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ABSENCE OF REPRODUCTIVE CONSEQUENCES OF HYBRIDIZATION IN THE NORTHERN FLICKER (*COLAPTES AURATUS*) HYBRID ZONE

D. T. TYLER FLOCKHART¹ AND KAREN L. WIEBE

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

ABSTRACT.—Two subspecies of Northern Flicker (*Colaptes auratus*), Yellow-shafted Flicker (*C. a. auratus*) and Red-shafted Flicker (*C. a. cafer*), form a hybrid zone that stretches the length of North America and is apparently stable. The most widely accepted hypothesis for the zone, the “bounded-hybrid superiority” hypothesis, predicts that the fitness of hybrids should be equal to or higher than that of parental types within the hybrid zone. We compared the reproductive performance at various stages of the reproductive cycle among Northern Flickers of different phenotypes at a location in the hybrid zone in which individuals are predominantly reddish. Individuals with red and yellow coloring showed similar levels of aggression toward taxidermy models of pure Red-shafted and Yellow-shafted flickers, and there was no association between phenotype (color class) and the likelihood of winning agonistic contests. In addition, the color of the male and female parents was not related to nest initiation date, clutch size, hatching success, risk of predation, or number of fledglings. These results do not support the tension-zone model, which predicts lower fitness of hybrids, but neither do they strongly support the concept of hybrid superiority, because all phenotypes had equivalent reproductive success. Annual changes in selection pressure, such as those caused by weather, could mask fitness differences between red and yellow individuals measured at a single geographic location and result in a hybrid zone that is variable in location and width over time. *Received 11 May 2008, accepted 8 December 2008.*

Key words: “bounded-hybrid superiority” hypothesis, *Colaptes auratus*, fitness, hybridization, Northern Flicker, reproductive success, territory defense.

Ausencia de Consecuencias Reproductivas de la Hibridación en la Zona Híbrida de *Colaptes auratus*

RESUMEN.—Dos subespecies de *Colaptes auratus*, *C. a. auratus* y *C. a. cafer*, forman una zona de hibridación que cubre toda la longitud de Norte América y es aparentemente estable. La hipótesis más ampliamente aceptada para esta zona, la de la superioridad limitada de los híbridos, predice que la adecuación de los híbridos debería ser igual o mayor a la de los tipos parentales dentro de la zona de hibridación. Comparamos el desempeño reproductivo en varias etapas del ciclo reproductivo entre aves con fenotipos distintos en una localidad de la zona de hibridación en la que los individuos son predominantemente rojizos. Los individuos con coloración roja y amarilla mostraron niveles de agresión similares ante modelos taxidérmicos representativos de individuos puros de ambas subespecies, y no existió una asociación entre el fenotipo (clase de color) y la probabilidad de ganar encuentros agresivos. Además, el color de los padres (macho y hembra) no estuvo relacionado con la fecha de iniciación de los nidos, el tamaño de la nidada, el éxito de eclosión, el riesgo de depredación o el número de volantones. Estos resultados no apoyan el modelo de zona de tensión, que predice una adecuación menor para los híbridos. Sin embargo, tampoco apoyan fuertemente el concepto de superioridad de los híbridos porque todos los fenotipos presentaron éxito reproductivo equivalente. Los cambios anuales en las presiones de selección, como aquellos causados por el clima, podrían enmascarar las diferencias en adecuación entre individuos rojos y amarillos estudiados en una sola localidad geográfica, y conducir a una zona de hibridación variable en ubicación y amplitud a través del tiempo.

WHEN TWO SPECIES interbreed in a hybrid zone, the relative fitness of the hybrids determines the persistence and stability of the zone (Barton and Hewitt 1985, Hewitt 1988, Price 2007), and it is important to understand the mechanisms involved (Buggs 2007). If hybrids are inferior and one parental type has higher

reproductive success than the other, the zone could move as a result of competitive exclusion (e.g., fitness-asymmetry model; Rohwer and Wood 1998). Alternatively, zones may be stable, and two main explanations exist for stability. The tension-zone model predicts that naïve, dispersing parental-type immigrants

¹E-mail: dt.tyler.flockhart@gmail.com

interbreed in a narrow zone characterized by reduced hybrid fitness (Barton and Hewitt 1985). The second model, the “bounded-hybrid superiority” hypothesis (BHS), suggests that hybrids have fitness equal to or greater than that of parental types in the hybrid zone, as dictated by ecological selection gradients within the zone of contact (Moore 1977, Good et al. 2000); hybrids do well in the transitional ecotone habitats but poorly in areas occupied by pure parental types. However, variable environmental factors (e.g., weather) may cause fluctuating selection pressures in the short term that favor hybrids in some years and parental forms in others (Grant and Grant 1992). Fitness patterns between phenotypes are, therefore, the primary measure to distinguish between hypotheses for hybrid zones.

