

COMPARATIVE REPRODUCTIVE SUCCESS OF YELLOW-SHAFTED, RED-SHAFTED, AND HYBRID FLICKERS ACROSS A HYBRID ZONE

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ABSTRACT.—Alternative hypotheses of hybrid zones make specific predictions about reproductive components of fitness in the hybrids. The dynamic-equilibrium and reinforcement hypotheses are premised on reduced hybrid fitness, which should be apparent as reduced clutch or brood size or as increased embryonic mortality. The hybrid-superiority and introgression hypotheses predict normal clutch and brood size and embryonic mortality.

Reproductive success was measured at four study sites on a transect across the hybrid zone between the Yellow- (*Colaptes auratus auratus*) and Red-shafted (*C. a. cafer*) subspecies of the Northern Flicker. Two additional clutch size samples representing pure Yellow- and Red-shafted flickers were obtained from museum egg collections. Mean clutch size did not differ significantly among the six samples. Factorial ANOVAs showed that early clutches and broods are larger than late clutches and broods, but no significant difference was detected between hybrid and parental study sites. Analyses of the effect of phenotype (yellow-shafted, red-shafted, hybrid) also suggest that neither clutch size nor brood size is affected, with the exception that hybrid males sired significantly smaller broods. Finally, there were no significant effects of type of cross (red-shafted male \times hybrid female, etc.) on the ratio brood-size/clutch-size.

The only evidence for reduced hybrid fitness was in the test where males with hybrid phenotypes appear to have sired small broods. This may indicate that abnormal behavior of hybrid males affects female fecundity, but it is also plausible that this marginally significant result is a type I statistical error. The overall lack of evidence for reduced hybrid fitness is inconsistent with either the dynamic-equilibrium or reinforcement models. Of the two remaining alternatives, the bounded hybrid-superiority model appears the more likely explanation of the Northern Flicker hybrid zone because earlier work (Moore and Buchanan 1985) showed that the hybrid zone is not becoming broader, as predicted by the introgression model. Received 20 February 1985, accepted 2 July 1985.

HYBRID zones often occur between avian populations that have diverged to near the species level but retain contiguous distributions as a result of either secondary contact or parapatric divergence (Short 1969, Moore 1977, Rising 1983a). Typically, hybridization is rampant in the zone but the zone itself is very narrow and seems to act as a barrier separating markedly divergent plumage patterns or song types, or both. Furthermore, the biogeography of most avian hybrid zones suggests that they arose in antiquity, probably as a result of Pleistocene glaciation, and therefore seem to be evolutionarily stable configurations (Short 1970, Moore 1977; but see Barrowclough 1980).

Three theories have been proposed to explain the existence of stable hybrid zones. Moore (1977) suggested that hybrid zones represent secondary contacts between taxa that had

diverged in isolation but not to the extent that hybridization would disrupt distinctly co-adapted gene complexes resulting in hybrid breakdown or hybrid unfitness. He further suggested that the secondary contact was established as distinct ecological communities expanded from refugia to form a "suture zone" in the sense of Remington (1968) and that the genes of the divergent characters are either adapted in their respective communities or closely linked to genes that are. The hybrid zone persists, then, because it occurs in an ecotone in which neither parental taxon is particularly well adapted. This was termed the hybrid-superiority model, although *bounded* hybrid superiority is more apt because it implies that hybrid superiority is restricted geographically.

Barton (1979) and Barton and Hewitt (1981)

developed an alternative hypothesis that explains stable hybrid zones by balancing opposing forces. The essential feature of the Barton-Hewitt *dynamic-equilibrium model* is hybrid unfitness, which prevents the hybrid zone from becoming broader through introgressive hybridization; less-fit hybrids form a narrower hybrid zone. Barton (1979) showed that hybrid unfitness itself can fix the width of the hybrid zone and further showed that variations in population density could prevent the hybrid zone from "flowing" geographically.

The third alternative is that the hybrid zone appears stable only to a short-lived observer but actually is growing broader through introgressive hybridization or becoming more restricted as premating reproductive isolation is reinforced by selection against hybrids (Wilson 1965, Remington 1968). Whether introgression or reinforcement is expected would depend on whether hybrid phenotypes are at least as fit as the parental phenotypes or less fit, respectively.

The three alternatives provide radically different explanations of hybrid zones, each with its own implications for speciation theory. Furthermore, the alternatives appear to be testable, as the dynamic-equilibrium and reinforcement models predict some measure of hybrid breakdown, whereas the hybrid-superiority and introgression models do not. More precisely, according to the dynamic-equilibrium and reinforcement models, one would expect increases in infertility and development aberrations in hybrid phenotypes. The pairs of alternatives can be tested further by studying the historical stability of the hybrid zone.

