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## THE ADAPTIVE BASIS OF GEOGRAPHIC VARIATION IN COLOR OF THE PURPLE MARTIN

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The North American Purple Martin (*Progne subis*) is a widely distributed but weakly polytypic species. The breeding range extends from coast to coast and from central and southern Canada to west-central México. In the west the species is found either in transition or higher montane woodlands or in extreme lowland desert habitats having saguaro or organ-pipe cacti. Partly as a consequence of the altitudinal semi-isolation of the western martins, we presently recognize two infraspecific differentiates: *Progne subis hesperia* (referring to Sonoran desert and Baja Californian populations) and *P. s. subis* (referring to eastern North American and montane western populations).

*Progne subis* is a Linnaean species, and it was not until the late nineteenth century that its morphological variation was formally recognized (Brewster, 1889). Brewster had 32 males (30 of them in adult plumage) from Sierra de la Laguna, Baja California del Sur, an unspecified number of females from that locality, and additional, unspecified material of the species from other localities. His description of *P. s. hesperia* was based solely on color characters of females. He ignored differences in linear dimensions of both sexes, but noted the coloristic inseparability of eastern and western adult males. Ridgway (1904) later mentioned size and spoke of small *P. s. hesperia* and large *P. s. subis*.

Grinnell (1928) eventually reviewed the western North American martins and provided a useful discussion of the clinal variation in color of females and in linear dimensions of both sexes. His study was chiefly concerned with the Pacific coast, but his findings applied also to martins from all of North America. The conclusions available at that time were: in eastern and montane western North America, martins are larger and females are dark; along the central Pacific coast, martins are slightly smaller and females are paler; in Baja California, martins are much smaller and females are much paler. Using additional material, Van Rossem (1931) later clarified the distribution of *P. s. hesperia*, but since 1931 no one has contributed appreciably to our knowledge of geographic variation in the species. The present report sets forth additional information on size and color of both eastern and western martins and discusses geographic variation in color in the species. Particular attention is given to the complex color dimorphism of martins.

Material used in colorimetric aspects of this study consists of 31 breeding martins from Guaymas (2) and Kino Nuevo (29), coastal Sonora, México, taken mostly in June 1963, and 14 birds from northeastern Kansas, taken from 1959 to 1964. This small number of specimens was sufficient to allow study of certain quantitative aspects of color variation.

All adult males (13 from Sonora and 5 from Kansas) were judged to be so by virtue of their steel-blue feather coat. The females (12 from Sonora and 5 from Kansas) may include both first-year and older birds; there are no tested criteria for separating these age groups. The remaining 10 specimens (6 from Sonora and 4

TABLE 1  
BREEDING SEASON WEIGHTS OF EASTERN AND WESTERN SAMPLES OF *PROGNE SUBIS*

Sample size	Males		Females	
	Kansas* 29	Sonora 16	Kansas* 10	Sonora 10
Weight:				
Range	48.1 - 62.5	40.5 - 50.1	51.6 - 63.4	40.6 - 56.0
Mean $\pm$ SE	54.9 $\pm$ 0.78	44.8 $\pm$ 0.89	56.2 $\pm$ 2.15	48.0 $\pm$ 1.64
Coef. variation	7.68	6.26	12.07	10.70

\* Excludes specimens labelled "fat" or "heavy fat," which indicates individuals in premigratory or immediate postmigratory physiologic states.

from Kansas) are first-year males, and were approximately one year old at time of death. Twenty-nine additional alcoholic or skeletal specimens from Kansas (24 males and 5 females) provided data on gross body weights. All 74 specimens are in the collections at the Museum of Natural History, The University of Kansas.