The Northern Flicker's (*Colaptes auratus*) hybrid zone has been known for ≥150 years (Allen 1892) and is considered stable (Moore and Buchanan 1985). Mating according to phenotype appears to be random in the southern part of the zone (Bock 1971, Moore 1987) and weakly assortative in the north but not driven by active choice (Wiebe 2000, Flockhart and Wiebe 2007), so there are numerous mixed pairs. Although Moore and Koenig (1986) documented that hybrid males had reduced brood size, they concluded that the analysis suffered from type I error. This apparent lack of fitness differences among phenotypes and the fact that the geographic location of the zone corresponds to environmental gradients make the BHS the leading hypothesis (Moore and Price 1993). Small sample sizes and the inability of previous studies to control for important factors such as age and annual variation that affect reproductive output (e.g., Smith et al. 2006) motivated our study of the reproductive success of Northern Flickers in a more northern population in which survival is not affected greatly by phenotype (Flockhart and Wiebe 2008).

Because of logistical constraints, fitness is usually estimated by surrogates, such as reproductive success (Grant and Grant 2000), and usually by one or two simple parameters such as clutch size or number of fledglings. However, a better understanding of mechanisms can be gained by quantifying reproductive performance at several pre- and postzygotic stages, for example infertility, embryonic mortality, developmental abnormalities, and incompatible behavior (Lanyon 1979, Kruuk et al. 1999, Veen et al. 2001). It is known that hybrid Northern Flickers are fertile, so comparing the reproductive performance of phenotypes in a hybrid zone should provide insight into (1) how the zone is maintained and (2) potential movement of the zone.

Several mechanisms can influence reproductive success in a hybrid zone. Social selection against the rare phenotype (Price 2007) predicts that yellow Northern Flickers, the less abundant phenotype on our study area, should be ignored as mates by red Northern Flickers, but this does not occur (Flockhart and Wiebe 2007). Behavioral dominance and the competitive ability to acquire territories and mates are important in determining reproductive success in avian hybrid zones of ducks (Brodsky et al. 1988), warblers (Pearson 2000, Leichty and Grier 2006), and chickadees (Bronson et al. 2003b). Dominance of individuals within a hybrid zone is often determined by comparing measures of aggression against experimentally presented models with different phenotypes (e.g., Pearson and Rohwer 2000, McDonald et al. 2001). If phenotype is important in aggressive responses, any differences should be most obvious when considering interactions between

the pure parental forms and not in hybrids that have a combination of phenotypic traits (Pearson and Rohwer 2000).

First, we tested for differences in levels of aggression between yellow and red Northern Flickers experimentally presented with taxidermic models of the subspecies Yellow-shafted Flicker (*C. a. auratus*) and Red-shafted Flicker (*C. a. cafer*). If one parental type is innately more aggressive than the other, we predicted that it would react more strongly to any color of model “intruder” other than the other parental type. If one parental type is likely to defer in contests, we predicted that it would react more strongly to a model of its own color than to a model Northern Flicker of the other color. Second, we tested for differences in reproductive performance among phenotypes of Northern Flickers at one geographic location within the hybrid zone. We examined several reproductive parameters, including territory retention, clutch initiation date, clutch size, nest-ing success, hatching success, and fledging success.

METHODS

Study site and species.—Yellow-shafted Flickers of eastern North America and Red-shafted Flickers of western North America interbreed in a wide hybrid zone that roughly parallels the Rocky Mountains for thousands of kilometers (Wiebe and Moore 2008). Northern Flickers in the hybrid zone usually show a mixture of intermediate plumage traits, the most obvious being the color of wings and tail. We studied Northern Flickers near Riske Creek, central British Columbia (51°52'N, 122°21'W), at approximately the 80% transition isocline between Yellow-shafted and Red-shafted flickers (see map in Wiebe and Moore 2008), where most individuals are reddish but many show hybrid traits (Erskine 1962, Wiebe and Bortolotti 2001). About 100–150 pairs have been monitored annually on the study area, which encompasses ~100 km² of grasslands and mixed forest and where Northern Flickers nest at high densities in discrete Quaking Aspen (*Populus tremuloides*) tree clumps. About 21% of nests fail annually because of predators such as Red Squirrels (*Tamiasciurus hudsonicus*) and competitors such as European Starlings (*Sturnus vulgaris*) (Wiebe 2003, Fisher and Wiebe 2006).

