Seattle temperatures ($r = 0.75$, $P = 0.02$) and this resulted in a weak negative correlation between HI1 and regional temperature ($r = -0.66$, $P = 0.056$) – that is, the mean hybrid index shifted towards *auratus*-type birds in warmer springs on the west coast. However, the annual coefficient of assortative mating did not vary with regional Seattle temperature ($r = 0.12$, $P = 0.75$).

Looking at more continental-scale weather patterns, NAO but not PNA correlated with the mean HI1 of flickers in our population in a given year (NAO: $r = 0.80$, $P = 0.01$; PNA:

$r = -0.26$, $P = 0.49$). In particular, there were more *auratus*-type (yellow) birds in years with low oscillation index values associated with below average winter temperatures in eastern North America (Fig. 4). Although mean HI1 was more 'yellowish' in years when the proportion of yellow birds was larger in our population ($r = -0.80$, $P = 0.01$), it was not clear that the movement of pure yellow individuals from eastern areas of the continent was driving the relationship with the NAO, as the correlation between proportion of yellow birds was not related to the NAO ($r = -0.50$, $P = 0.17$; Fig. 4). Low annual NAO values, as well as being associated with more yellowish individuals on our study area, were weakly related to a higher prevalence of assortative mating ($r = -0.62$, $P = 0.072$; Fig. 4). Again, however, the actual proportion of pure yellow individuals in the population was not related to the prevalence of assortative mating ($r = 0.57$, $P = 0.11$; Fig. 5).

DISCUSSION

Reproductive timing and assortative pairing

In the pooled data set collected over 9 years in the northern part of the flicker hybrid zone, positive assortative mating was weak ($r^2 = 0.08$) but significant, consistent with Wiebe (2000) ($r^2 = 0.12$). Pairing appears random in the southern part of the zone (Short, 1965; Bock, 1971; Moore, 1987) ($r^2 < 0.001$), but small samples in some of those studies may limit the ability to detect trends. Assortative pairing or the lack of it is not a critical prediction of the bounded hybrid superiority hypothesis, but based on this idea hybrids have the greatest fitness in the hybrid zone and so the best strategy could, in fact, be disassortative pairing in the hybrid zone in order to produce hybrid offspring (Moore, 1977).

Differences in reproductive timing among sympatric populations are known to influence reproductive isolation in a range of taxa (Hendry and Day, 2005). For example, different flowering and pollination schedules between plant populations reduce the likelihood of cross-breeding and aid in assortative mating (Fox, 2003). However, among animals that are mobile, differences in migration timing can be a mechanism that influences temporal isolation, the timing of reproduction, and hence further accelerates divergence between groups (Quinn *et al.*, 2000).

Migration and reproductive timing have also been shown to influence reproductive isolation in several bird species. For example, European willow warblers (*Phylloscopus trochilus*) that breed in Scandinavia migrate to either southern or western Africa depending on their breeding latitude (Chamberlain *et al.*, 2000; Bensch *et al.*, 2006). It is assumed that populations pair assortatively because there is a 2-week difference in arrival times between them (Bensch *et al.*, 1999) leading to reduced gene flow and a low production of hybrids, resulting in traits diverging quickly between the populations (Bensch *et al.*, 1999). These populations have quite distinct migration routes or at least respond differently to photoperiod cues that influence migration such that arrival times are always distinctly separated, and thus weather patterns that delay arrival of one group by a few days will not result in mixing of the two gene pools.

Influence of weather on migration and spring arrival

We hypothesized that different wintering areas interacting with large-scale weather patterns could influence arrival after migration, and hence proportions of phenotypes during mate choice and assortative pairing. In contrast to the previous avian examples, arrival schedules

