

VARIABLE WEATHER PATTERNS AFFECT ANNUAL SURVIVAL OF NORTHERN FLICKERS MORE THAN PHENOTYPE IN THE HYBRID ZONE

D. T. TYLER FLOCKHART¹ AND KAREN L. WIEBE

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

Abstract. Fitness in a hybrid zone is determined both by the reproductive success and the survival of phenotypes. The hybrid zone of Northern Flickers (*Colaptes auratus*), a common woodpecker, is one of the largest and most well-known hybrid zones in North America. Bounded-hybrid superiority, the most widely accepted hypothesis for the persistence of the zone, suggests hybrids should have equal or higher reproduction or survival than parental types in the zone, but the latter life history trait has never been examined. We analyzed the apparent survival of 1117 flickers over nine years using capture-recapture models and found no evidence that the phenotypic hybrid index influenced survival. Instead, annual adult apparent survival was best modeled according to large-scale weather patterns such as the North Atlantic Oscillation (NAO). During warm phases of the NAO, adult flickers had lower survival compared to cooler phases of NAO. There was no evidence that phenotype influenced the local recruitment of yearling flickers to the study area and no effect of NAO on this relationship. These results suggest survival in the flicker hybrid zone is largely influenced by annually variable weather patterns and that if there are differences in survival according to phenotype, they are extremely small for the flicker hybrid zone in the north.

Key words: *bounded-hybrid superiority hypothesis, Colaptes auratus, fitness, hybridization, North Atlantic Oscillation, recruitment.*

Los Patrones Climáticos Variables Afectan la Supervivencia Anual Más que el Fenotipo de *Colaptes auratus* en la Zona de Hibridación

Resumen. La adecuación biológica en una zona de hibridación está determinada tanto por el éxito reproductivo como por la supervivencia de los fenotipos. La zona de hibridación de *Colaptes auratus*, un pájaro carpintero común, es una de las zonas de hibridación más grandes y mejor conocidas de América del Norte. La superioridad limitada de los híbridos, la hipótesis más aceptada para la persistencia de la zona, sugiere que los híbridos deberían presentar una reproducción o supervivencia igual o mayor que los tipos parentales en la zona, pero estos rasgos de las historias de vida jamás han sido analizados. Analizamos la supervivencia aparente de 1117 individuos a lo largo de nueve años usando modelos de captura-recaptura y no encontramos evidencia de que el índice de fenotipo híbrido influya la supervivencia. Al contrario, la supervivencia aparente anual de los adultos fue modelada mejor de acuerdo con patrones climáticos de gran escala como la Oscilación del Atlántico Norte (OAN). Durante las fases cálidas de la OAN, los individuos adultos tuvieron menor supervivencia que durante las fases más frías de la OAN. No hubo evidencia de que el fenotipo influyera el reclutamiento local de los jóvenes al área de estudio y la OAN no afectó esta relación. Estos resultados sugieren que la supervivencia en la zona de hibridación de *C. auratus* está influenciada principalmente por los patrones climáticos anuales variables y que si hay diferencias en la supervivencia de acuerdo al fenotipo, éstas son extremadamente pequeñas para la zona de hibridación de *C. auratus* en el norte.

INTRODUCTION

Patterns of survival, reproduction, and dispersal of individuals across a hybrid zone determine whether the zone is stable or moving. Stable hybrid zones may exist although there is selection against hybrids because naive parental forms continually immigrate into the zone and interbreed (the tension-zone model; Barton and Hewitt 1985, 1989). Alternatively, the bounded-hybrid superiority hypothesis predicts that hybrids have equal or higher fitness relative to parental forms within the contact zone (Moore 1977), but the zone is maintained by ecological selection gradients such that phenotypes

have maximum fitness within the habitat for which they are best adapted (Moore and Price 1993). To distinguish between these two hypotheses, fitness differences between hybrids and parental types must be assessed to determine how selection operates in the zone (Arnold and Hodges 1995).