Calculating a hybrid index.—Breeding adults were captured in a net placed over the entry hole to the nest either during incubation or as they provisioned young. Adults were color-banded, to enable individual recognition, and aged, weighed, measured, and scored on various plumage attributes. Northern Flickers can easily be sexed by plumage and were assigned to an age category of 1, 2, or ≥2 years on the basis of feather molt (Pyle 1997). Between 1998 and 2006, both adults were banded at >95% of nests each summer.

Because phenotypic indices usually reflect genotypes at least in ordinal rankings (Shriver et al. 2005), we summed the scores of five plumage traits: throat, ear, nape, tail color, and malar patch (males only) using categories for each trait that ranged from 0 for a pure Yellow-shafted Flicker to 4 for a pure Red-shafted Flicker, following Short (1965). These scores were standardized from 0 (pure Yellow-shafted Flicker) to 1 (pure Red-shafted Flicker) to form the hybrid index (HI; see Flockhart and Wiebe 2007). An individual's HI did not change over time, and the scoring of HI and plumage traits was repeatable (Flockhart 2007). Individuals were categorized as yellow (HI < 0.33), orange (0.34 < HI < 0.66), or red (HI > 0.67), and pairs were categorized by the difference between the male and female HI as more ($|\Delta\text{HI}| < 0.33$) or less similar ($|\Delta\text{HI}| > 0.33$).

Agonistic behavior.—During territory establishment, Northern Flickers of the same sex often engage in conspicuous agonistic displays that involve “mock” fencing duels with bills and flicking the bright undersides of wings and tail toward the opponent (Wiebe and Moore 2008). These “wicka-dances” can last several hours and may result in chases through the trees or direct physical fights. We monitored territory turnover and intrasexual agonistic interactions (wicka-dances and chases) during 2005 and 2006 and classified these interactions collectively as “contests.” Starting shortly after birds arrived on the study area after migration in the last two weeks of April, we censused breeding territories using tape-recorded territorial calls and recorded the general phenotype (yellowish, orangish, reddish) and sex of responding individuals (Flockhart and Wiebe 2007). A given territory was revisited, on average, every four or five days for two weeks. A territory turnover was recorded when a bird with a different phenotype was observed subsequently on that territory. By this method we may have missed some turnovers between two birds of similar phenotypes, but our goal was to test for a directional shift between different color classes that differed from random. If two individuals were initially detected on a territory, we recorded both and then considered the phenotype that remained on the territory, or that was trapped at the nest in a subsequent visit, the winner. For wicka-dances and chases, we classified the phenotype that was the aggressor as the winner. We recorded both male–male and female–female interactions, and we pooled all observations over both years because of small sample sizes.

Experimental tests of aggression toward models.—Defense of nesting trees and parental attentiveness increase during egg laying (Wiebe 2008), so we presented all models during the egg-laying stage when there were at least two eggs. The taxidermy models were either pure yellow-shafted ($HI = 0$) or pure red-shafted ($HI = 1$) and were presented to yellow and red male territory-holders using a paired experimental design. We chose territory holders that were phenotypically as purely yellow- or red-shafted as possible, and although pure Yellow-shafted Flickers were rare, the chosen yellow males all had yellow rectrices and scored in the most yellow 28% of the index. We used two red and two yellow taxidermic models (the model used in a trial was determined randomly), but it was not logically possible to have a new model for each trial. The model birds were prepared in an upright posture with the head to one side to display the face and malar patch, whereas the tail and wings were slightly spread to show the conspicuous undersides of the remiges as is common in wicka-displays. The order of model-color presentation was also randomly assigned and separated by at least one day. All trials were conducted by the same observer (D.T.T.F.).

A model was placed on a wooden stake ~1.5 m above the ground and ~5 m in front of the cavity entrance, where a returning territorial Northern Flicker should see it easily. To make the models more lifelike, we jiggled them slightly with an attached fishing line. A 5-min silent period at the beginning of the trial was followed by a 5-min territorial call from a tape recorder placed beneath the model. The vocalizations used were recorded in California and presumably were from Red-shafted Flickers (Cornell Lab of Ornithology 1999); however, vocalizations are not believed to differ between Northern Flicker subspecies (Wiebe and Moore 2008), so our results should not be biased. Reactions of the territorial males were observed from a camouflage blind 10–20 m from the cavity entrance, which did not seem to inhibit Northern

Flicker responses, because several times territorial males landed <2 m from the observers between the model and the blind.