Colorimetric readings were made on a Bausch and Lomb Spectronic 20 colorimeter with reflectance bulb, which was made available by Robert K. Selander. The use of this instrument in the analysis of colors of vertebrate specimens is described by Selander *et al.* (1964) and Lubnow and Niethammer (1963). The scanning port on the reflectance bulb was stopped down to an opening 2 mm  $\times$  2 mm square by means of a bushing with 2 mm optical glass seated in the opening. Reflectance of monochromatic light from feather surfaces in terms of per cent of a standard was determined at 10 wavelengths for each specimen. The data have been used both in standard bivariate plots of reflectance against wavelength (figs. 1 and 2) and to calculate trichromatic and brightness coefficients (Bowers, 1956; Lubnow and Niethammer, 1963; Selander *et al.*, 1964), wherein colors are considered as to hue (dominant wavelength), value (brightness or amount of black-and-white), and chroma (purity). These readings for study specimens are presented in figures 3 and 4 and in table 2.

## RESULTS

*Body size.* Ridgway (1904), Grinnell (1928), van Rossem (1931), Hellmayr (1935), and Brandt (1951) presented data concerning linear dimensions in Purple Martins which support the generalization that northern and eastern populations are of larger average size than are southwestern. The data have suggested that in such characters as length of wing the southwestern birds were perhaps 4 or 5 per cent smaller than birds from other populations. Such a differential agrees with information on body weight presented here. Table 1 contains data on gross weight of martins that were in or approaching breeding condition at time of death. The difference in mean weight of males is 10.1 g, or about 22 per cent; the cube root of the difference amounts to 4.8 per cent, or of the same order of magnitude as differences in linear dimensions.

For both sexes the differences in weights of the two samples are significant ( $P < 0.001$  for both males and females). This is so in spite of the enormous variation in weight of the females. Such variability is evident in most of the statistical parameters used in table 1 and is a consequence of the fact that most of the females in each sample were laying eggs, were approaching laying of eggs, or had just finished laying eggs.

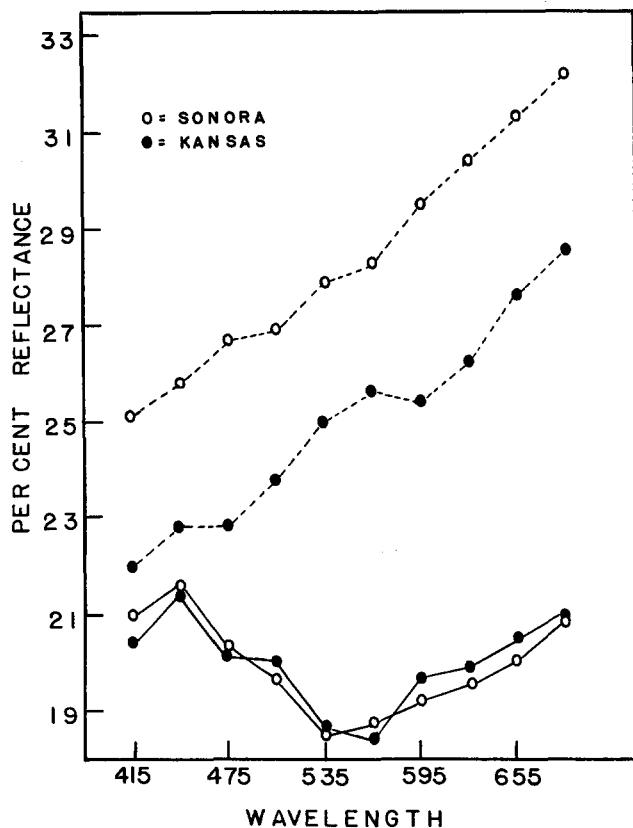


Figure 1. Spectral reflectance curves for eastern and western samples of Purple Martins. The top two curves represent reflectance readings as a function of wavelength for breast feathers of females; the lower two curves are for back feathers of adult males. Wavelength scale is in millimicrons.