The idea that hybridization between distinctly coadapted gene pools results in hybrid breakdown is an old idea in evolutionary biology that is of particular importance to speciation theory. Collectively, the assorted maladies that are expected to result are termed postmating reproductive isolating mechanisms. Although hybrid breakdown could manifest at any stage in the life cycle, the maladies most often mentioned affect the early development or fertility of hybrid phenotypes. Thus, where natural hybridization has disrupted coadapted gene complexes, one would expect higher frequencies of developmental anomalies and reduced fertility. In birds this should appear as reduced brood and clutch sizes, respectively.

We report clutch- and brood-size data for four

populations of the Northern Flicker (*Colaptes auratus*) along a transect across the hybrid zone between the Yellow- and Red-shafted flickers (*C. a. auratus* and *C. a. cafer*) in western Nebraska and eastern Wyoming. The two central locales support hybrid populations, whereas the distal locales represent parental populations (see Fig. 1). Our purpose is to determine whether hybridization between these well-marked subspecies has disrupted coadapted gene complexes and whether hybrid breakdown is essential to understanding this hybrid zone. Data pertaining to historical stability were reported earlier (Moore and Buchanan 1985).

The structure of the hybrid zone has been reported by Short (1965) and Moore and Buchanan (1985). To summarize briefly, the Yellow-shafted Flicker is broadly distributed in diverse woodland types across eastern North America, whereas the Red-shafted Flicker is the western North American counterpart. The hybrid zone occurs on the western Great Plains, primarily in riparian woodlands (cottonwood, peach-leaved willow, and green ash) but also in the coniferous forests of the Black Hills, the Pine Ridge region of Nebraska and South Dakota, and in the Cypress Hills of Saskatchewan. The hybrid zone may be continuous in the solidly forested montane regions of Alberta, British Columbia, and southern Alaska (Short 1965, Moore pers. obs.). The two subspecies exhibit contrasting conditions for 6 (5 in females) plumage characters; e.g. red-shafted males have a red malar stripe, whereas that of the yellow-shafted is black. Hybrids exhibit intermediate variations. These characters are easily scored, even with binoculars. Mating is random with regard to the plumage characters (Short 1965, Bock 1971, Moore and Buchanan 1985). The hybrid zone varies in width and is asymmetrical, with introgression evident farther west of center than east (see Fig. 1). Population densities are uniformly high along the study transect (Moore and Buchanan 1985).

MATERIALS AND METHODS

Active nests were located throughout May and June in 1981–1984 at four study sites on a transect across the hybrid zone (Fig. 1). The study sites are: Sutherland (James Haugland farm on the south bank of the South Platte River between the river and interstate highway I-80, 1.75 km south-southeast of Sutherland, Lincoln Co., Nebraska, R33W, T14N, secs. 32, 33); Bridgeport (Blanchard-Lindgren ranch on the