Trials lasted for ≤15 min or until the territorial male struck the model. We started to record the “response time” from when we thought the territorial male could see the model and used this time to calculate rates of agonistic responses. We assumed that a more aggressive (and potentially dominant) male would attack more frequently, approach the model more closely, and exhibit more agonistic behaviors (Rohwer 1982, Fisher and Wiebe 2006). We recorded a variety of aggressive calls and responses, but because of small sample sizes in each behavior category, we calculated “pooled behaviors” as the sum of *peahs*, *wickas*, and *whurdles* (i.e., territorial vocalizations; Wiebe and Moore 2008) and tree drums and bill fences. We also recorded whether the territorial male blocked the cavity, whether it struck the model, the minimum distance it moved toward the model, and its mean distance from the model using 30-s intervals. Minimum distance and pooled behaviors were analyzed with nonparametric Wilcoxon signed-rank tests because they were non-normal. Binary data (cavity blocking and striking model) were analyzed with McNemar change tests that compare paired proportions of the same subject under two different conditions (model color) using dichotomous response data (yes–no; Siegel and Castellan 1988). Mean distance was log-transformed and analyzed with repeated-measures analysis of variance (ANOVA; Zar 1999).

Reproductive success.—Active cavities were monitored with a mirror and flashlight every three to four days to determine laying date, clutch size, hatching date, nest fate (successful or depredated), and number of fledglings. A small replaceable door was cut into the tree trunk to allow access to the eggs and nestlings. Because there were no extrapair copulations in Northern Flickers (Wiebe and Kempenaers 2009), reproductive parameters should not be influenced by females searching for better genetic partners (e.g., Veen et al. 2001, Reudink et al. 2006).

Reproductive success could vary with the phenotype of either the male or the female or could be influenced by the degree of phenotypic difference between members of the pair. Therefore, for each dependent variable, we conducted two ANOVAs, the first with both male and female color category (yellow, orange, or red) and the second with the difference between the HI of members of a pair (more vs. less similar). Because the BHSH and tension-zone models predict that the fitness of hybrids is greater or less than that of both parental types and are best represented as quadratic functions, we graphed all data and checked for nonlinear trends, but none was apparent. Therefore, we used general linear models for the dependent variables: laying date (first clutches only), clutch size (all complete clutches), and number of fledglings (for nests with ≥1 fledgling). We controlled for parental age and year in the models by entering them as covariates. Initial models included all two-way interactions, but nonsignificant effects were eliminated in a backward-stepwise procedure to obtain a final model. A few pairs returned to breed in subsequent years, but analyses with and without such pairs were qualitatively the same, so we retained all samples (Flockhart and Wiebe 2007).

Hatching success (brood size–clutch size, for nests that hatched ≥1 egg) and fledging success (number of fledglings–brood size, for nests that fledged ≥1 nestling) were arcsine transformed and analyzed with Kruskal-Wallis tests between the color categories of males, females, and pairs. Finally, we analyzed a binary

variable “nest success” (i.e., whether or not ≥ 1 nestling fledged) with a forced-entry logistic regression containing the following independent variables: parental color, parental age, and year. Again, two-way interaction terms were included initially but were deleted if not significant. All data fit their respective model according to goodness-of-fit tests (Hosmer and Lemeshow 2000). Only first nesting attempts were considered, and all statistical tests were two-tailed and considered significant at $\alpha = 0.05$.

RESULTS

Aggression levels.—Of 47 natural aggressive interactions between Northern Flickers where we could designate phenotypes and a winner, no phenotype won more encounters than expected by chance (Table 1). We presented models to 21 red and 20 yellow territorial males over two summers. Model color was not associated with the probability of blocking cavities by either red (McNemar change test: $P = 0.29$) or yellow ($P = 1.0$) territorial males. Similarly, the likelihood of striking the model did not depend on model color for red males ($P = 0.5$), whereas there was a weak trend that yellow males struck red models more often than yellow models ($P = 0.07$). However, with model types pooled, yellow males did not strike models more often than red males ($\chi^2 = 0.4$, $df = 1$, $P = 0.58$), which suggests that one phenotype was not generally more aggressive. The minimum approach distance did not vary according to model color for red males ($Z = -1.54$, $P = 0.12$), but yellow males approached red models more closely than they approached yellow models ($Z = -2.99$, $P = 0.003$).