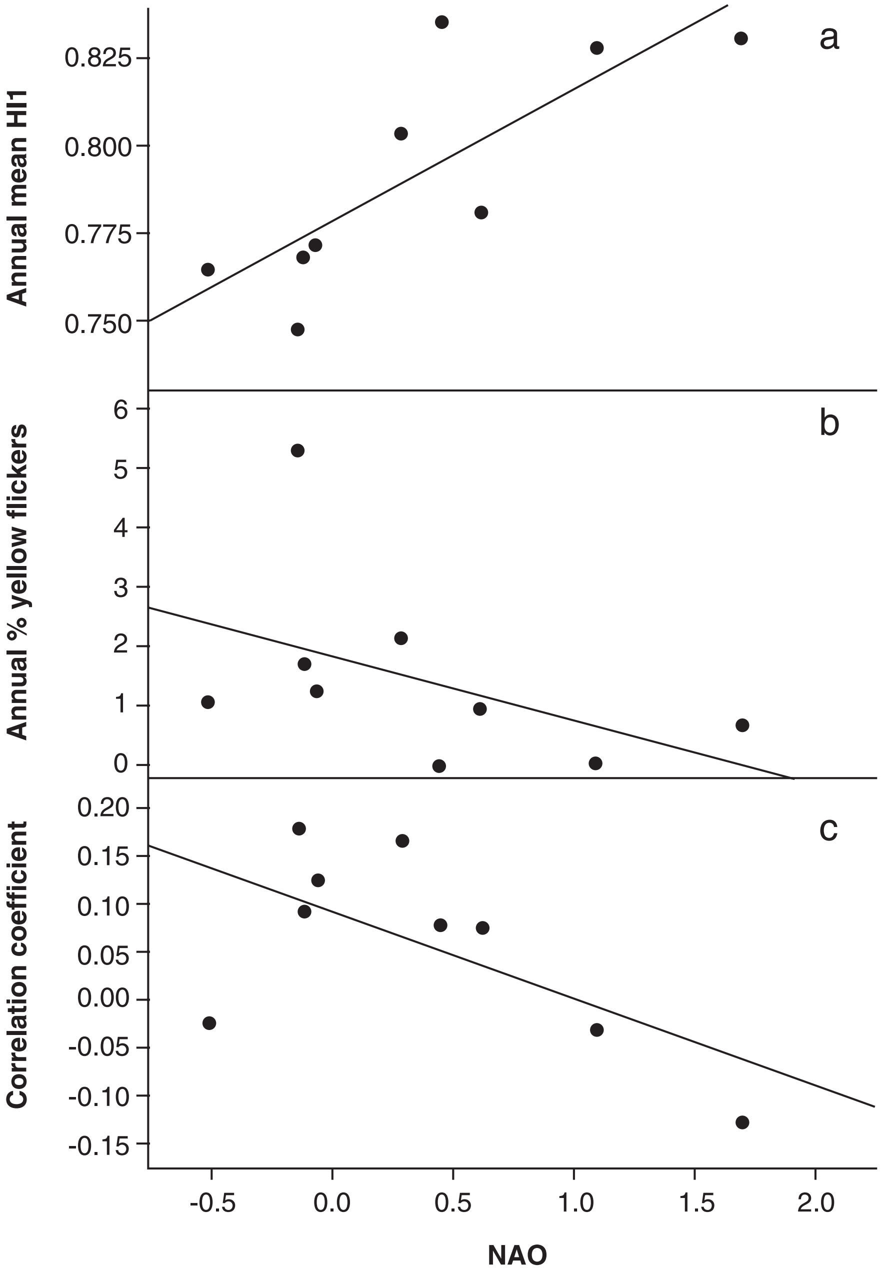

Fig. 4. Relationships between the North Atlantic Oscillation (NAO) and (a) average annual phenotype (HI1), (b) annual proportion of yellow (*auratus*-type) flickers breeding at Riske Creek, and (c) annual correlation coefficient of the hybrid index between members of a mated flicker pair. A positive NAO results in above average winter temperatures and a negative NAO results in below average winter temperatures in eastern North America.