Lifetime reproductive success increases with the number of offspring per reproductive event or with continued survival to breeding over many years (Grant and Grant 2000). Where phenotypes do not differ in annual reproductive success, differences in survival could still affect lifetime success and hence could affect hybrid zone stability, rate of introgression, and hybrid fitness. In relatively short-lived species and where

Manuscript received 24 April 2008; accepted 24 September 2008.

¹E-mail: dt.tyler.flockhart@gmail.com

The Condor, Vol. 000, Number 0, pages 1–8. ISSN 0010-5422, electronic ISSN 1938-5129. © 2008 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, <http://www.ucpressjournals.com/reprintInfo.asp>. DOI: 10.1525/cond.2008.8613

breeding is annual, surviving an additional one or two years may double or triple the number of breeding attempts, and so survival may be the best overall measure of fitness (Grant and Grant 1992, 2000, Crone 2001).

The Northern Flicker (*Colaptes auratus*) is the most common woodpecker in North America. Once considered different species, the western Red-shafted Flicker (*C. a. cafer*) and eastern Yellow-shafted Flicker (*C. a. auratus*) are subspecies that hybridize in a zone that is 300 to 500 km in width and stretches over 4000 km in length from Texas to Alaska (AOU 1983, Wiebe and Moore 2008). The flicker hybrid zone is often cited as an example of hybrid superiority because southern portions of the zone appear stable (Moore and Buchanan 1985), mating seems to be random with respect to phenotype (Bock 1971, Moore 1987), and hybrids do not have smaller clutch sizes than parental types (Moore and Koenig 1986). However, the dynamics of the northern part of the zone may be different from those of the south because both subspecies are migratory and pairing is weakly assortative in at least one area of the hybrid zone (Wiebe 2000, Flockhart and Wiebe 2007). Although we could not detect any differences in reproductive success according to phenotype (DTTF and KLW, unpubl. data), there may still be fitness differences among phenotypes if there are differences in survival. For example, while annual reproductive success was found to be similar between hybrid and pure-parental individuals, survival was lower in hybrid sapsuckers (*Sphyrapicus* spp.; Trombino 1998) and higher in hybrid Darwin's finches (*Geospiza* spp.; Grant and Grant 1992).

Although it is ideal to track birds with known pedigrees over their entire life spans to discern survival rates (Grant and Grant 1992), this is often impossible for migratory species and those which disperse. Instead, survival of hybrids has been inferred from differences in abundances over different life stages (Vamosi et al. 2000, Rohwer 2004, Albert et al. 2006), return rates of marked individuals (Trombino 1998), or experimental evidence of susceptibility to predators (Vamosi and Schluter 2002). Few studies of survival in hybridizing populations have used a hybrid index, but rather have simply categorized individuals as pure or hybrid. Long-term capture-recapture studies allow robust apparent survival estimates to be calculated, and recent advances in information-theoretic analyses allow one to calculate how specific covariates (i.e., phenotypic hybrid indices) can influence an individual's apparent survival (Burnham and Anderson 2002, Cam et al. 2002). Although mark-recapture models are powerful, they cannot distinguish mortality from permanent emigration (Cilimburg et al. 2002), but several lines of evidence suggest that apparent survival estimates of adult flickers from program MARK (White and Burnham 1999) are accurate estimates of true survival in our population (Fisher and Wiebe 2006a). This is not true for fledglings, which disperse long distances. For fledglings, if the probability of permanent

emigration is independent of phenotype, then we can assume differences in local recruitment among phenotypes should reflect differences in mortality.

Our objective was to investigate how phenotype (i.e., hybrid index) and weather patterns may influence the survival of Northern Flicker fledglings and adults. The tension-zone model predicts that hybrids have lower survival than either parental type (Barton and Hewitt 1985). The bounded-hybrid superiority hypothesis predicts that hybrids have either higher survival than parental types, or in a special case outlined by Moore and Price (1993), equal survival in the center of the zone. However, because our study area is located on about the 80% cline of the hybrid zone, in this special case, we would predict survival of Red-shafted Flickers to be greater than that of hybrids, while survival of Yellow-shafted Flickers should be the lowest. We tested for differences in local recruitment among phenotypes of offspring hatched on the study site and also used mark-recapture data to derive apparent survival estimates of adults according to phenotype.