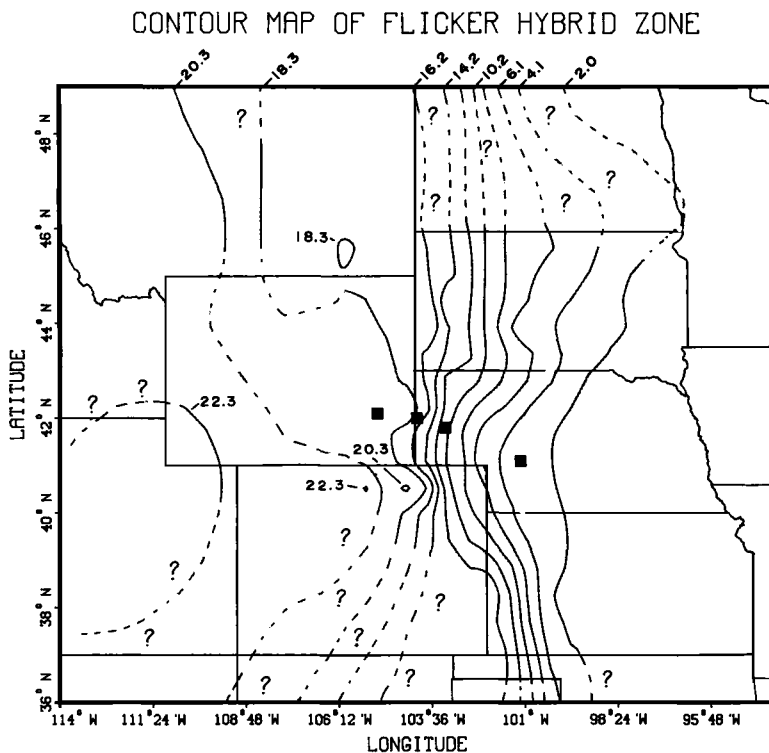


Fig. 1. Provisional contour map of the Northern Flicker hybrid zone on the western Great Plains. The solid squares mark the four live-study sites (from east to west: Sutherland, Bridgeport, Morrill, and Wheatland). The contour levels indicate the transition in Short's (1965) hybrid index (HI) from yellow-shafted in the east (HI = 0) to red-shafted in the west (HI = 23). The dashed contours and question marks indicate poorly collected areas that cannot be accurately mapped. The map is accurate in the region of the live-study sites.

south bank of the North Platte River, 7.5 km west-northwest of Bridgeport, Morrill Co., Nebraska, R51W, T20N, secs. 21, 22, 23); Morrill (north bank of the North Platte River, 4.8 km west-northwest of Morrill, Scottsbluff Co., Nebraska, R58W, T23N, secs. 13, 14); and Wheatland (Laramie River at the confluence of Sybille Creek, 13 km west-northwest of Wheatland, Platte Co., Wyoming). Bridgeport and Morrill were established as study sites in 1981; Sutherland and Wheatland were not established until 1982.

Nest cavities were reached with the aid of a 9.6-m extension ladder and climbing gaffs where necessary. Cavity interiors were viewed with a 6-cm circular mirror on a handle and a penlight.

The following data were collected for each nest: score for each plumage character for both parents (see below), clutch size, brood size, and, when possible, date when the first egg was laid.

Clutch size.—It was necessary to establish that the clutches were complete at the times of the final counts. With rare exceptions, flickers lay one egg per day (Sherman 1910, Moore pers. obs.). To establish com-

pleteness, the eggs in a given nest were counted over several days as laying progressed and incubation began. When clutch size remained the same for at least two successive days, the clutch was considered complete. In some cases it was apparent that the clutch was complete at the time the nest was discovered because clutch size did not increase or the eggs hatched in less than 11 days, the normal incubation period for flickers (Sherman 1910, Moore pers. obs.).

Brood size.—An access port was cut into the nest cavity during the brooding period. At that time, the hatchlings were banded and counted, and the adults were trapped, banded, and scored phenotypically. Usually, the access port was cut and the hatchlings banded in the afternoon of one day, and the adults were trapped the following morning. Adults were trapped in the nest cavity by a remote-activated trap door modified from a common rat trap. The trapped adult was then removed through the access port. Follow-up observations on numerous nests suggest that the trapping and banding activities did not permanently disrupt the nesting process; nevertheless,

brood size was based on the number of hatchlings in the nest at the time it was first disturbed rather than the number that subsequently fledged. The ages of the broods at the time hatchlings were counted varied between 10 and 17 days after hatching.

In most cases, Short's (1965) hybrid index (HI) was determined for both adults at the time the nest was discovered. This initial phenotypic determination was done by observing the adults around the nest with binoculars. In those cases where the adults were subsequently trapped, the HI was redetermined on the bird in hand. Priority was given to HIs determined on hand-held birds, but in some cases when it was not possible to trap one of the adults (usually the female), the HI determined using binoculars was used. The concordance between scores determined using binoculars and in the hand was strong.

Short's (1965) hybrid index is based on 6 plumage characters in males. The 6 characters are listed according to the following format: character (abbreviation, *auratus/cafer*), where *auratus* and *cafer* represent the relative states for the parental subspecies. The plumage characters are: crown color (CROWN, gray/brown); ear covert (EAR, brown/gray); throat color (THROAT, brown/gray); red nuchal patch (NUCHAL, present/absent); shaft color (SHAFT, lemon-yellow/salmon-red); and malar stripe (MALAR, black/red). All of these characters except MALAR can be scored in females; females lack the malar stripe. Each character is given an integer score on the scale 0-4, where 0 and 4 represent the *auratus* and *cafer* parental states, respectively, and the integers 1-3 represent proportionally intermediate conditions. In theory, then, pure *auratus* males and females would have HIs of 0, and *cafer* males and females would score 24 and 20, respectively. In practice, however, CROWN scores are never higher than 3 in this portion of the species range. We reserved the score of 4 for the deeper brown crown color of the northwestern race (Short 1965), but this variation appears unrelated to hybridization. In any case, pure red-shafted males and females would have hybrid indices of 23 and 19, respectively, at the latitude of our transect.

