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VARIATION IN CAROTENOID-BASED COLOR IN NORTHERN FLICKERS IN A HYBRID ZONE

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ABSTRACT.—We studied variation in the carotenoid color of flight feathers of hybrid Northern Flickers (*Colaptes auratus*) and its correlation with reproductive performance and survival. Color scores provided by a digital camera revealed in 218 individuals a continuous spectrum from yellow to red. Males tended to be slightly redder than females. Within individuals, an analysis of color change with age revealed that males, but not females, became redder with age. Except for yearling females, body condition did not improve with age, suggesting that color is not linked to body condition measured during incubation. We did not detect any correlations between feather color and measures of reproductive performance, such as clutch size, hatching success, or fledging success, or return rate to the study area. In a hybrid population where intraspecific variation in color is controlled partly by genes, hue or brightness may not be a useful signal of individual quality, contrary to other studies of birds. About 25% of flickers had one or more tail feathers that differed from the rest of the plumage. In each case, the ''odd'' feathers were paler or yellower in color and may have been caused by diet or stress when the feathers were lost and regrown during winter. Such odd colors support the hypothesis that red carotenoid pigments are costly to maintain under stressful conditions. *Received 25 January 2002, accepted 5 August 2002.*

''The flicker situation will puzzle all the naturalists in the world'' (Audubon 1843:71).

Documentation of variation in plumage color, whether across a species' range or within a population, has been the foundation for many subdisciplines in ornithology. Trends in coloration are the raw material in avian systematics, allow us to describe the demography of populations, and more recently in behavioral ecology, reveal the power of sexual selection in shaping bird morphology (Hill 1991, Gray 1996). In general, males are more brightly colored than females, and juveniles have a drab appearance compared to adults (Butcher and Rohwer 1989). Bright colors in birds may function in numerous ways as signals to conspecifics or predators (reviews in Burtt 1981, Butcher and Rohwer 1989, Savalli 1995, Fitzpatrick 1998). Of particular interest in recent years are the bright yellows, oranges, and reds, so common in the feathers of birds, that are a product of carotenoids. These pigments are of such interest because the same molecules have a variety of important physiological functions related to the health of birds (see Lozano 1994, Olsen and Owens 1998, Möller et al. 2000). In this paper, we examine intrapopulation plumage variation in the Northern Flicker (*Colaptes auratus*), a woodpecker with extensive and conspicuous carotenoid pigmentation on the undersides of the flight feathers of both the wing and tail. Two subspecies (formerly species) are recognized: *C. auratus auratus*, the Yellow-shafted Flicker of eastern North America and the Great Plains, and *C. a. cafer*, the Red-shafted Flicker of western North America. As the common names suggest, the color of flight feathers is yellow or red and has a genetic basis (Short 1965, Moore 1995). The two subspecies groups hybridize along a zone extending along the Rocky Mountains from Texas to Alaska; birds with an intermediate feather color, shades of orange, are identified as hybrids (Moore 1995, Wiebe 2000).

The bright colors of the flight feathers of the Yellow-shafted Flicker are derived from three carotenoids that are absorbed untransformed from the diet: lutein, zeaxanthin, and β-cryptoxanthin. In contrast, the colors of the Red-shafted Flicker are derived from oxidation of ingested carotenoids such that the predominant pigments are astaxanthin, adonirubin, α-doradexanthin, and canthaxanthin (Stradi 1998). In a previous study (Wiebe and Bortolotti 2001), we examined the frequency of yellow-orange-red color morphs in a hybrid population by using color scores from a digital camera.

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Relationships between color and individual traits have not been examined in flickers; however, the potential role of color in communication is suggested by ritualized displays during which both males and females fan their wings and tails and expose the colored undersides of their flight feathers in exaggerated motions (Moore 1995). The display may be directed either to a member of the same sex, in which case it probably is agonistic, or to the opposite sex, in which case it may function in mate choice. Thus, it is not implausible that color variation may be used to select an appropriate mate either with regard to species, or in selection of a high quality partner. In the latter case, it is predicted that color may correlate with traits such as age and body condition.