For mean distance, there was a significant interaction between phenotype of the defending male and model color ($F = 4.19$, $df = 1$ and 38, $P = 0.048$; Fig. 1), so we examined territorial red and yellow males separately. There was no significant difference in distance according to model color for red males ($t = 0.39$, $df = 20$, $P = 0.70$), but yellow males stayed closer to red models than to yellow models ($t = -3.67$, $df = 18$, $P = 0.002$). Red males did not behave differently according to model color ($Z = -1.01$, $P = 0.31$), but yellow males showed more aggressive agonistic behaviors toward red models ($Z = -1.98$, $P = 0.048$; Fig. 1). However, the average measure of aggression with model types pooled was not different between territorial red and yellow males ($Z = -1.33$, $P = 0.18$).

Reproductive success.—In all, 865 breeding attempts for which the phenotype of both parents could be determined were monitored between 1998 and 2006 at Riske Creek. After controlling for year, parental age, and laying date where appropriate, the phenotype of the male or female parent was not a significant predictor of laying date, clutch size, or number of fledglings (Table 2), but the sample

TABLE 1. The number of contests (agonistic behaviors and territory turnovers) won between pairs of Northern Flickers of different phenotypes at Riske Creek, British Columbia, 2005–2006. P values are from a binomial test ($P = 0.5$) to determine whether the winning phenotype won more contests than expected. The phenotype listed first won the most contests.

Phenotype interaction	n	Percentage of contests won	P
Red–Orange	25	60	0.42
Yellow–Red	17	59	0.63
Yellow–Orange	5	80	0.38

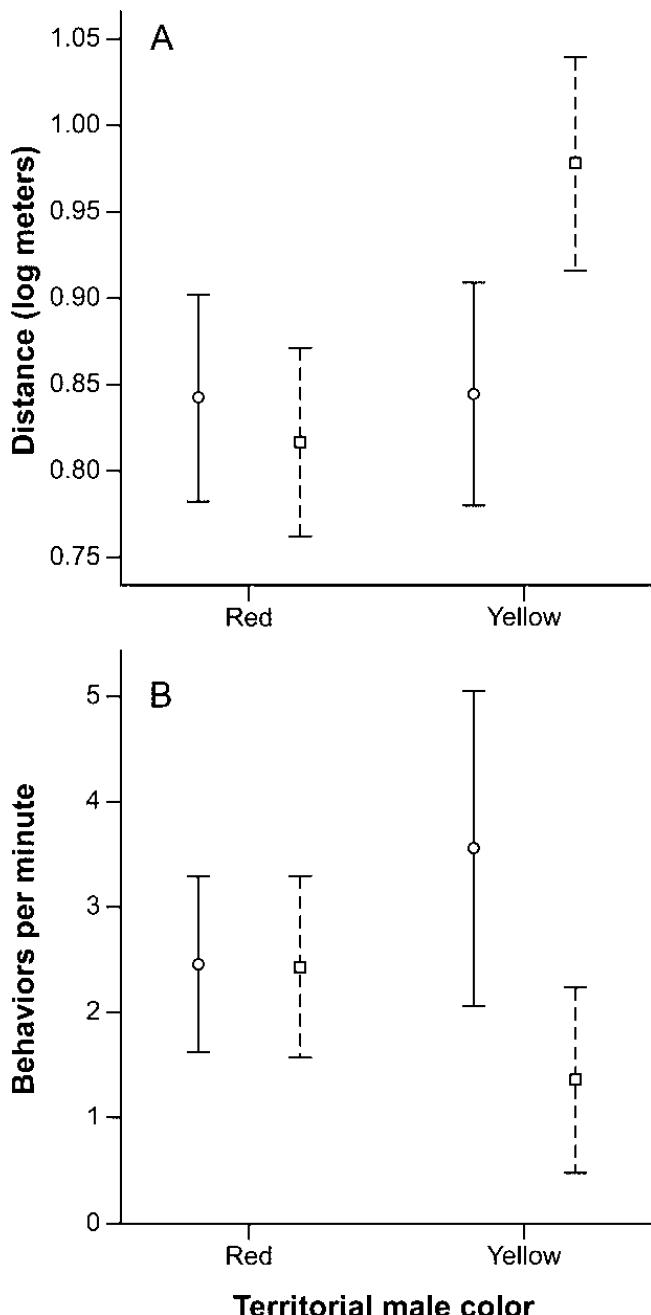


FIG. 1. Yellow territorial male Northern Flickers were more aggressive toward Red-shafted Flicker models than toward Yellow-shafted Flicker models: they approached them more closely (A) and had a higher rate of aggressive behaviors (B). Bars represent means (\pm SE) for responses to Red-shafted Flicker models (circles, solid line) and Yellow-shafted Flicker models (squares, dashed line) for red or yellow territorial male Northern Flickers. Behaviors include vocalizations, bill drums, and bill fences. Means of behavior rates are shown for illustration, but statistical tests were nonparametric (see text).