*Plumage color.* Figures 1 and 2 show plots of relative reflectances of monochromatic light from feather surfaces as functions of wavelengths for six samples of Purple Martins. Successive readings are connected by lines in order to suggest the curve depicting continuous variation (the spectral reflectance curve) that might be obtained with other equipment. It should be noted that the pairs in each set of curves are essentially parallel to each other; this means that differences in colors of Sonoran and Kansan martins are chiefly a result of differential brightness, or amount of melanin in the feathers, rather than of differences in hue or chroma. Therefore, females (and young males, see below) of the Sonoran martins are brighter, or paler, than Kansan martins, as students of geographic variation have maintained for many years (*e.g.*, Grinnell, 1928, p. 123-124). In fact, the relative differences in brightness at given wavelengths vary from 10 to 15 per cent of the Kansan values. It is worth emphasizing that the differences between Sonoran and Kansan females are not so conspicuous on breast feathers as they are on feathers of the gular, frontal, nuchal, and belly regions; determinations were made on breast feathers because readings could be obtained from that region with little operating error. Hence, the greater

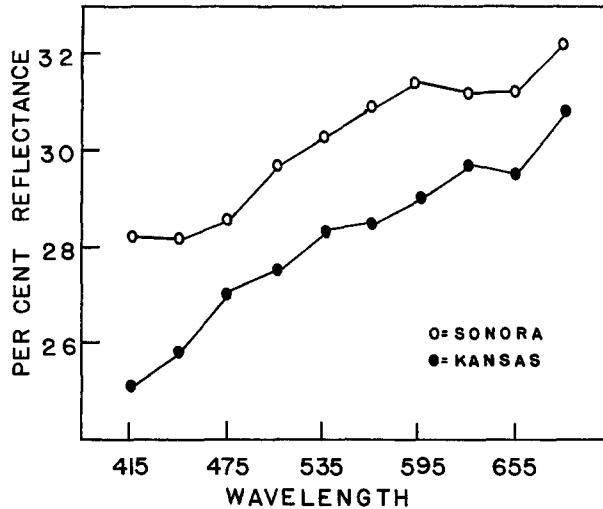


Figure 2. Spectral reflectance curves for breast feathers of first-year male specimens in two samples of Purple Martins. Wavelength scale is in millimicrons.

mean value in brightness of Sonoran breast feathers of about 13 per cent is nearer the minimum than can be found between the two samples.

The curves (fig. 1) for back color of males are practically identical with one another, a fact conspicuous in the plotting and in table 2. Brightness values also are closely similar (and are not entered on the points in fig. 4). Such overall parallelism indicates that there is virtually no visually detectable difference between Sonoran and Kansan adult males. It is, as will be discussed below, most instructive to see the degree to which dorsal coloration is uniform in the two samples. The slight percentage differences are not statistically significant. Also, first-year males strongly resemble females in color of breast feathers; colorimeter readings made on a few such males are close to values obtained from females, and Sonoran specimens are paler than the Kansan (fig. 2). First-year males as a class are paler than females as a class, a fact also evident to the unassisted eye in both samples.

TABLE 2  
TRICHROMATIC COEFFICIENTS AND BRIGHTNESS VALUES FOR  
EASTERN AND WESTERN SAMPLES OF *PROGNE SUBIS*

Sample	N	Trichromatic coefficients				Brightness	
		x		y		Mean	Range
		Mean	Range	Mean	Range		
<b>Males: back</b>							
Kansas	5	0.301	0.292-0.309	0.312	0.308-0.314	19.3	18.4-19.7
Sonora	13	0.304	0.297-0.308	0.311	0.306-0.315	19.4	19.0-20.0
<b>Females: breast</b>							
Kansas	5	0.322	0.318-0.326	0.333	0.331-0.337	25.3	23.4-28.1
Sonora	12	0.323	0.314-0.329	0.330	0.321-0.338	28.6	23.6-32.1