METHODS

TRAPPING AND RESIGHTING EFFORT

We studied flickers over nine years at Riske Creek in central British Columbia, Canada (51°52'N, 122°21'W) on a study area that covered about 100 km². This is the site of a long-term population study in which 80–150 nests have been monitored annually since 1998. For a general description of habitat and nests sites, see Wiebe and Swift (2001) and Fisher and Wiebe (2006b). Each year between 1998 and 2006, the study area was surveyed daily in spring, starting in mid-April as flickers settled after migration, until about June, when nestlings were hatching. We used tape-recorded territorial calls to solicit responses from flickers that were defending territories. Vocalizations used were recorded in California and presumably were from Red-shafted Flickers (Cornell Lab of Ornithology 1999); however, there are no known differences in the vocalizations between Red-shafted and Yellow-shafted Flickers (Wiebe and Moore 2008), and so our detections should not be biased towards particular phenotypes. When a flicker responded, we recorded its sex and, if present, its color-band combination. We trapped unbanded and otherwise unknown adults on their nests as they incubated eggs or provisioned young after we found their nests (Wiebe 2002). Most adults that breed on the study area (>95%) are identified each year. We also banded all nestlings at approximately 20 days of age just prior to fledging.

CALCULATING A HYBRID INDEX

Most studies of hybrid zones quantify an individual's hybrid status (phenotype) by characterizing plumage or morphological traits and assume that these traits are the result of underlying genotypic differences, an assumption that

usually seems justified (Shriver et al. 2005). Hybrid flickers show variable intermediate phenotypic traits that seem to assort independently between Red-shafted and Yellow-shafted Flickers (Erskine 1962, Moore 1987). Coloration in flickers is likely under genetic control (Stradi et al. 1998), and therefore, scoring plumage traits to derive a composite index should approximate a ranking of genotypes in our population.

When adults were captured, we calculated two different hybrid indices (HI) for each. The first (HI_A) was the sum of categorical scores for up to five plumage traits (four in females): ear, throat, nape, tail color (mean of tail rachis and vane), and moustache (males only; Short 1965). Each trait was scored on a five-point scale, where 0 = pure Yellow-shafted Flicker and 4 = pure Red-shafted Flicker. The sum of these traits was then divided by the maximum possible score so that it varied between 0 for a pure Yellow-shafted and 1 for a pure Red-shafted Flicker (Flockhart and Wiebe 2007). We scored plumage traits of nestlings when they were banded and calculated HI_A as outlined above; however, when certain plumage traits had not yet developed (e.g., malar patch), those variables were omitted for that individual. This index was not continuous or normally distributed, so we calculated a second index (HI_B) for adults, which was derived from a tail feather scanned with a CM-2600d spectrophotometer (Konica Minolta Sensing, Inc., Ramsey, New Jersey). The spectrophotometer produced reflectance spectra values between 360 and 740nm at 10nm intervals, and we used principal component analysis (PCA) to extract data on two axes using the reflectance data between 570nm and 700nm, because most variation in color differences among flicker feathers was explained by wavelengths in this range (DTTF, unpubl. data). Following Cuthill et al. (1999), where the score on the first axis (PCA1) measures brightness values that are largely independent of color, we used the scores of the second axis (PCA2) to quantify feather color and standardized the scores to range from 0 for a pure Yellow-shafted Flicker to 1 for a pure Red-shafted Flicker (Flockhart and Wiebe 2007). Tail feathers were collected only from adult flickers, and sample size for HI_A ($n = 1117$) was larger than for HI_B ($n = 591$) because not all individuals had feather samples collected in each year.

We conducted separate apparent-survival analyses for adults using HI_A and HI_B as individual covariates and assumed that the indices remained consistent throughout the life span of the individual. Scoring of HI_A and HI_B was consistent, and statistical tests showed that hybrid indices calculated for the same individual in multiple years were highly repeatable and did not change over time (Flockhart 2007). If a flicker was trapped more than once, we used the HI_A and HI_B score from its initial capture.