TABLE 2. ANOVA models for various reproductive parameters of Northern Flickers in the hybrid zone at Riske Creek, British Columbia. A hybrid index (HI) designates Northern Flickers as yellow, orange, or red (see text). Data are from 865 reproductive attempts monitored from 1998 to 2006. Only first nesting attempts are included.

Model, variable	df	MS	F	P
Laying date				
Male HI	2	47.28	0.87	0.42
Female HI	2	18.48	0.34	0.71
Male age	2	636.41	11.77	<0.001
Female age	2	390.80	7.23	0.001
Male age* female age	4	236.86	4.38	0.002
Year	8	452.66	8.37	<0.001
Clutch size				
Male HI	2	0.75	0.45	0.64
Female HI	2	2.11	1.27	0.28
Male age	2	7.37	4.44	0.012
Female age	2	4.04	2.43	0.089
Year	8	7.88	4.75	<0.001
Laying date	1	185.79	111.95	<0.001
Fledglings				
Male HI	2	0.06	0.02	0.98
Female HI	2	3.35	0.98	0.38
Male age	2	5.73	1.68	0.19
Female age	2	2.91	0.85	0.43
Year	8	5.48	1.60	0.12
Laying date	1	94.14	27.53	<0.001

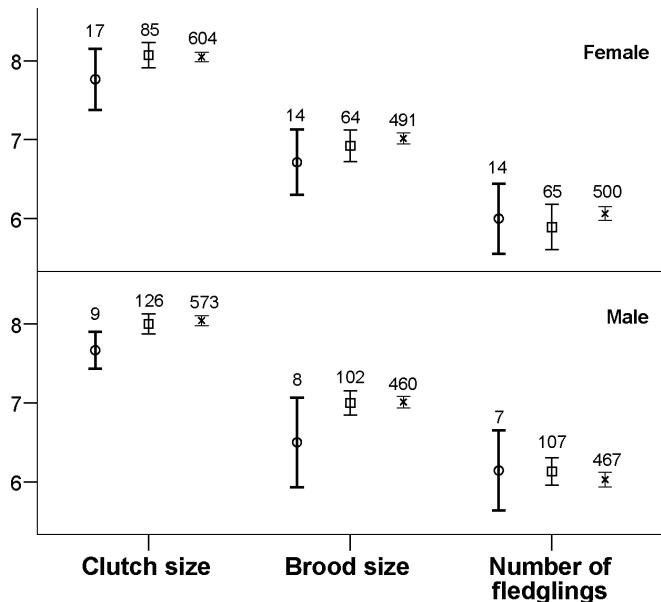


FIG. 2. Phenotype class of male (bottom panel) or female (top panel) parents was not related to reproductive output. Bars represent the mean (\pm SE) of reproductive parameters for yellow (circles, thick bar), orange (squares, medium bar), and red Northern Flickers (star, thin bar). “Clutch size” includes all first nesting attempts, whereas “brood size” and “number of fledglings” include only nests that hatched at least one egg. Sample sizes are above error bars.

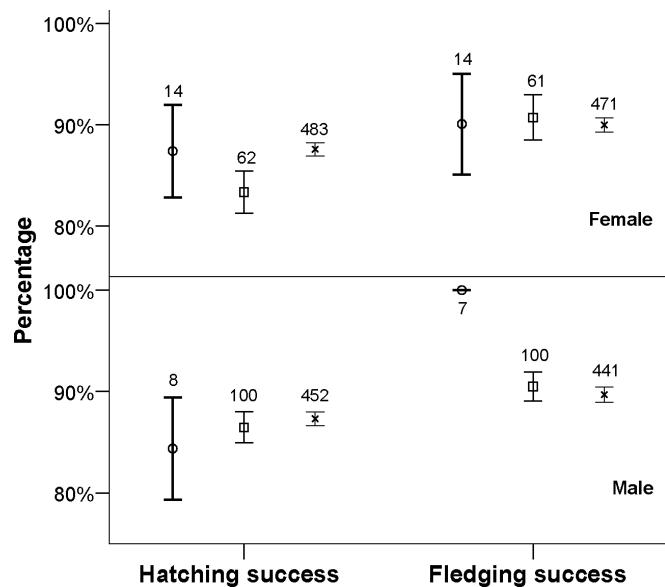


FIG. 3. Hatching and fledging success did not differ according to phenotype class of the male (bottom panel) or female (top panel) parent. Bars represent the mean (\pm SE) for yellow (circles, thick bar), orange (squares, medium bar), and red Northern Flickers (star, thin bar). “Hatching success” is brood size divided by clutch size and excludes failed nests. “Fledging success” is the number of fledglings divided by the brood size at hatching and excludes nests that failed to produce any fledglings. Sample sizes are above error bars.