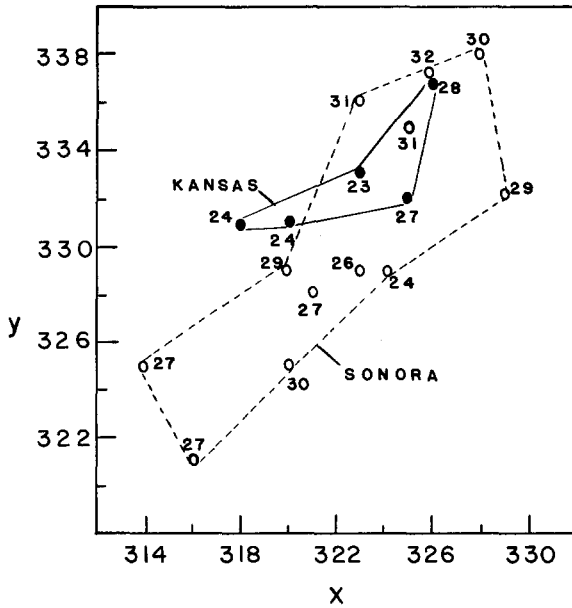


Figure 3. Chromaticity diagrams for breast feathers of females in two samples of Purple Martins. Each point represents one specimen plotted according to its trichromatic coefficients, with  $y$  values on the ordinate and  $x$  values on the abscissa; the tristimulus value  $Y$  (brightness) is indicated beside each point.

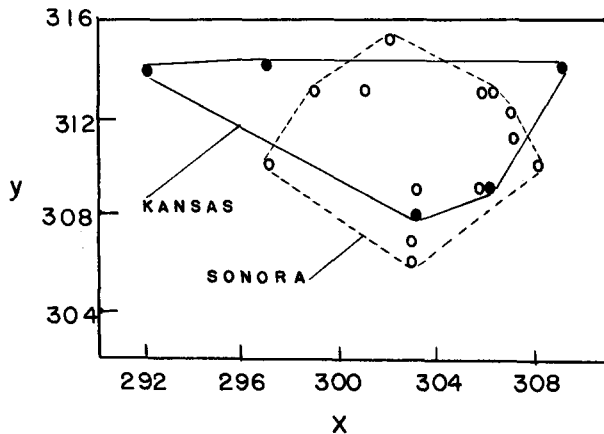


Figure 4. Chromaticity diagrams for back feathers of adult males in two samples of Purple Martins. See figure 3 for explanation. Brightness values ( $Y$ ) are not here indicated (but see table 2).

Another way of presenting these colorimetric data is to convert the reflectance values to tristimulus values ( $X$ ,  $Y$ , and  $Z$ ) and trichromatic coefficients ( $x$  and  $y$ ). Such conversion shows quantitatively which of the three aspects of variation in color accounts for the greatest amount of difference in working samples. Trichromatic coefficients  $x$  and  $y$  and the brightness coefficient  $Y$  are presented for the Sonoran and Kansan samples of females and adult males in figures 3 and 4 and in table 2.

It is evident, especially in the plots of individual specimens, that none of the paired, mean trichromatic coefficients differ significantly from one another, and neither do the brightness coefficients for back color of males. But the mean brightness values for breast color of females from the two localities are significantly different from each other; the likelihood that they have been drawn from the same sample is extremely small ( $P < 0.001$ ).

Thus, concerning color in Purple Martins, it appears that the following statements can be made:

1. Earlier conclusions on the coloristic identity of northern and southwestern adult males are fully warranted.
2. Earlier conclusions on the differences in colors of females are also warranted and should be extended to include first-year males.
3. The apparent differences seen by our eyes are functions of brightness or amounts of melanins laid down in the feathers.

#### DISCUSSION

*Possible controls of color variation.* Two ways in which variation in pigment color of bird feathers can be brought about are changes in the kinds of pigments laid down (that is, changes in hue and chroma), and changes in the amount of pigment laid down (changes in value). There is no way of knowing a priori which of these mechanisms is most readily workable physiologically because pigment deposition is known to be influenced by a range of biochemical factors (Rawls, 1960), at least including both sets of gonadal hormones, epinephrin, and the enzymes contingent on presence of certain genes. Of possible pertinence in considering this question are data on variation in color of martins. The colorimetric data here presented show fairly clearly that the birds have essentially the same melanins in their feathers regardless of their locality of origin. Since the obvious differences in color of these birds are results of differing amounts of pigments in the feathers, it is suggested that rate of deposition of melanins is more labile as a phenomenon subject to hereditary change than is change in kind of pigment.