In a hybrid zone, correlations between color and reproductive success are especially interesting. If a wide range of color variation is controlled by genes in a hybrid zone, it may be a poor signal of age or experience. On the other hand, if the fitness of hybrids is higher or lower than parental types in the hybrid zone, color could be an excellent indicator of potential fitness. The leading hypothesis for the stability of the hybrid zone in flickers is that hybrids have higher fitness than pure types in the hybrid zone (Moore and Buchanan 1985). Therefore, orange flickers should have greater success than yellow or red birds there. Despite potential fitness differences among flickers of different colors related to their genetic makeup, most previous studies have failed to detect mate choice according to color (Bock 1971, Moore 1987, but see Wiebe 2000). In this paper, our aim is not to test the function of color, but to examine proximate correlates of color variation such as age, sex, body condition, reproductive success, and return rates of adults. It is our hope that this baseline information will be useful in future studies that may focus on the adaptive significance of color variation in Northern Flickers.

METHODS

Study site and field methods.—The study area near Riske Creek, in central British Columbia (51° 52′ N, 122° 21′ W) within the hybrid zone of Northern Flickers, encompassed approximately 75 km^2 of grassland with scattered patches of trembling aspen (*Populus tremuloides*) and mixed coniferous forest (Martin and Eadie 1999). Flickers were observed during 1998 and 1999 from the time they arrived on territories during late April until the young fledged during late July. Potential territories and peripheral regions were searched intensively every 2–3 days during spring using tape-recorded calls. Because the habitat was fairly open and flickers were responsive to the tapes, we believe nearly all nesting birds were located. We also trapped most birds each year (see below) to estimate return rates. During 1998, 111 breeding adults were banded, of which 36 returned in 1999. As we detected only one bird from 1998 in 2000 but not in 1999, we are confident that we detected most color-banded birds (36/37 = 97%) if they returned and therefore our return rates are an accurate measure of local survival.

Adult flickers were trapped at the nest either by stuffing the nest hole during incubation, or by pulling a net over the hole with an attached string during brood rearing (see Wiebe and Swift 2001). We trapped ≥96% of nesting adults each year, and there is no reason to think trapping success was biased according to plumage color. Flickers were aged as 1, 2, or 3 years old by molt of upper primary coverts (Pyle et al. 1997) but for some analyses we used two age classes by combining all birds ≥2 years as ‘‘adults.’’ We entered six body size measurements, bill length, bill depth, wing chord, tarsus, central rectrix, and ninth primary length, in a principal components analysis and used the first component (PC1) as a measure of overall body size (Rising and Somers 1989). Because of sexual dimorphism, we performed separate analyses for each sex and made PC1 values positive by scaling them to a hypothetical individual of zero size (Bortolotti and Iko 1992). The third rectrix on the right side was collected from each adult flicker when it was trapped in May or June, and saved in a paper envelope to be photographed later. If the individual had multiple colors in its tail, we collected two feathers.

Determining color.—Quantifying subtle variation in feather color is difficult because observers’ perceptions depend upon the context, the degree of illumination, and individual differences (Endler 1990). Previous studies of flicker subspecies ranked the color of feather shafts and vanes into 3–5 categories (Short 1965, Bock 1971), or named the feather vane color according to standardized color chips (Test 1940). Such categories are too coarse for many questions. In a previous paper (Wiebe and Bortolotti 2001), we used a digital camera to measure color on a continuous scale (Villafuerte and Negro 1998). A Nikon Coolpix E900s digital camera was used to photograph each rectrix. We photographed all feathers during November 1999 alongside two gray scale reference cards so that we could adjust colors to control for differences in illumination (Villafuerte and Negro 1998). Although the camera did not record UV reflectance, we do not believe this was a serious drawback as carotenoids reflect light mainly in the visible range, and red tail coverts of the Great Spotted Woodpecker (*Dendrocopus major*) did not show UV reflectance (Burkhardt 1989).

To derive a single color variable, we plotted feathers on the red and blue brightness axes provided by the camera. That scatter plot revealed that a single axis (e.g., the "red" axis) was not sufficient to distinguish color hues perceived by us. Rather, color hues were segregated in tight diagonal bands across both axes. We used the reduced major axis technique to fit a regression line through the median red and blue values and then used residuals from this regression as the new single color variable (Wiebe and Bortolotti 2001). These color residuals corresponded well to a scale of paint chips ranked from yellow through orange and red; higher residuals indicated more reddish feathers and lower residuals indicated yellow hues. Wiebe and Bortolotti (2001) also confirmed that feather hues as ranked by human test subjects matched the ranking of the feather color residuals as calculated by us.