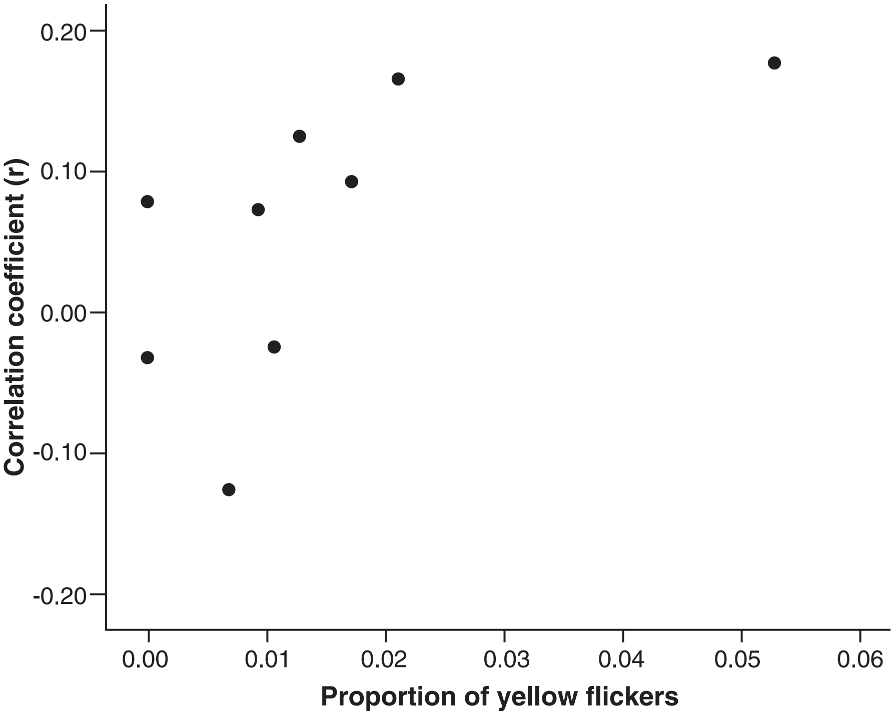

Fig. 5. The annual correlation coefficient of the hybrid index (HI1) between members of a mated flicker pair according to the proportion of yellow (*auratus*-type) individuals in the population at Riske Creek that year. Each data point represents correlations between 50–129 pairs annually.

of the flicker subspecies were not distinctly staggered. It could be that geographical separation of phenotypes on the wintering grounds is not as dramatic as in the other examples. Migratory 'pure' yellow-shafted and 'pure' red-shafted flicker populations wintered in the eastern and western United States, respectively. Reddish-orange hybrids at Riske Creek wintered along the west coast south to California but there were no band recoveries of yellowish hybrids from our population, so it is still unclear whether phenotypes in the hybrid zone migrate along different routes or segregate in different wintering areas.

Casual observation of flicker phenotypes on the study area in early spring in previous years confirms that arrival times of reddish and yellowish birds are never completely segregated and do not differ by the 2-week margin reported in the example of willow warblers (see above). Although we were unable to detect a difference in arrival times between phenotypes at Riske Creek in 2006, or a difference in date of first egg according to phenotype in the larger data set, it is still possible that small but significant differences in arrival times occur in some years, depending on weather patterns. Furthermore, there is substantial variation in laying dates not accounted for by arrival time, so nest initiation may be a too coarse measure to detect differences in arrival that may only vary by a few days.

Although direct evidence of staggered arrival between phenotypes was lacking, regional and continental weather patterns were related to spring breeding phenology, annual variation in phenotypes, and patterns of assortative pairing in our population. As anticipated, higher April temperatures in Seattle were linked to earlier egg-laying dates in the population at Riske Creek as a whole, suggesting that benign weather in the Pacific Northwest in spring generally accelerated arrival. Warmer springs on the west coast and colder than average winters in eastern North America indicated by a negative NAO resulted in a more yellow (*auratus*-like) annual phenotype and a stronger prevalence of assortative mating. Because the proportion of 'strongly yellow' individuals was not driving these relationships, it did not seem that the weather patterns increased the influx of pure parental *auratus*-types from great geographic distances (i.e. from central and eastern North America). Instead, the shift in mean hybrid index appeared to be driven by changes in settlement in the hybrid zone on a smaller scale, with the position of the zone shifting slightly to the west following cold eastern winters.