Because some nests were depredated after clutch size was determined and others were found after the eggs hatched, there is variation in sample size for clutches and broods. Sample sizes are given in the results section in the context of specific tests. SPSS (release 9.2) was used to perform statistical tests (Nie et al. 1975).

Sutherland and Wheatland were intended to serve as yellow-shafted and red-shafted reference samples, respectively. However, there is some evidence of introgression at both localities. Two additional reference samples were extracted from the clutch-size data compiled by Koenig (1984). One sample represents pure yellow-shafted and includes clutches within the block delineated by longitudes 89-96°W and latitudes 38-42°N; the second sample includes clutches

TABLE 1. Average hybrid index scores, percentage transition from pure yellow-shafted (0%) to pure red-shafted (100%) scores, and sample sizes (*n*) on a transect across the Northern Flicker hybrid zone.

Study site	Average hybrid index		Percentage of pure red-shafted score	
	Female (<i>n</i>)	Male (<i>n</i>)	Female	Male
Sutherland	0.73 (11)	0.69 (13)	3.8	3.0
Bridgeport	4.85 (26)	7.09 (32)	25.5	30.8
Morrill	13.64 (25)	16.22 (27)	71.8	70.5
Wheatland	15.71 (14)	18.19 (16)	82.7	79.1

within longitudes 105-113°W and latitudes 38-42°N. These two blocks are roughly contiguous with the eastern and western ends of the study transect; they are narrow so as to avoid variance resulting from the strong latitudinal gradient in clutch size in *Colaptes* (Koenig 1984). Koenig's data were extracted from the egg collections of museums, and we followed his protocol for determining the completeness of clutches. Only clutches where incubation was evidenced by embryonic development were included in our samples.

RESULTS

Phenotypes of adults at the four study sites.—The average hybrid index (HI) scores for nesting adults at the four study sites are presented in Table 1. The two end sites, Sutherland and Wheatland, ideally represent pure yellow- and red-shafted locales for comparison with the hybrid locales, Bridgeport and Morrill. Sutherland is close to pure yellow-shafted, but significant numbers of hybrid phenotypes are included in the Wheatland samples. For this reason and because sample sizes from Wheatland are small, greater consideration should be given to Sutherland as a parental population for comparison.

Descriptive statistics.—The distributions of clutch and brood sizes for the six samples are illustrated in Fig. 2, along with the means, standard deviations, and sample sizes. Brood-size data were not available for pure red- and yellow-shafted samples based on museum egg collections and so only clutch-size data are given for these samples.

The distributions of clutch and brood sizes at all locales appeared sufficiently close to normal distributions that parametric statistical tests

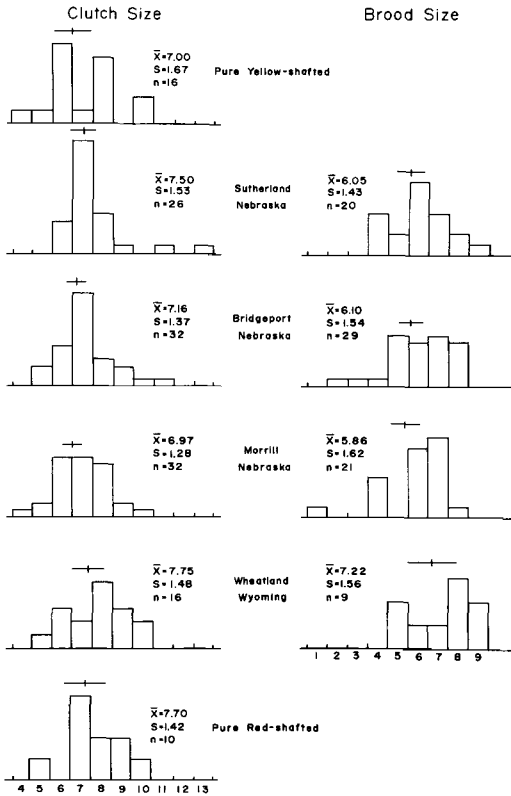


Fig. 2. The distributions of clutch and brood sizes across the Northern Flicker hybrid zone. The extreme upper and lower clutch panels are based on museum egg collections; the other distributions are based on the four live-study sites. The horizontal line above each histogram is a 95% confidence interval centered at the mean.

were valid in most instances and provided more sensitive statistical tests than did corresponding nonparametric tests.