*Dimorphic nature of geographic variation.* Only one aspect of martin morphology, plumage color of the adult males, is presently known not to vary geographically. To phrase it another way, the degree to which martins show geographic variation in color is a function of sex. It is here assumed to be adaptive for female martins to show gradual color change from eastern and northern populations to those of the desert southwest. Such variation conforms with the ecogeographic rule of Gloger. It is additionally also assumed here that it is likewise adaptive for adult males not to show such color variation. Phrased positively, it is assumed to be adaptive for adult males to have precisely the same plumage color irrespective of their locality of origin. The maintenance of such coloristic uniformity runs counter to Gloger's rule, and it is a question of no little interest as to why adult males can be exempt from known environmental pressures (see Bowers, 1960) and maintain a unicolor plumage.

One approach to this question would be to examine the superficial box cells of the cortical regions of feathers. It is conceivable that these bases for blueness in martins are somehow less available to modification than is amount of deposition of melanin pigment. But this seems to be an unlikely possibility, and in the absence of any pertinent information it is permissible to examine other alternatives.

A second approach to the problem of coloristic uniformity in males is through examination of the significance of plumage colors in the species. Sex-related plumage

dimorphism in birds usually has behavioral functions at both epigamic and agonistic levels, and it is likely that martin plumages are of signal function. Martins, of course, are not merely sexually dimorphic. Adult males differ in plumage from first-year males almost as much as they do from females, and first-year males appear at a distance to be in female plumage. In the following discussion any reference to dimorphism in martins will include both sexual and age dimensions.

If plumage dimorphism has epigamic function, we may expect one or both of the sexes to note the differences and to modify the behavior of formation and maintenance of the pair bond. Females seem not to note colors of males, and females form pairs with almost any males that have control of nesting cavities (Johnston and Hardy, 1962). It is evidently the behavior of males that is of importance to females. Males, contrariwise, actually note the plumage differences, but the distinction is not used to organize epigamic behavior.

Males act aggressively, or territorially, toward other adult males and almost ignore first-year males. In any event, they treat them as though they were females, which is exceedingly nonaggressively, and in the absence of an attack by a first-year bird the adults effectively ignore them. Hence, the behavioral modifications consequent on perception by adult males of plumage differences are aggressive modifications, and these almost exclusively have to do with fighting. The only external morphologic feature correlated with such adult male behavior is the entire steel-blue feather coat; every feather is dark, and almost no variation occurs. The rigid expression of this character may well mean that a fully functional adult male must have an entire steel-blue plumage. Departure toward the subadult condition would therefore represent a less effective plumage as far as display and fighting are concerned. The steel-blue plumage color of adult males is assumed to be functional as a signal of masculinity.

Fighting in martins is almost always centered around a nesting cavity. Males fight with other males when trespass occurs or is threatened, whereas trespass by females is permitted, and seemingly encouraged, by unmated males. In fights between old and young males (always initiated by the young males), adults win. Adults have further advantages: they arrive at nesting sites earlier than first-year birds, they gain possession of nesting sites first, and they first form pairs with females. Adults are, in short, the birds most likely to leave offspring. Therefore, the disposition of morphology into both age and sex dimorphism in association with the distribution of aggressive and reproductive activity is very nearly what Darwin (1871) ultimately talked of in referring to sexual selection (see also Sibley, 1957).

If the steel-blue plumage of adult male martins represents one result of sexual selection, it may be presumed that selection pressure for that plumage is relatively heavy. It would appear necessary that relatively heavy selection pressures run counter to environmental pressures in order to select for pale southwestern and dark northern female and first-year male martins.

These environmental pressures as they pertain to Wrentits (*Chamaea fasciata*) have been extensively examined quantitatively by Bowers (1960). He found that darker birds inhabited coastal brush that was dark, and paler birds lived in paler inland brush or chaparral. The positioning of any locality in the environmental spectrum of darker to paler seemed to be a function of the biological and physical concomitants of humidity, and the occurrence of birds that tended to match the environmental colors seemed to be a function of natural selection by visual predators. For these reasons, and in respect to a larger geographic region, it is assumed that

part of the color variation in martins is also a consequence of selection by visual predators.