Positive phases of the NAO that coincide with warmer winter temperatures in Europe result in earlier arrival of many migratory species (Hüppop and Hüppop, 2003; Vähätalo *et al.*, 2004). Gunnarsson *et al.* (2006) suggested that NAO influenced timing of migration by affecting feeding conditions in the months before spring migration, the effects being more pronounced closer to spring migration. Similarly, warmer winter conditions associated with NAO allowed earlier arrival for European long-distance migrants through improved foraging conditions on the wintering grounds and for short-distance migrants through both improved foraging conditions and weather conditions during migration (Forchhammer *et al.*, 2002). Because flickers forage mainly on the ground (Moore 1995), they may migrate according to patterns of disappearing snow cover, but until the wintering ground and migration routes are mapped more precisely, it is impossible to confirm the exact aspect of the weather pattern responsible for flicker movements in western North America.

Annual variation in phenotype and assortative pairing

Weather patterns were associated with annual variation in phenotypes, which, in turn, was related to the prevalence of assortative pairing. Years with more yellowish individuals, the rarest phenotype on our study area, meant a greater range and variation in phenotypes and this may have increased the strength of assortative pairing. Such annual variation in phenotypes has implications for the dynamics of hybrid zones. While studies in the south suggest that the flicker hybrid zone has been stable for centuries at least (Rising, 1983; Moore and Buchanan, 1985), evidence from northern populations suggests there may be increasing introgression (McGillivray and Biermann, 1987). A time-series long enough to detect a directional shift in the hybrid zone is unavailable in British Columbia, but at Riske Creek the distribution of phenotypes fluctuates annually, apparently in response to large-scale weather patterns. Wiebe and Bortolotti (2001) argued that the complex mountainous topography in British Columbia may not produce the smooth and continuous environmental clines hypothesized to keep the subspecies separate in the United States. Instead, weather and migratory movements may determine the proportion of phenotypes that breed in different geographic locations in the north.

Different proportions of phenotypes or differences in arrival times are linked to the annual strength of assortative pairing in our population. Since assortative mating is a mechanism of pre-mating reproductive isolation, it will act as a barrier to introgression regardless of the subsequent reproductive performance of the pair (Coyne and Orr, 2004). Migration can therefore influence how gene flow progresses or is impeded in the flicker hybrid zone. However, it is unlikely that the overall weak assortative pairing at Riske Creek is a major force of reproductive isolation even in this northern population. Further data on reproductive performance of breeding pairs according to their phenotypes is needed to determine if any reproductive isolation occurs at later stages of breeding, as this can be another mechanism that prevents introgression and keeps hybrid zones stable (Moore, 1987).

In summary, we did not detect a large difference in arrival times of flicker subspecies like the distinct 1–2 week difference reported in some other avian species. However, there may be more subtle variation in arrival that is influenced more by weather patterns, which in turn can vary from year to year. This could explain annual variation in phenotypes and strength of assortative pairing in this northern portion of the flicker hybrid zone. Further data on the timing and speed of migration of the different subspecies in relation to large-scale weather events on a continental scale (e.g. reporting rates of passage through migratory bird banding stations) is needed to refine our picture of how weather affects migration timing, assortative pairing, and the long-term dynamics of the flicker hybrid zone.

ACKNOWLEDGEMENTS

We thank numerous field assistants over the years for helping to find and monitor flicker nests. D.T.T.F. was supported financially by a University of Saskatchewan Graduate Scholarship and the study was funded by an NSERC discovery grant to K.L.W.

REFERENCES

Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K., and Lehikoinen, E. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. *Glob. Change Biol.*, **10**: 1610–1617.

Allen, J.A. 1892. The North American species of the genus *Colaptes*, considered with special reference to the relationships of *C. auratus* and *C. cafer*. *Bull. Am. Mus. Nat. Hist.*, **4**: 21–44.

Barton, N.H. and Hewitt, G.M. 1985. Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.*, **16**: 113–148.

Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J. *et al.* 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science*, **310**: 502–504.