Clutch-size comparisons across study sites.—Variances in clutch size were homogeneous across the four study sites and two museum samples (Bartlett-Box F -test, $P < 0.87$). This is of interest because disruption of coadapted gene complexes via hybridization might be expected to increase variance in clutch size. Although not significant, clutch-size variances were lowest at the two hybrid locales. Because the variances were homogeneous, we compared mean clutch size across locales by completely randomized-design ANOVA. In this analysis, the mean clutch size did not differ significantly in any of the six samples ($P < 0.363$).

As the data were collected from the four live-

study sites, it seemed as though clutch sizes of early-nesting pairs were larger than those of late nesters and that there was also variation between years. Uncontrolled sources of variance could obscure any underlying difference between locales or alternatively could bias the test. We tested for the effects of seasonal variation (early vs. late clutches) and between-year variation by a factorial ANOVA with site (1–4), season (early, late), and year (1982, 1983, 1984) as factors.

Three problems in the design of this three-factor ANOVA should be mentioned. First was how to separate early and late clutches. We plotted a histogram of first-egg dates. A conspicuous bimodality was manifest, with a valley around 20–21 May. This is consistent with the field observation of a period in late May during which new nests are more difficult to find than earlier or later. Thus, two levels were defined for the factor season; early comprises nests in which laying began 20 May and earlier, and late comprises nests in which laying began 21 May and later. The second problem is that Sutherland and Wheatland were not established as study sites until 1982; thus, data are available at Bridgeport and Morrill for 4 yr, 1981–1984, but for only 3 yr at Wheatland and Sutherland. For this analysis, then, only the years 1982–1984 were considered. The third problem is that the numbers of observations (clutches or broods) in the 24 cells resulting from the cross classification of the three factors are unequal, which means that the effects are not orthogonal. The regression approach of adjusting sums of squares was used to correct for nonorthogonality (Nie et al. 1975).

The results of this analysis are that the effect of season was very significant ($P < 0.002$), but neither site ($P < 0.382$) nor year ($P < 0.240$) was significant, nor were any of the interaction terms.

Because the factor year was not significant but season was, the most parsimonious ANOVA model for the final comparison of mean clutch size between sites considered just two factors, site and season. In this ANOVA (Table 2), again using the regression approach to correct for nonorthogonality, the effect of season remained significant ($P < 0.001$), with early clutches averaging 7.82 eggs vs. 6.80 for late clutches, whereas the effect of site was even less significant ($P < 0.561$) than in previous tests.

Brood-size comparisons across study sites.—Brood size was analyzed in exactly the same manner as clutch size with similar results. The analysis of clutch size provided no statistical evidence for reduced hybrid fitness, and the brood-size statistics were even less compelling. Mean brood size was actually greater at Bridgeport than Sutherland (Fig. 2), although, again, there were no significantly different means. Brood size was correlated with clutch size ($r = +0.62$, $P < 0.0001$), and so the more refined factorial designs yielded much the same results as the clutch-size analyses, viz., year did not affect brood size but season did ($P < 0.014$). In the two-factor ANOVA, site did not affect brood size ($P < 0.651$).

The analyses of clutch and brood size were similar, but it is important to note that clutch and brood size probably would be affected by different components of fitness. Although abnormal male behavior conceivably could affect the female reproductive cycle (Lehrman 1965), clutch size should be affected primarily by female fertility, whereas brood size could be affected by male fertility as well as zygotic mortality. It is possible to assess the effect of hybridization on development alone by analyzing brood size while statistically controlling for clutch size. This might be accomplished by comparing the slopes of lines of brood sizes regressed on clutch sizes for the four sites by analysis of covariance. However, such an analysis may not be valid; brood sizes are not normally distributed for a given clutch size because in too many cases brood size is equal to clutch size. A cruder but safer test can be accomplished by comparing the ratios of brood-size/clutch-size across sites by the nonparametric Kruskal-Wallis test. The test of the null hypothesis that the central tendencies (means) of this ratio are identical across sites cannot be rejected ($P < 0.485$; sample sizes: Sutherland = 20, Bridgeport = 26, Morrill = 18, Wheatland = 8). Although the validity of an analysis of covariance is suspect, such an analysis gave a very similar result. Thus, there is not evidence of hybrid unfitnes in the form of reduced brood size at hybrid locales.