STATISTICAL ANALYSES

Local recruitment. We tested if the distribution of phenotypes of nestlings that were eventually recruited into the population (i.e., recaptured as breeding adults in subsequent years) was

different from phenotypes of all nestlings that fledged in their particular cohort (year). To increase sample sizes in the analysis involving weather, we categorized years as either positive or negative North Atlantic Oscillation (NAO) values (mean September–April) and tested if the phenotype of local recruits from those years differed from the phenotypes of all fledglings from those years. All statistical tests were two-sample Kolmogorov-Smirnov tests (Siegel and Castellan 1988) and conducted with SPSS 13.0 (2004). Significance was set at $\alpha = 0.05$ for all statistical tests.

Survival estimates using program MARK. For adult flickers, we used a Cormack-Jolly-Seber capture-recapture model in program MARK to determine apparent survival (Φ) and resighting probability (p), which incorporated individual and cohort-level covariates over nine years. Philopatric nestlings were considered new to the study for this analysis when they were first captured as adults, and therefore, these apparent survival estimates apply only to flickers at least one year old. Previous analyses suggested small differences in apparent survival between males and females but little support for time or adult age-class effects (Fisher and Wiebe 2006a), so we retained sex-dependent variation in our models (Φ_{sex}) in addition to constancy models (Φ). We then modeled survival according to the hybrid index both with linear dependence (Φ_{HI}) and with quadratic dependence (Φ_{HI^2}), since the bounded-hybrid superiority hypothesis suggests hybrids may have higher fitness than pure parental types. We included annual weather variation in the form of the NAO index (mean September to April data, Φ_{NAO} ; Climate Prediction Center Internet Team 2006) because it influences mating patterns in flickers (Flockhart and Wiebe 2007) and because large-scale weather patterns are known to affect the survival of migratory birds (Sillett et al. 2000, Mazerolle et al. 2005). Lastly, we incorporated linear and quadratic HI relationships in both interactive and additive models of NAO (e.g., Φ_{NAO*HI}) and sex (e.g., Φ_{sex*HI}). Recapture probability was considered either as constant (p) or sex-dependent (p_{sex}) in addition to linear (p_{HI}) and quadratic (p_{HI^2}) effects of HI. Therefore, our candidate model list included 13 parameterizations for apparent survival and 4 parameterizations for recapture or resighting, for a total of 52 models each for both HI_A and HI_B .

A necessary first step in model selection is to determine the goodness-of-fit of a global model. Program MARK does not allow goodness-of-fit testing on covariates, so we assessed the most parameterized model without covariates ($\Phi_{sex} p_{sex}$). We used the median $\hat{c}$ procedure to determine if the global model fit the assumptions of mark-recapture analysis using 700 simulations (White and Burnham 1999). A variance inflation factor ($\hat{c}$) of 1 suggests perfect model fit, while a $\hat{c}$ between 1 and 3 suggests acceptable fit (Burnham and Anderson 2002).

We used Akaike's information criterion adjusted for overdispersion and small sample size (QAIC_c) to determine the most parsimonious model in the candidate list (Burnham and Anderson 2002). To distinguish between competing models, we used the difference between the model of interest and the best fitting model (ΔQAIC_c). Models within two Akaike units ($\Delta\text{QAIC}_c \leq 2$) were considered as competing models to explain variation in the data (Burnham and Anderson 2002). Parameter estimates were derived through model averaging of Akaike weights (w_i) that determine the relative support of the various effects (e.g., HI) in the candidate set of models (White and Burnham 1999, Burnham and Anderson 2002).

RESULTS

PHENOTYPES OF RECRUITED NESTLINGS

A total of 127 of 3501 fledglings (3.6 %) hatched on the study area were recruited into the local population between 1998 and 2006. There was no difference between the hybrid index (HI_A) of local recruits compared to the cohort of fledgling young both in individual years (all $P > 0.30$) and all years combined (Kolmogorov-Smirnov test: $Z = 0.8$, $n = 122$, $P = 0.50$). The analysis with years categorized as either positive or negative with respect to the NAO resulted in no significant differences between phenotypes of recruiting offspring versus fledged offspring (negative NAO years: $Z = 0.6$, $n = 60$, $P = 0.90$; positive NAO years: $Z = 1.1$, $n = 62$, $P = 0.17$). The year of our study with the greatest positive NAO value was 1999, and between 1950 and 2006, there were only two years (1993, 1989) with more extreme positive NAO values. In contrast, there were several years (1952, 1955, 1970, 1962, 1968) with more extreme negative NAO values than that observed in 2002 during the study. The number of fledglings that were recruited into the local population was lower than expected following the extreme positive NAO year compared to the extreme negative NAO year observed during our study ($\chi^2_1 = 5.5$, $P = 0.02$).