Statistical analyses.—We analyzed body size because the Red-shafted Flicker was reported to be larger than the yellow-shafted subspecies (Moore 1995) and also because body size may influence social dominance and territory acquisition, and therefore quality of the individual. As an index of body condition, we used the residuals of a reduced major axis regression of body mass on PC1 (Green 2001). We recaptured 27 flickers during 1998 and 1999. To avoid pseudoreplication in analyses involving color frequencies and reproductive performance, we randomly chose one observation per individual in the dataset except when analyzing within individual variation. For analyses of return rates and changes in body condition within individuals between years, recaptured birds from 2000 were included. We performed statistical analyses using SPSS, and all tests were two tailed. Means are reported ± SE. Initial ANOVA models included all higher order interaction terms, but in order to increase power these were dropped from the model if nonsignificant.

RESULTS

Not counting "odd" colored feathers but including recaptures, we collected and photographed 245 flicker tail feathers: 111 from 1998 and 133 from 1999. Using the reduced dataset with one feather per individual, a three-way ANOVA revealed no significant effect of year ($F_{1,213} = 0.12$, $P = 0.72$) or age (ages 1–3; $F_{2,213} = 0.56$, $P = 0.57$) on feather color but a significant sex effect ($F_{1,213} = 4.6$, $P = 0.032$). After pooling years, males were slightly more reddish ($n = 107$, mean color residual $= 0.0064 \pm 0.01$) than females ($n = 111$, mean color $= -0.026 \pm 0.01$; Fig. 1). For both sexes, the modal color in the population was about 0.05, a dark orangish red (approximately the "Chrome Orange" of Smithe 1975).

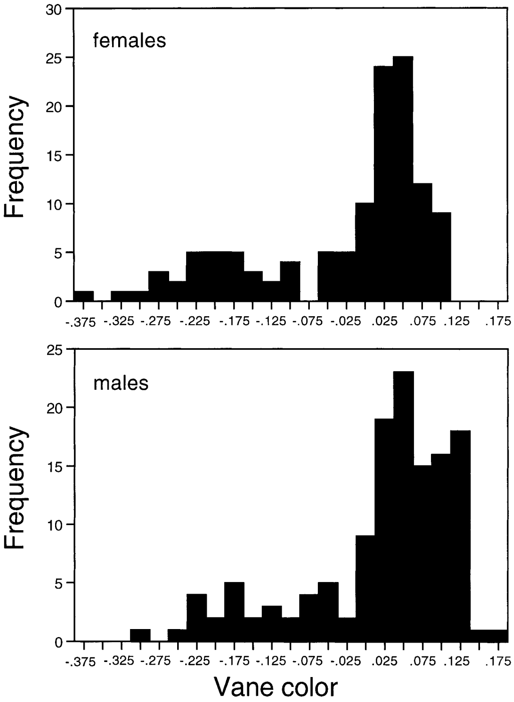

FIG. 1. Distribution of color scores in the hybrid flicker population at Riske Creek, British Columbia, 1998–2000, as determined with a digital camera. Males were redder than females as shown by the greater frequency of higher (positive) color scores.

A fraction of individuals trapped during spring during the two years (22% of 114 females and 25% of 105 males) had one or more flight feathers that differed conspicuously in color from the majority of their rectrices and primaries. In the tail, these odd feathers often were shorter or stunted, but not more worn compared to other feathers, suggesting they had been lost and regrown after the normal period of postbreeding molt during the fall. One third of these odd feathers had a "washed out" appearance, (i.e., pale pink or pale yellow), but 66% of odd feathers were still of a vibrant hue, but yellower. The shift in color was sometimes extreme; "red-shafted" flickers could have a feather almost as yellow as typical yellow-shafted *C. a. auratus* birds. In one case, a bird was bilaterally asymmetrical with one entire side of the tail red and the other yellow. Paired *t*-tests confirmed that such regrown feathers were significantly yellower ($t_{15} = 4.13$, $P = 0.001$; Fig. 2). Of 19 birds with odd feathers that were trapped in two consecutive years, only four (21%) had odd feathers in both years, which was expected based on the overall frequency of odd