Clutch- and brood-size comparisons by phenotype.—Males and females can be classified as pure yellow-shafted, pure red-shafted, or hybrid based on HI scores. Clutch and brood sizes can then be compared between phenotypic classes as opposed to between locales, as in the

TABLE 2. The effect of site and season on mean clutch size along a transect across the Northern Flicker hybrid zone.

Source	Sum of squares	df	Mean square	F-statistic	Attained significance
Total	180.39	95	—	—	—
Site	3.63	3	1.21	0.69	$P < 0.561$
Season	22.00	1	22.00	12.52	$P < 0.001$
Site by season	0.12	3	0.04	0.02	$P < 0.995$
Error	154.64	88	1.76	—	—

previous analysis. Females with HI scores of 3–17 inclusive were classified as hybrids, those with scores <3 as yellow-shafted, and those >17 as red-shafted. For males, individuals scoring between 3 and 21 inclusive were classified as hybrids, those <3 as yellow-shafted, and those >21 as red-shafted.

The results of these analyses are summarized in Table 3. Adults from the four study sites were pooled and reclassified by phenotype. Again, to control the effect of early vs. late nesting, a two-factor ANOVA, season (early, late) \times phenotype (yellow-shafted, hybrid, red-shafted), was employed for the comparisons of clutch and brood sizes. However, because there were no data for late broods sired by red-shafted males, the ANOVA of male brood was restricted to two phenotypic classes, i.e. season (early, late) \times phenotype (yellow-shafted, hybrid). In the four tests of the effect of phenotype on clutch and brood size, hybrid males sired significantly ($P < 0.04$) smaller broods than nonhybrids; the other three tests were not significant.

This result provided some evidence for reduced hybrid fitness. However, a more detailed examination of this apparent reduction in brood size was enigmatic. Either reduced fertility in hybrid males or increased frequency of developmental abnormalities in zygotes sired by hybrid males may be the cause. In either case, clutch size should *not* be reduced, but the effects should be apparent in a reduced ratio of brood-size/clutch-size. A paradox is then apparent in Table 3 because the brood-size/clutch-size ratio was not significant in itself (Kruskal-Wallis test), and both a reduced clutch size and an increased zygotic mortality seemed to contribute about equally to the statistically significant reduction in brood size. It is possible that

TABLE 3. Average clutch and brood sizes and their ratios for pure Yellow-shafted, pure Red-shafted, and hybrid flickers (sample sizes in parentheses).

	Clutch size		Brood size		Brood/clutch
	Early	Late	Early	Late	
Female phenotype					
Yellow-shafted	7.42 (12)	6.63 (8)	6.11 (9)	5.00 (6)	0.835 (15)
Hybrid	7.84 (25)	6.71 (17)	6.53 (28)	5.83 (12)	0.833 (34)
Red-shafted	7.40 (5)	8.00 (2)	6.80 (5)	6.00 (1)	0.903 (5)
Test					
Phenotype	$P < 0.61^a$		$P < 0.39^a$		$P < 0.68^c$
Season	$P < 0.37$		$P < 0.18$		
Male phenotype					
Yellow-shafted	8.06 (16)	7.50 (2)	7.00 (15)	7.00 (2)	0.898 (16)
Hybrid	7.27 (30)	6.61 (26)	6.14 (28)	5.40 (20)	0.826 (42)
Red-shafted	8.60 (5)	7.00 (2)	8.00 (4)	—	0.866 (4)
Test					
Phenotype	$P < 0.15^a$		$P < 0.04^b$		$P < 0.17^c$
Season	$P < 0.09$		$P < 0.53$		

^a ANOVA: phenotype (yellow, hybrid, red) × season (early, late).

^b ANOVA: phenotype (yellow, hybrid) × season (early, late).

^c Kruskal-Wallis test.

two sampling errors compounded to produce a false rejection of the null hypothesis or, alternatively, that hybrid males somehow affected the egg-laying capacity of their mates—perhaps through behavior (Lehrman 1965).

The effects of particular crosses on hatchling success.—The data set allowed one additional set of tests for reduced hybrid fitness: the effects of specific crosses (e.g. yellow-shafted female × hybrid male, etc.) on clutch and brood size (Table 4). Of the nine possible types of crosses, none involved red-shafted × yellow-shafted and only one involved red-shafted × red-shafted. The average ratio (brood-size/clutch-size) for all nests was pooled from the four sites (Table 4). The ratio for hybrid males weighted and averaged across all types of females was 0.826. The grand mean for all crosses was 0.838. The means (central tendencies) were compared by the Kruskal-Wallis test. The null hypothesis that the sum of ranks for the six classes (excluding the cross where $n = 1$) are identical could not be rejected ($P < 0.336$). Although not significant, the hatchling survival rate (brood-size/clutch-size) was lowest for the cross hybrid × hybrid. A similar analysis was made for clutch size, but there were no significant differences between classes as defined by the type of cross. This is not surprising because the female alone probably determines clutch size.