SURVIVAL ESTIMATES USING PROGRAM MARK

After correcting for overdispersion (HI_A: $\hat{c} = 1.29$; HI_B: $\hat{c} = 1.25$), the top models for both HI_A and HI_B suggested that apparent survival varied annually according to NAO but that there was little effect of sex or hybrid index (HI; Table 1). Three of the top six models for HI_A included NAO, and in years with positive NAO, which correlate with above-average temperatures in North America (Thompson and Wallace 2001), winter apparent survival was estimated to be lower than in negative years, but error bars overlapped among all years (Fig. 1). Resighting probability was best modeled as sex dependent with males (0.84) more likely to be detected than females (0.81), but differences were slight, as there was also some support for constant resighting rates (Table 1).

TABLE 1. Supported models ($\Delta\text{QAIC}_c < 2$) to explain variation in apparent survival (Φ) and resighting (p) probability of adult Northern Flickers at Riske Creek, British Columbia between 1998 and 2006. QAIC_c is Akaike's information criterion adjusted for overdispersion and small sample size, and ΔQAIC_c is the difference in QAIC_c value from the top model. Models for two different hybrid indices are presented: HI_A is the sum of categorical scores for up to five plumage traits, and HI_B is the score of a tail feather scanned with a spectrophotometer. Models include parameters for constancy (.), annual North Atlantic Oscillation (NAO), sex, linear effects of hybrid index (HI), and quadratic effects of hybrid index (HI2) on apparent survival and resighting. The total QAIC_c, difference of QAIC_c of each model relative to the top model (ΔQAIC_c), Akaike model weight (w_i), number of parameters (K) and quasi deviance (QDeviance) are presented for each model. The correction for overdispersion was $\hat{c} = 1.29$ for HI_A and $\hat{c} = 1.25$ for HI_B.

Model	K	QDeviance	ΔQAIC_c	w_i
HI_A				
$\Phi_{\text{NAO}} p_{\text{sex}}$ ^a	4	1704.6	0.00	0.12
$\Phi_{\text{NAO}} p_{\cdot}$	3	1707.0	0.38	0.10
$\Phi_{\cdot} p_{\text{sex}}$	3	1707.5	0.91	0.08
$\Phi_{\cdot} p_{\cdot}$	2	1709.9	1.34	0.06
$\Phi_{\text{sex}} p_{\cdot}$	3	1708.1	1.52	0.06
$\Phi_{\text{NAO+HI}} p_{\text{sex}}$	5	1704.4	1.85	0.05
HI_B				
$\Phi_{\cdot} p_{\text{HI2}}$ ^b	4	716.7	0.00	0.11
$\Phi_{\text{NAO}} p_{\text{HI2}}$	5	715.0	0.37	0.09
$\Phi_{\cdot} p_{\cdot}$	2	721.8	1.05	0.06
$\Phi_{\cdot} p_{\text{sex}}$	3	720.1	1.37	0.05
$\Phi_{\text{NAO}} p_{\cdot}$	3	720.1	1.40	0.05
$\Phi_{\text{NAO}} p_{\text{sex}}$	4	718.5	1.79	0.04
$\Phi_{\text{sex}} p_{\text{HI2}}$	5	716.6	1.93	0.04
$\Phi_{\cdot} p_{\text{HI}}$	3	720.7	1.99	0.04
$\Phi_{\text{HI}} p_{\text{HI2}}$	5	716.7	2.00	0.04

^a QAIC_c of the top model using HI_A was 1712.61.

^b QAIC_c of the top model using HI_B was 724.78.