size of yellow birds was small (Fig. 2). The difference in HI between members of a pair was not associated with laying date ($F = 0.76$, df = 1 and 678, $P = 0.38$), but there was a weak trend that more similar pairs had larger clutches ($F = 3.26$, df = 1 and 649, $P = 0.07$). The probability that a nest was successful or depredated was not associated with the phenotype of the male (Wald = 2.91, df = 2, $P = 0.23$) or the female (Wald = 5.02, df = 2, $P = 0.08$) or with the difference in pair phenotype (Wald = 0.01, df = 1, $P = 0.93$).

Hatching success was 80–90% (Fig. 3) and was not influenced by the male’s ($\chi^2 = 3.00$, df = 2, $P = 0.22$) or the female’s ($\chi^2 = 4.76$, df = 2, $P = 0.09$) phenotype or by the difference between pairs ($\chi^2 = 0.39$, df = 1, $P = 0.53$). Yellow males tended to have higher fledging success than other phenotypes ($\chi^2 = 5.61$, df = 2, $P = 0.06$; Fig. 3), because all pairs that had a yellow male fledged all offspring (Table 3).

TABLE 3. Fledging success (mean proportion \pm SE, with sample size in parentheses) of male and female Northern Flickers of different phenotypes in the hybrid zone at Riske Creek, British Columbia, 1998–2006. The color of the parents was determined by their hybrid index (see text). There were no pure yellow–yellow pairs.

	Female		
	Yellow	Orange	Red
Male			
Yellow	—	1.00 \pm 0.00 (2)	1.00 \pm 0.00 (5)
Orange	0.87 \pm 0.13 (5)	0.91 \pm 0.05 (16)	0.91 \pm 0.01 (78)
Red	0.92 \pm 0.03 (9)	0.90 \pm 0.03 (43)	0.90 \pm 0.01 (384)

Otherwise, fledgling success did not differ for females ($\chi^2 = 0.19$, $df = 2$, $P = 0.91$) or pairs ($\chi^2 = 0.12$, $df = 1$, $P = 0.73$). At the end of the brood-rearing period, there was no difference in the number of fledglings according to the color of either parent (Table 2 and Fig. 2) or the difference between members of a pair ($F = 0.01$, $df = 1$ and 547, $P = 0.93$).

DISCUSSION

Aggression and territory-holding potential.—Observations of Northern Flickers in the hybrid zone in central British Columbia suggested that phenotype was not associated with the ability to win an aggressive encounter or with higher reproductive success. The experimental presentation of models showed that overall aggression levels (model types pooled) of red versus yellow territory defenders did not differ. It could be that immigrant yellow Northern Flickers, as a rare phenotype, have difficulty defending territories because red Northern Flickers are not intimidated by them and, therefore, yellow birds may suffer lower fitness because of social selection (Price 2007). However, red Northern Flickers did not behave differently toward taxidermic models of different colors. Although yellowish males were slightly more agonistic toward red models than toward yellow ones, this does not necessarily suggest that yellow Northern Flickers could dominate red ones in the hybrid zone, because red Northern Flickers were more aggressive toward yellow models than yellow Northern Flickers were (Fig. 1), which indicates that an intruding yellow bird would face greater resistance from a red than from a yellow territory-holder. Some of the variation in responses to models is probably related to an individual's past history of encounters with certain phenotypes. For example, yellow defenders, which are less numerous on our study area, may behave more aggressively toward red intruders because they encounter them more often. In the future, it would be useful to replicate the model presentations in the core geographic ranges of both parental types to see whether any differences in responses to phenotypes may be learned and based on the frequency of contacting different phenotypes. We conclude that there is little difference in dominance or territory-holding potential between phenotypes of Northern Flickers.