DISCUSSION

Several points concerning ecologically and geographically adaptive variation in clutch size need to be considered, as they may be confounding our attempt to identify the effects of hybridization (Koenig 1982, 1984). Latitudinal variation across the four study sites, which spanned about 1°, is minimal. According to Koenig's (1984) regression of clutch size on latitude for the Northern Flicker, the expected difference in clutch size between Sutherland and Wheatland is only 0.1 egg. However, ecological differences between study sites may have influenced our results. In particular, there is both an elevational increase from Sutherland (902 m) to Wheatland (1,448 m) and an ecological gradient of increasing aridity and harsher winter conditions. These differences may produce greater seasonality in productivity, found by Koenig to significantly influence clutch-size variation in the Northern Flicker, and thus may be partially responsible for the (nonsignificantly) larger clutch sizes found in Wheatland and in the pure red-shafted samples.

Such an effect is likely to be minimal for several reasons. Winter actual evapotranspirations (AE), defined as the sum for the three consecutive months yielding the lowest AE values, are 0 for all sites (Thorntwaite Assoc. 1964). AE was used by Ricklefs (1980) and Koenig

TABLE 4. Hatchling survivorship as measured by the ratio of brood size to clutch size for various natural crosses from the hybrid zone (sample sizes in parentheses).

	Phenotype of male parent			Weighted mean ^a
	Yellow-shafted	Hybrid	Red-shafted	
Phenotype of female parent				
Yellow-shafted	0.838 (21)	0.823 (12)	—	0.833 (33)
Hybrid	0.911 (5)	0.811 (26)	0.888 (3)	0.833 (34)
Red-shafted	—	0.929 (4)	0.800 (1)	0.903 (5)
Weighted mean ^a	0.852 (26)	0.826 (42)	0.866 (4)	0.838 (72)

^a Weighted means for each phenotype averaged over all crosses.

(1984) as an index of winter productivity. Other factors potentially influencing seasonality of resources either did not vary among sites (population density) or do not influence geographic patterns of clutch size in this species (summer AE; Koenig 1984). Thus, we feel that sources of ecological variation in clutch size are as comparable among these sites as possible in any study encompassing a geographical gradient.

One ecological factor, date, had a significant influence on clutch size, with clutch size being significantly lower in late clutches. Koenig (1984) found that clutch size increases with date, whereas there was a highly significant decrease in late clutch sizes at the four live-study sites reported here. The obvious, although not necessarily correct, explanation for this seemingly contradictory result is that Koenig's sample included clutches from a broad range of latitudes; clutches from low latitudes are smaller, and they are also initiated earlier, on average, because breeding commences earlier in the south.

Our goal was to determine whether there is reduced fertility or increased developmental failure in flickers from the Northern Flicker hybrid zone. Evidence of reduced hybrid fitness would suggest that this apparently stable hybrid zone is best explained by a dynamic-equilibrium model. Failure to find this kind of dysgenesis would favor a bounded hybrid-superiority model or some other explanation (Moore 1977). In testing the alternatives, it is important to point out that the hybrid-superiority model refers to ecological or exogenous fitness parameters, whereas the dynamic-equilibrium model requires depression of endogenous fitness parameters in hybrids, i.e. infertility, developmental aberrations, failure to maintain physiological homeostasis, etc. Thus, the bounded hybrid-superiority hypothesis does not predict increased clutch size, etc., but

rather a failure to find a reduction in these reproductive parameters in hybrid phenotypes.

If reduced hybrid fitness were a factor maintaining the Northern Flicker hybrid zone, we would expect a reduction in one or more of the three reproductive parameters (clutch size, brood size, or the ratio of the two) at the two central hybrid locales (Bridgeport and Morrill) relative to the two distal locales (Sutherland and Wheatland) and the two museum egg collection samples. This was not the case. Reshuffling the data such that the reproductive parameters were compared across adult phenotypes (Table 3) resulted in one significant test. Specifically, males with hybrid phenotypes seemed to be associated with reduced brood size, but, as discussed in the results, this was an enigmatic result when explained in terms of reduced hybrid fitness. When the data set was reshuffled again, such that developmental success (brood-size/clutch-size) could be compared between different types of cross (Table 4), there were no significant differences. Considering comparisons for clutch size, brood size, and the ratio between the two, 10 statistical tests were performed where reduced hybrid fitness might have manifested. Only one test was significant ($P < 0.04$), and this could be attributed reasonably to chance alone.