Apparent survival estimates of males (HI_A: 0.47; HI_B: 0.46) and females (HI_A: 0.47; HI_B: 0.46) were nearly identical between the two indices. For HI_B, several other models were within two QAIC_c units of the most parsimonious model, indicating they held some support but, again, apparent survival was best modeled by the annual effects of NAO without sex or HI dependence (Table 1).

A post-hoc survival analysis with respect to weather and HI considering only the two most extreme positive and the two most extreme negative NAO years from our study produced similar results. The best-supported model with a NAO and HI interaction was greater than two QAIC_c units from the most parsimonious model and had lower support compared the original analysis using all NAO values. Overall, there was no evidence that HI terms held any more support to explain survival when only extreme NAO years were considered.

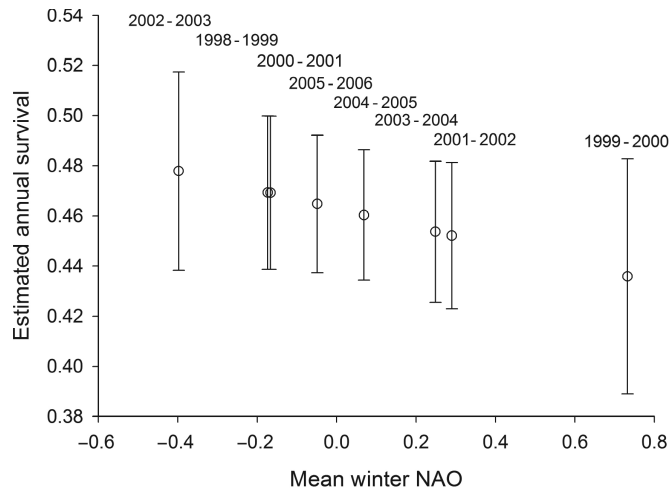


FIGURE 1. Estimated annual winter apparent survival ($\pm$ SE) of adult Northern Flickers from Riske Creek, British Columbia, and mean winter North Atlantic Oscillation (NAO) index (September–April) between 1998 and 2006. Survival estimates are derived from models using the hybrid index (HI_A ; pooled plumage trait scores) and are for the interval August–April in the years indicated.

Although there was no overwhelming evidence that HI greatly influenced apparent survival, we derived survival estimates with regard to HI to better understand the selection pressures operating on the various phenotypes at Riske Creek. Overall, linear relationships of HI held more support (HI_A : $w_i = 0.29$; HI_B : $w_i = 0.27$) than quadratic relationships (HI_A : $w_i = 0.13$; HI_B : $w_i = 0.15$). Linear relationships predicted that Yellow-shafted Flickers had lower apparent survival than Red-shafted Flickers, whereas quadratic relationships suggested that hybrid flickers had the highest apparent survival (Fig. 2).

DISCUSSION

Overall, there was little evidence that survival of flickers was linked to their hybrid index; survival was best explained without phenotype as a covariate. Instead, the factor with the greatest influence on annual survival was weather. Strong positive phases of the NAO result in above average temperatures in the Pacific Northwest (Thompson and Wallace 2001) and were associated with low adult flicker survival and low recruitment of nestlings, while the negative phases with their cooler temperatures and increased precipitation were associated with high apparent survival of adults. If the flickers of different phenotypes from Riske Creek overwinter in different areas, weather events might affect the phenotypes differently, but only one model supported an interaction effect between NAO and HI.

Large-scale climatic variations, such as NAO and El Niño–Southern Oscillation (ENSO), can influence survival of birds during the wintering periods, likely through increased or decreased precipitation that influences food availability.