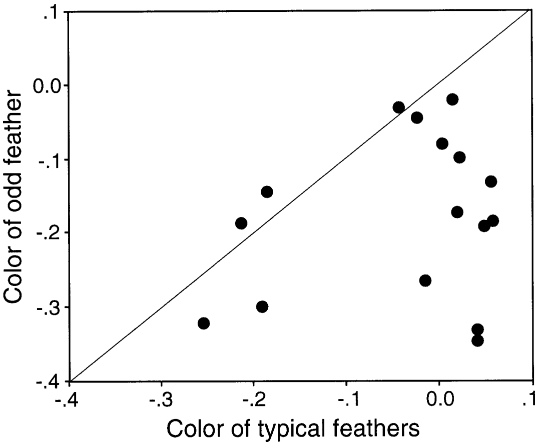

FIG. 2. The color of odd feathers and typical feathers collected from an individual flicker's tail at the same time, Riske Creek, British Columbia, 1998–2000. A shift to yellower hues in the odd, regrown feathers is shown by points below the diagonal line.

feathers in the population. In these four individuals, the odd feather in the tail was at a different location each year. It also is clear that replacement feathers did not always grow in as a different color. Nine adults that were retrapped on the study area in July (i.e., after their extracted tail feather had begun to regrow), had replacement feathers that were indistinguishable to our eye from the older rectrices.

For age-related changes in color within individuals, we used paired *t*-tests to compare feathers of individuals trapped in both years. With all ages pooled, there was no significant change in color with age for females (t_{11} = 0.29, $P = 0.78$; Fig. 3a) but a significant increase in redness for males (t_{15} = 2.92, P = 0.014; Fig. 3b). This age effect was not simply a product of a change in age class (i.e., from first to second year), as the relationship was still significant when only males two years of age and older were analyzed (t_7 = 2.4, P = 0.044). The degree of color change with age (mean difference in residual = 0.045 ± 0.06) was not as marked as the differences in color with odd regrown feathers (mean difference 0.14 ± 0.13; compare Figs. 2 and 3).

Color was not associated with our measures of individual quality. There was no association between PC1 and feather color for either males ($r = 0.03$, $n = 107$, $P = 0.75$) or females ($r = -0.02$, $n = 111$, $P = 0.82$). Because color extremes had a genetic basis in the population, simple correlations between color and body condition at the population level may have little value. Instead, we analyzed longitudinal changes in body condition with age to test whether the increase in redness with age (see above) might be explained by a proximate mechanism of an increase in body condition. Including recapture data from 2000 and pooling all ages, body condition measured during incubation improved with age for females (paired-t_{29} = 2.83, $P = 0.007$) but not males (paired-t_{39} = 0.68, $P = 0.58$). Thus, within each gender, any changes in body condition with age did not correspond with an increase in redness with age.

With respect to reproductive performance, color was not associated with clutch size (r_s = 0.05, $n = 216$, $P = 0.54$) in the hybrid population and feather color was not related to the number of nestlings that eventually fledged (r_s = 0.03, $n = 212$, $P = 0.73$). Thirty-six of 111 (32%) individuals examined in 1998 returned to the study area in 1999, and 41 of 134 (31%) from 1999 returned the subsequent year. Return rates did not differ significantly between years (χ^2_1 = 0.10, P = 0.83) or between sexes (χ^2_1 = 1.4, $P = 0.27$). Color did not differ significantly between birds that returned and those that did not (t_{243} = 1.1, $P = 0.23$).