Because of limited sample sizes we cannot state conclusively that there is no reduction in hybrid fitness in the Northern Flicker hybrid zone; however, we can state that if it is there, it is very slight. This overall lack of evidence for hybrid unfitness is inconsistent with either the dynamic-equilibrium or the reinforcement model. Of the two remaining alternatives (Moore 1977), the bounded hybrid-superiority model appears the more likely explanation of the Northern Flicker hybrid zone because the hybrid zone is not growing broader, as pre-

dicted by the introgression model (Moore and Buchanan 1985).

The Northern Flicker hybrid zone is one of a substantial number of avian hybrid zones (see Short 1969, Moore 1977, and Rising 1983a for reviews). Although few of these have been studied in detail, it is apparent that the flicker hybrid zone is *not* paradigmatic for *all* avian hybrid zones. For example, the hybrid zone between the Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers has moved substantially in historical times (Gill 1980). Reproductive isolation appears to have evolved in a portion of the Northern Oriole (*Icterus galbula*) hybrid zone (Corbin and Sibley 1977), although major portions of the hybrid zone remain unchanged (Rising 1983b). Johnson and Johnson (1985) described natural hybridization between the Red-breasted (*Sphyrapicus ruber daggetti*) and Red-naped (*S. nuchalis*) sapsuckers. This is presumably an old secondary contact and hybridization persists, but this situation is best described as a zone of overlap and hybridization (Short 1969) because parental phenotypes predominate numerically. The sapsuckers clearly mate assortatively, and Johnson and Johnson (1985) argued from indirect evidence that hybrids assorted from the F₁s were selected against. The Northern Flicker hybrid zone, in contrast, appears stable, and there is no evidence of preferential mating (Moore and Buchanan 1985) or of hybrid breakdown. Furthermore, hybridization is rampant, one infrequently sees a pure Red- or Yellow-shafted Flicker in the center of the hybrid zone, and the zone covers a large geographical area (Short 1965).

A monumental question is whether one type of hybrid zone evolves into another, particularly as a result of selection forces operating within the hybrid zone. This appears to be the case in the Northern Oriole. On the other hand, the flicker hybrid zone must be at least as old, but evolution of reproductive isolation has not progressed there (Moore and Buchanan 1985). Dowling and Moore (1984, 1985) described a zone of overlap and hybridization between the common and the striped shiner (*Notropis*) that is comparable to the sapsucker hybrid zone in a number of respects. Despite the antiquity of that zone and clear evidence for selection against hybrids, reproductive isolation between the shiners is far from complete. This raises the possibility that pre mating reproduc-

tive isolating mechanisms do not evolve in hybrid zones even when the hybrids are selected against. When some measure of pre mating reproductive isolation (assortative mating) is seen in a hybrid zone, it is possible that it evolved *in situ* as an adaptive response to selection against hybrids. Alternatively, it is possible that its evolution was incidental to the hybrid zone. In the case of the sapsuckers, for example, the red-breasted are known to return to seasonal nesting areas earlier than the red-naped, and this no doubt contributes to the low level of interspecific matings. It is possible that selection has favored early and late migration in the respective species and this, incidentally, has resulted in a reduced level of hybridization in the limited areas of sympatry. Although it is important to recognize these alternatives as a guide to future research, the present data are too few to develop a reasoned inference as to the relationships among different kinds of hybrid zones.

ACKNOWLEDGMENTS

We thank James Haugland of Sutherland, Nebraska; Donald Lindgren of Bridgeport, Nebraska; Sam Masid of Morrill, Nebraska; and Buddy Wilson of Wheatland, Wyoming for allowing us to conduct this research on their property. We thank Thad Grudzien for critically reading the manuscript and Lori Merlotti for helping with the preparation of the manuscript. We thank Ned K. Johnson, Peter G. Connors, and an anonymous reviewer for many thoughtful and useful comments that were incorporated into the revised manuscript. This research was sponsored by NSF grants BSR 81-05195 and BSR 83-20605 to William S. Moore. Compilation of the museum data was made possible by a grant from the Frank M. Chapman Memorial Fund to Walter D. Koenig.

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