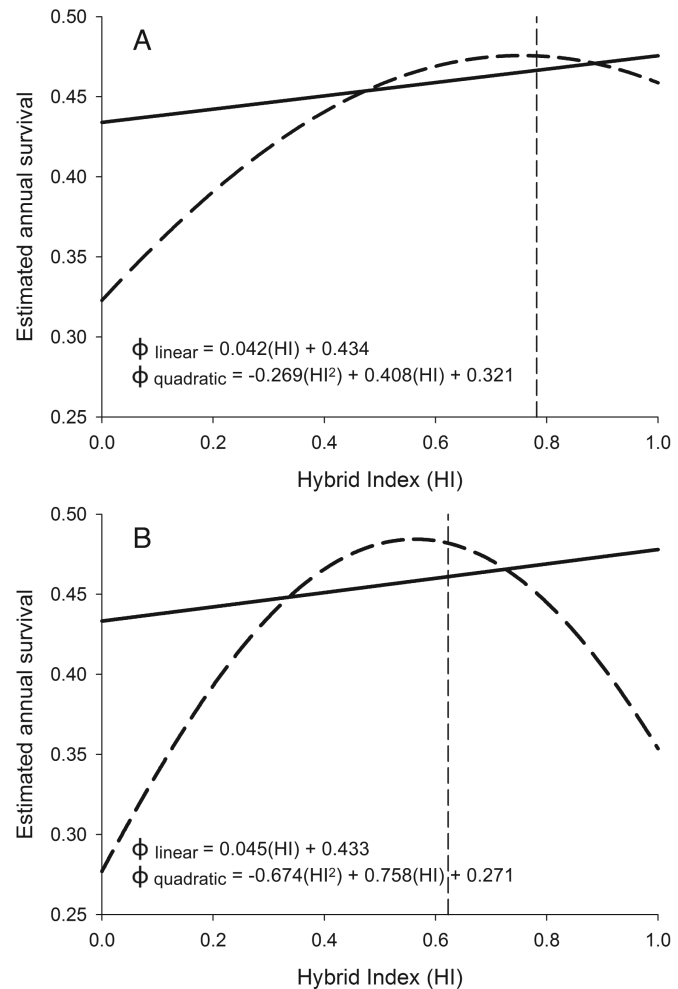


FIGURE 2. Estimated annual apparent survival of adult Northern Flickers at Riske Creek, British Columbia, between 1998 and 2006 based on linear (solid line) and quadratic (dashed line) relationships of the hybrid index (HI) for (A) pooled plumage trait scores (HI_A) and (B) tail color score (HI_B). The vertical dashed line indicates the population mean for each HI, and HI ranges from 0 (pure Yellow-shafted Flicker) to 1 (pure Red-shafted Flicker).

Although North American effects of NAO are centered over the eastern United States and Canada (Wallace and Gutzler 1981), Nott et al. (2002) found relationships between winter NAO and reproductive success for temperate migrants breeding in the Pacific Northwest. Therefore, it is reasonable that NAO also influences western areas of the continent, where flickers from our population at Riske Creek seem to overwinter, and influences survival patterns and other activities in the annual cycle such as migration (Flockhart and Wiebe 2007). For such migrating species, the dynamics of so-called stable hybrid zones could be greatly influenced by continental weather patterns that vary annually because such weather may affect the time and location that individuals settle to breed.

Furthermore, these large-scale weather patterns could influence ecological variables, such as temperature and moisture, hypothesized to affect fitness of flickers according to the bounded-hybrid superiority hypothesis (Moore 1977, Moore and Price 1993). Such selection gradients have been considered static on the landscape but may not be static from year to year.

Survival of hybrids under natural conditions is insufficiently studied because the best estimates require long-term data, large sample sizes, and great effort to resample (re-sight) individuals. Nevertheless, one needs to measure both survival and fecundity to estimate fitness because the parameters sometimes show conflicting patterns. For example, Rowher (2004) used age ratios to determine that survival of pure Townsend's Warblers (*Dendroica townsendi*; $\Phi = 0.65$) and hybrids ($\Phi = 0.65$) was lower than that of pure Hermit Warblers (*D. occidentalis*; $\Phi = 0.73$). Despite this, the range of Hermit Warblers is retracting because Townsend's are socially dominant and reproductively superior (Pearson and Rohwer 1998, 2000). Given that annual reproductive success does not differ among flicker phenotypes (DTTF and KLW, unpubl. data) and survival also does not seem to vary significantly, the overall fitness of hybrid flickers on our study area seems to be equivalent to parental types, and the tension-zone model can therefore be rejected as an explanation of the flicker hybrid zone. This agrees with Moore and Koenig (1986), who, although they did not measure survival, rejected the tension-zone model based on reproductive success of flickers in the southern part of the hybrid zone.