Differences in ability to hold a territory or obtain a mate are common in other moving avian hybrid zones. Introgression that promotes one phenotype can occur through male dominance or female choice resulting in greater reproductive potential of individuals possessing genes characteristic of hybrids (McDonald et al. 2001, Stein and Uy 2006) or one parental type (Brodsky et al. 1988, Pearson 2000). McDonald et al. (2001) found that hybrid manakins (*Manacus candei* and *M. vitellinus*) were more aggressive than either parental type and suggested that hybrids with yellow collars received more mating opportunities; however, counterselection against hybrids later in the reproductive cycle appeared to restrict introgression and expansion of the manakin hybrid zone (Stein and Uy 2006). By contrast, the introgression of Carolina Chickadee (*Poecile carolinensis*) genes into the range of pure Black-capped Chickadee (*P. atricapillus*) genes may be driven by behavioral dominance of male Carolina Chickadees over male Black-capped Chickadees (Bronson et al. 2003b) and by the fact that females paired with male Black-capped Chickadees preferentially seek male Carolina Chickadees for extrapair copulations

(Reudink et al. 2006). Dominance unrelated to phenotype, a lack of strong mate choice for one phenotype, and a lack of differences in reproductive success all suggest that there is no directional movement of the Northern Flicker hybrid zone in the north related to fitness of the phenotypes.

Hybrid fitness.—At least until the time of fledging, we detected no significant differences in reproductive performance according to phenotype for either males or females, and there was little evidence that dissimilar pairs performed less well than similar pairs. This agrees with other studies of Northern Flicker reproduction from the southern part of the hybrid zone (Short 1965, Moore and Koenig 1986) and, together with the lack of a density trough within the hybrid zone (Moore and Buchanan 1985), provides strong evidence against the tension-zone hypothesis. Although there were few "pure" yellow Northern Flickers at Riske Creek, sample sizes of orange and red phenotypes were large and we were able to control for age and year effects, so a lack of statistical power cannot explain a failure to detect differences, at least between the latter phenotypes. Instead, models showed that male and female age, seasonal timing, and annual variation explained reproductive performance. Bronson et al. (2003a) used a strong experimental approach of reciprocal introductions of pure and hybrid chickadees across the contact zone and found reduced hatching success among hybrids due to genetic effects (endogenous selection), but such an experiment is unrealistic for Northern Flickers because of the large size of the zone and because Northern Flickers are migratory and breeding individuals may disperse widely.

Although the tension-zone hypothesis was not supported, neither did we find strong support for the BHSH, because hybrids did not perform better than parental types in the hybrid zone at any stage of nesting. Although equivalent fitness of all phenotypes at the center of the zone is consistent with the BHSH (see Moore and Price 1993), our study area is in the "red" side of the hybrid zone at about the 80% cline, and yet we did not find that yellow Northern Flickers had lower success than red Northern Flickers. The BHSH suggests that fitness of different phenotypes depends on environmental gradients across the hybrid zone, such as temperature, evapotranspiration rates, and precipitation, either directly or through adaptations to vegetation communities that are determined by climate variables (Moore and Price 1993). Several avian hybrid zones, including that of Northern Flickers, occur in the Great Plains (Rising 1983, Swenson and Howard 2004), which suggests a common environmental-gradient-based selection (exogenous selection) linked to geographic changes from the hot, dry west to the cool, moist east (Swenson 2006). However, Wiebe and Bortolotti (2001) suggested that the complex intermountain habitats characteristic of the northern portion of the Northern Flicker hybrid zone in British Columbia may lead to environmental gradients that are not as smooth or predictable as those in the south. Thus, it is unknown whether, or how, exogenous selection operates in the north.

Dynamics of the hybrid zone in the north.—Aspects of the hybrid zone in the north still remain a puzzle and are complicated because individuals here are migratory, not resident (Flockhart and Wiebe 2007). Along with the complex topography, annual variation in weather (temperature and precipitation) may be more extreme and unpredictable in northwestern North America than in the south. Therefore, exogenous selection gradients, which are an

assumption of the BSH, may be somewhat stochastic and selection pressures on phenotypes at any location may vary from year to year (see Grant and Grant 1992, Bell 1997). Pooling data across years may, therefore, obscure a relationship between phenotype and success, but we did not find any year*phenotype interactions in any analyses that suggested that weather influenced the relative success of phenotypes differently. By contrast, variable weather patterns influence pairing patterns (Flockhart and Wiebe 2007) and annual survival on our site (Flockhart and Wiebe 2008). However, nine years of data may not be sufficient to detect subtle shifts in selection associated with cyclic or variable weather patterns.

The lack of a difference in reproductive success among phenotypes suggests that there is no barrier to gene introgression and that the hybrid zone could widen in the north. Museum records indicate that the northern part of the Northern Flicker hybrid zone in Alberta may have shifted over time (McGillivray and Biermann 1987), but such detailed historical records for central British Columbia near our study area are lacking. What keeps the northern part of the zone stable, if indeed it is stable, remains unclear. It is possible that selection gradients as proposed by the BSH are sufficient to keep populations of Northern Flickers apart throughout much of their central and southern range, but the hypothesis may break down in northern regions with complex topography and migratory individuals.

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