DISCUSSION

Color in relation to age and sex.—Unlike many species of birds that have bright plum-

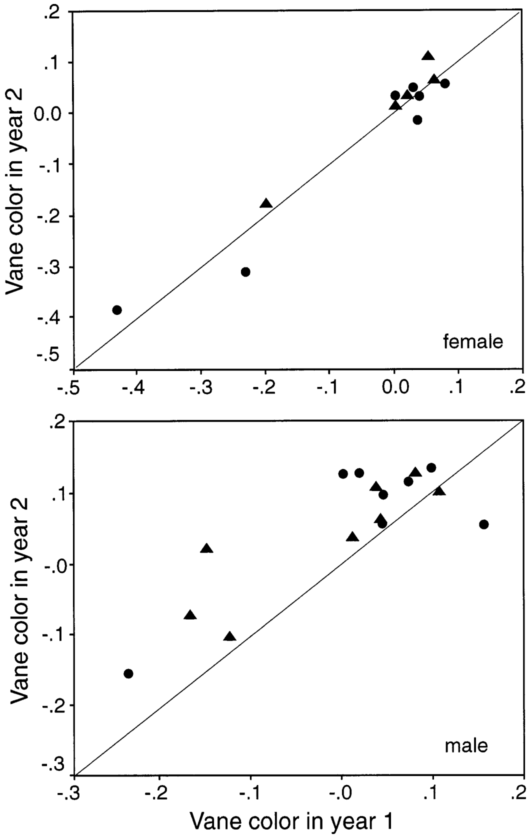

FIG. 3. A longitudinal comparison of feather color in Northern Flickers as they age from one year to the next, Riske Creek, British Columbia, 1998–2000. Circles indicate yearlings and triangles indicate birds >2 years old. The feathers of males but not females became redder with age as shown by the position above the diagonal line.

age (Butcher and Rohwer 1989, Gray 1996, Badyaev and Hill 2000), carotenoid-based coloration in flickers does not play a major role in variation with regard to age or sex. Instead, the melanin-based malar stripe is important for sex recognition (Noble 1936). The brighter red score of males in our population of hybrids (Fig. 1) could be merely the result of different proportions of individuals of each sex along the hybrid continuum, rather than a difference related to the biology of the sexes. The fact that only males became redder with age (Fig. 3) may explain how the difference arose in mean coloration between the sexes. However, the relatively subtle shifts in color with age means that it is not possible to age flickers in the field based on color. Villafuerte and Negro (1998) also found a subtle difference between the brightness of captive male and female Red-legged Partridges (*Alectoris rufa*) that was revealed only by a digital camera. A sex difference in age-related carotenoid coloration also has been reported for American Kestrels (*Falco sparverius;* Bortolotti et al. 1996).

Color variation and reproductive performance.—Subtle variation in color within an age class or sex is of interest because it may indicate a bird's quality as measured by body condition, immunocompetence, or survivorship (Hill and Montgomerie 1994, Bortolotti et al. 1996, Nolan et al. 1998, Hill 2000, Lindström and Lundström 2000, Hõrak et al. 2001). We did not find any evidence that body condition, reproductive output, or return rate varied along the color spectrum in a hybrid flicker population. In contrast to our results, redder male Northern Cardinals (*Cardinalis cardinalis*) obtained higher quality territories and produced more offspring than paler males (Wolfenbarger 1999). Redder male House Finches (*Carpodacus mexicanus*) had higher provisioning rates to nestlings and higher survival (Hill 1991, Nolan et al. 1998). However, the genetic basis of color variation in this hybrid population complicates the analysis and interpretation of potential relationships with condition. While it still is plausible that flickers within the core range of the pure subspecies may show subtle variation in color that functions in social situations (e.g., mate choice), the reliability of color as an honest signal of quality may have been compromised in the hybrid zone.

The second aspect of color that complicates our analysis is that the variation we observed is unlike that of most populations of birds. In other species, the size of the carotenoid-based color patch (Hill 1993) or the intensity of hue along a gradient of dull to bright (Bortolotti et al. 1996, Wolfenbarger 1999) is quantified. In such studies, brighter birds likely had more circulating carotenoids, which in turn may explain why there was a correlation between color and health (Lozano 1994). In contrast, flickers varied along a continuum of hues from bright yellow to bright red, displaying different, but not necessarily more, carotenoids. Instead, our find of yellow odd feathers is consistent with the hypothesis that the expression of red pigments *per se* is costly (Hill 1996, 2000).

Regardless of any potential signaling functions, the leading hypothesis about the flicker hybrid zone suggests there should be a relationship between color and reproductive performance (Moore and Buchanan 1985, Wiebe and Bortolotti 2001). However, we did not find support for the idea that intermediate phenotypes performed better in terms of reproduction than parental types in the hybrid zone, and return rates to the study area were not associated with color. Similarly, with a smaller sample size and categorical classification of phenotypes, Moore and Koenig (1986) did not detect differences in clutch size within a hybrid population in the central United States.