Recruitment, which is a function of both postfledging mortality and natal philopatry, is difficult to measure in open populations when juveniles disperse great distances. We did not model survival of fledglings because it is clear that the 3.6% return rate of nestlings to the local population is mainly a result of high dispersal. Since no banded fledglings were subsequently recovered breeding outside our study area, it is impossible to test whether natal dispersal distances differ among phenotypes. Assuming it does not, the fact that the phenotypes of local recruits was the same as the phenotypes of the fledging cohort the previous year suggests no differences in survival of fledglings according to phenotype. In other words, there is no evidence that postfledging mortality differs according to hybrid status and, in particular, hybrids do not suffer increased mortality through obvious genetically based (endogenous) selection.

Understanding natal dispersal, settlement, and survival is necessary to understanding the stability of hybrid zones and how selection operates in them. Where there is selection against hybrids, individuals dispersing in a hybrid zone limit the width of the zone (Barton and Gale 1993) and also introgression of genes. On the other hand, hybrid zones explained by hybrid superiority should be located in vegetation transition areas (i.e., ecotone habitats), where exogenous

(environmental) selection should favor hybrid individuals (Moore 1977, Barton and Hewitt 1985). In this case, dispersal should be independent of zone width because the zone is dictated by ecological parameters; however, selection will favor individuals that do not disperse outside the habitats to which they are best adapted.

In contrast to many other studies of hybrid zones such as in mammals (*Thomomys* spp.; Hafner et al. 1983), anurans (*Bombina* spp.; Szymura and Barton 1986), and plants (*Pinus* spp.; Millar 1983), where dispersal distances per generation do not exceed the width of the zones, flickers seem to have high dispersal abilities. Although the width of the flicker hybrid zone nears 300 km in most places (Wiebe and Moore 2008), it is certainly narrower in areas of Nebraska and Alberta. Average natal dispersal distances of flickers have been estimated at 100 km, but this is based on only three individuals (Moore and Buchanan 1985). Regardless, gene flow appears to be high in this species (Grudzien et al. 1987). With such a large proportion of offspring dispersing long distances, we should expect and have recorded pure Yellow-shafted (1 of 631) and especially Red-shafted Flickers (43 of 631) yearling immigrants settling and recruiting locally into our population.

In sum, we found no differences in survival according to phenotype among a population of flickers in the northern part of the hybrid zone. Together with equivalent reproductive success among phenotypes (DTTF and KLW, unpubl. data), these data fail to support the tension-zone model, which stipulates that hybrids are inferior. Although our results do not disprove the bounded-hybrid superiority hypothesis, neither do they provide strong support for it; if we did not find that hybrids were superior, we should have at least documented lower survival of Yellow-shafted Flickers relative to Red-shafted Flickers given the position of our study area on the hybrid gradient. Perhaps small survival differences among phenotypes do exist and we could just not detect them, but one wonders about the role of such small exogenous selection given the large apparent influence of other factors, such as weather, on survival and settlement of flickers in the north. Admittedly, a more powerful approach would be to compare survival in multiple populations along a transect across the hybrid zone, but this is nearly logistically impossible given the geographic and temporal scales required.

Therefore, although we cannot completely dismiss that the bounded-hybrid superiority hypothesis operates in the north, exogenous selection gradients appear to be patchier on the landscape and more temporally unpredictable in intermountain habitats of British Columbia (Wiebe and Bortolotti 2001) compared to the Great Plains in the United States (Moore and Price 1993). In the future, survival analyses should be conducted on resident flickers on the Great Plains to investigate whether stronger selection gradients in southern zone could lead to greater differences in survival among phenotypes there, and explain the persistence of the hybrid zone.

ACKNOWLEDGMENTS

We thank K. Dufour for analytical suggestions and W. S. Moore, B. K. Sandercock, and two anonymous reviewers for comments on an earlier draft. DTF was supported by a Graduate Scholarship and Graduate Teaching Fellowship from the University of Saskatchewan. This study was funded by an NSERC discovery grant to K.L.W.

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