Bensch, S., Andersson, T., and Akesson, S. 1999. Morphological and molecular variation across a migratory divide in willow warblers, *Phylloscopus Trochilus*. *Evolution*, **53**: 1925–1935.

Bensch, S., Bengtsson, G., and Akesson, S. 2006. Patterns of stable isotope signatures in willow warbler *Phylloscopus trochilus* feathers collected in Africa. *J. Avian Biol.*, **37**: 323–330.

Berthold, P., Helbig, A.J., Mohr, G., and Querner, U. 1992. Rapid microevolution of migratory behavior in a wild bird species. *Nature*, **360**: 668–670.

Bock, C.E. 1971. Pairing in hybrid flicker populations in eastern Colorado. *Auk*, **88**: 921–924.

Bronson, C.L., Grubb, T.C., and Braun, M.J. 2003. A test of the endogenous and exogenous selection hypothesis for the maintenance of a narrow avian hybrid zone. *Evolution*, **57**: 630–637.

Burley, N. 1983. The meaning of assortative mating. *Ethol. Sociobiol.*, **4**: 191–203.

Chamberlain, C.P., Bensch, S., Feng, X., Akesson, S., and Andersson, T. 2000. Stable isotopes examined across a migratory divide in Scandinavian willow warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. *Proc. R. Soc. Lond. B*, **267**: 43–48.

Coyne, J.A. and Orr, H.A. 2004. *Speciation*. Sunderland, MA: Sinauer Associates.

Craig, T.P., Itami, J.K., Abrahamson, W.G., and Horner, J.D. 1993. Behavioral evidence for host-race formation in *Eurosta solidaginis*. *Evolution*, **47**: 1696–1710.

Cuthill, I.C., Bennett, A.T.D., Partridge, J.C., and Maier, E.J. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *Am. Nat.*, **153**: 183–200.

Dobzhansky, T. 1937. Genetic nature of species differences. *Am. Nat.*, **71**: 404–420.

Erskine, A.J. 1962. Some new data on introgression in flickers from British Columbia. *Can. Field-Nat.*, **76**: 82–87.

Ferrer, M. and Penteriani, V. 2003. A process of pair formation leading to assortative mating: passive age-assortative mating by habitat heterogeneity. *Anim. Behav.*, **66**: 137–143.

Fisher, R.J. and Wiebe, K.L. 2006a. Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. *Oecologia*, **147**: 744–753.

Fisher, R.J. and Wiebe, K.L. 2006b. Effects of sex and age on survival of northern flickers: a six-year field study. *Condor*, **108**: 193–200.

Forchhammer, M.C., Post, E., and Stenseth, N.C. 2002. North Atlantic Oscillation timing of long- and short-distance migration. *J. Anim. Ecol.*, **71**: 1002–1014.

Fox, G.A. 2003. Assortative mating and plant phenology: evolutionary and practical consequences. *Evol. Ecol. Res.*, **5**: 1–18.

Good, T.P., Ellis, J.C., Annett, C.A., and Pierotti, R. 2000. Bounded hybrid superiority in an avian hybrid zone: effect of mate, diet, and habitat choice. *Evolution*, **54**: 1774–1783.

Gunnarsson, T.G., Gill, J.A., Atkinson, P.W., Gélinaud, G., Potts, P.M., Croger, R.E. *et al*. 2006. Population-scale drivers of individual arrival times in migratory birds. *J. Anim. Ecol.*, **75**: 1119–1127.

Hendry, A.P. and Day, T. 2005. Population structure attributable to reproductive time: isolation by time and adaptation by time. *Mol. Ecol.*, **14**: 901–916.

Hill, G.E. 1998. An easy, inexpensive means to quantify plumage coloration. *J. Field Ornithol.*, **69**: 353–363.

Hobson, K.A. 2005. Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *Auk*, **122**: 1037–1048.

Horel, J.D. and Wallace, J.M. 1981. Planetary-scale atmospheric phenomena associated with the southern oscillation. *Mon. Weather Rev.*, **109**: 813–829.