Causes of odd-colored rectrices.—In many species, the brightness of carotenoid colors may be influenced by a number of environmental factors. Since birds must obtain carotenoid molecules from their food, and they grow pale feathers on artificial diets lacking carotenoids (Brush 1978), different diets in the wild have been implicated in intraspecific variation (Slagsvold and Lifjeld 1985, Hill 1992, Eeva et al. 1998). However, the idea that carotenoids are limiting in the wild is controversial (Hudon 1994, Thompson et al. 1997, Bortolotti et al. 2000). Instead, physiological capabilities to absorb and use carotenoids in the diet may be influenced by physical condition, stress, or degree of parasitism (Weber 1961, Thompson et al. 1997). Gender, age, and seasonality influenced circulating carotenoids and color in American Kestrels even when diet was controlled (Bortolotti et al. 1996, Negro et al. 1998).

Surprising to us was the high prevalence (nearly 25%) of flickers with odd colored feathers in their wings or tail. Fading in sunlight does not change the hue of flicker feathers (Wiebe and Bortolotti 2001). Odd feathers must be explained by differences in diet or physiology (or both) at the time the feathers were regrown compared to conditions during the normal period of postbreeding molt from August to October. Feathers pulled in May and examined in July matched the normal color of the other rectrices. This suggests that there is a seasonal window, at least between May and October, during which carotenoids were deposited in feathers in a typical color for the individual. Pale pink or pale yellow feathers also occur in nestling flickers, which often share the nest with normal, brightly colored siblings. Such uniformly pale chicks often are the smallest of the brood (KLW pers. obs.), but probably receive the same types of food items as bright siblings. Therefore, paleness in nestlings appears to be caused by a general lack of food and poor health rather than different dietary items. We can not rule out seasonal diet changes as a cause of pale feathers in adults because the diet of flickers shifts from nearly 100% insect prey (ants) during summer, to mainly fruits and seeds during winter (Beal 1911, Test 1969). However, many fruits contain abundant carotenoids (Gross 1987), so it is more probable that pale, regrown feathers indicate greater energetic or physiological stress during winter.

It is more difficult to explain odd feathers that were still bright, but yellower than normal. Red flickers grew odd bright yellow feathers, but yellow birds never grew odd red feathers. Test (1969) also reported flickers with mixed plumages but was not clear whether these were red-shafted individuals growing yellow feathers or vice versa. It is well documented that diverse avian taxa are capable of metabolic conversion of ingested carotenoids into other forms (Goodwin 1984, Brush 1990). Red-shafted Flickers have a biochemical pathway, probably lacking in yellow-shafted individuals, which oxidizes yellow carotenoid pigments into red ones (Stradi 1998). Such biochemical pathways may be costly (Hudon 1991, review in Hill 1996) and the amount of yellow carotenoids converted to red ones may depend upon a bird's physical condition. For example, male Eurasian Bullfinches (*Pyrrhula pyrrhula*) experimentally fed a constant amount of yellow pigments produced brighter red feathers when given an energy rich diet (Schereschewsky 1929). If Red-shafted Flickers are energetically stressed during winter, costly pigment conversion may be limited, causing feathers grown during winter to be yellower than normal. Test (1969) found that Red-shafted Flickers fed ground carrots in captivity produced orange feathers. Psychological stress associated with being held in captivity may reduce the expression of red pigment in birds even though carotenoid rich diets are provided (Weber 1961 cited in Hudon 1994).

Plumage color has been a basis for the classification of flicker subspecies, but our study suggests caution is needed because there are nongenetic components to color variation. For example, Short (1965) interpreted ‘‘off-color’’ feathers reported by Test (1942) as indicators of hybridization. However, odd-colored feathers within a bird's tail probably result from environmental or physiological effects during feather molt rather than mixed parentage. It seems that a wild flicker with uniformly orange flight feathers is likely a hybrid, but the orange color of flickers raised in captivity could indicate stress rather than hybridization. The subtle differences in redness associated with age and sex probably are not large enough to influence classification based on human perception. Further study is needed to determine whether such subtle differences predict reproductive performance in pure parental populations.

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