Hüppop, O. and Hüppop, K. 2003. North Atlantic Oscillation and timing of spring migration in birds. *Proc. R. Soc. Lond. B*, **270**: 233–240.

Hurrell, J.W. 1995. Decadal trends in the North-Atlantic Oscillation – regional temperatures and precipitation. *Science*, **269**: 676–679.

Kinnison, M.T., Bentzen, P., Unwin, M.J., and Quinn, T.P. 2002. Reconstructing recent divergence: evaluating nonequilibrium population structure in New Zealand Chinook salmon. *Mol. Ecol.*, **11**: 739–754.

Liou, L.W. and Price, T.D. 1994. Speciation by reinforcement of premating isolation. *Evolution*, **48**: 1451–1459.

Martin, K. and Eadie, J.M. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. *For. Ecol. Manage.*, **115**: 243–257.

Mayr, E. 1942. *Systematics and the origin of species*. New York: Columbia University Press.

McGillivray, W.B. and Biermann, G.C. 1987. Expansion of the zone of hybridization of northern flickers in Alberta. *Wilson Bull.*, **99**: 690–692.

Moore, W.S. 1977. Evaluation of narrow hybrid zones in vertebrates. *Q. Rev. Biol.*, **52**: 263–277.

Moore, W.S. 1987. Random mating in the northern flicker hybrid zone – implications for the evolution of bright and contrasting plumage patterns in birds. *Evolution*, **41**: 539–546.

Moore, W.S. 1995. Northern flicker (*Colaptes auratus*). *The birds of North America*, No. 166 (A. Poole and F. Gill, eds.). Philadelphia, PA: Academy of Natural Sciences/Washington, DC: American Ornithologists' Union.

Moore, W.S. and Buchanan, D.B. 1985. Stability of the northern flicker hybrid zone in historical times – implications for adaptive speciation theory. *Evolution*, **39**: 135–151.

Moore, W.S. and Koenig, W.D. 1986. Comparative reproductive success of yellow-shafted, red-shafted, and hybrid flickers across a hybrid zone. *Auk*, **103**: 42–51.

Pyle, P. 1997. *Identification guide to North American birds*. Bolinas, CA: Slate Creek Press.

Quinn, T.P., Unwin, M.J., and Kinnison, M.T. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution*, **54**: 1372–1385.

Rising, J.D. 1983. The great plains hybrid zones. *Curr. Ornithol.*, **1**: 137–157.

Short, L.L. 1965. Hybridization in the flickers (*Colaptes*) of North America. *Bull. Am. Mus. Nat. Hist.*, **129**: 307–428.

Shriver, W.G., Gibbs, J.P., Vickery, P.D., Gibbs, H.L., Hodgman, T.P., Jones, P.T. *et al.* 2005. Concordance between morphological and molecular markers in assessing hybridization between sharp-tailed sparrows in New England. *Auk*, **122**: 94–107.

Siegel, S. and Castellan, N.J. 1988. *Nonparametric statistics for the behavioral sciences*, 2nd edn. New York: McGraw-Hill.

Vähätalo, A.V., Rainio, K., Lehikoinen, A., and Lehikoinen, E. 2004. Spring arrival of birds depends on the North Atlantic Oscillation. *J. Avian Biol.*, **35**: 210–216.

Wallace, J.M. and Gutzler, D.S. 1981. Teleconnections in the geopotential height field during the northern hemisphere winter. *Mon. Weather Rev.*, **109**: 784–812.

Wiebe, K.L. 2000. Assortative mating by color in a population of hybrid northern flickers. *Auk*, **117**: 525–529.

Wiebe, K.L. 2002. First reported case of classical polyandry in a North American woodpecker, the northern flicker. *Wilson Bull.*, **114**: 401–403.

Wiebe, K.L. and Bortolotti, G.R. 2001. Variation in colour within a population of northern flickers: a new perspective on an old hybrid zone. *Can. J. Zool.*, **79**: 1046–1052.

Wiebe, K.L. and Bortolotti, G.R. 2002. Variation in carotenoid-based color in northern flickers in a hybrid zone. *Wilson Bull.*, **114**: 393–400.