Such a mechanism probably does not account for all the variation found in the species. It is possible that the increase in white in feathers of the nuchal, frontal, gular, belly, and breast regions in females and young is useful in increasing the amount of solar radiation reflected by the feathers. Intense solar radiation characterizes the desert regions inhabited by *P. s. hesperia*, and it is permissible to think that mechanisms increasing the amount of that radiation reflected by feathers would be advantageous to the birds. Conversely, darker plumages to the north or east would seem to be advantageous in increasing the amount of radiation absorbed by the feathers, and extremely dark birds would be at a selective advantage in high montane and northern Canadian regions. Temperature differentials tend to occur as gradients, and color variation partly tied to such gradients should itself occur in gradient form. As was noted earlier, color in female martins varies clinally.

In regard to adult males, the view here presented is that the dark signal plumage of males is more adaptive than would be a paler plumage that could confer some cryptic advantage or some thermoregulatory advantage. It needs thus to be demonstrated that adequate thermoregulatory capacity is available otherwise to these males. In addition to regulating the amount of heat absorbed by feathers, birds can regulate body temperature by evaporation of water and by radiation of heat at the body surface.

Perhaps the most significant regulation of heat flow from the body in birds with large gapes occurs as a result of evaporation of water from the respiratory tract (Dawson and Schmidt-Nielsen, 1964). Rate of flow can be modified in accord with size of the bucco-gular area and the behavioral tendencies to gape or otherwise expose the mouth and throat, and in accord with body temperature, as may be seen from the following equation:

$$H_{es} = \frac{K_{es}(P_s - p_a)}{r_a} w,$$

where  $H_{es}$  is rate of heat loss per unit of area,  $K_{es}$  is a constant,  $P_s$  is the saturation vapor pressure at skin temperature,  $p_a$  is vapor pressure of the ambient air,  $r_a$  is the resistivity of the ambient air to the outward passage of water vapor, and  $w$  is the proportional wetness of the skin (modified from Lee, 1964). Hence, the most rapid heat loss by evaporation of water will occur when body temperatures are high (when  $P_s$  is large), when the evaporative surface is saturated (when  $w$  is at maximum), and in dry air (when  $p_a$  and  $r_a$  are small). The mechanism is clearly most efficient in xeric regions, but a lower limit to its utility is suggested by the fact that rate of loss of evaporative water varies inversely with body weight (Dawson and Schmidt-Nielsen, 1964).

An important amount of heat flow can occur as a result of conduction and convection. Such flow may be modified by changes in body temperature and the insulating qualities of the feather coat, as can be seen from the following generalized formula:

$$H_{cs} = \frac{K_{cs}(t_s - t_a)}{I_a + I_f},$$

where  $H_{cs}$  is heat loss per unit of area,  $K_{cs}$  is a constant,  $t_s$  is the surface temperature of the skin,  $t_a$  is the ambient air temperature,  $I_a$  is the resistivity of the ambient air to heat flow, and  $I_f$  is the resistivity of the feather coat to passage of heat (modified from Lee, 1964). Such heat loss is greatest at low temperatures (when  $t_a$  is small),



at high body temperatures (when  $t_s$  is large), in humid air (when  $I_a$  is small), and when the feather coat is tightly appressed to the body surface or wings are raised, etc. (when  $I_f$  is small). Birds of the xeric southwest regularly increase body temperature some 2° to 4°C (Dawson and Schmidt-Nielsen, 1964), which, as noted above, also increases evaporative heat loss as well as that by radiation. Moreover, hyperthermia itself, as a phenomenon of temporary storage of heat, is also of advantage to desert birds in addition to increasing heat-transfer gradients (Schmidt-Nielsen, 1964:208).

In connection with radiative heat loss, it is appropriate to recall that surface-volume ratios are of significance, and that smaller bodies may be considered to be better radiators because of their larger proportional surface areas. However, because small body sizes are expensive of water, there must be a limit for most bird species as to how small they may evolve.

Thus, in thinking of the Purple Martin as a species found over a wide range of environments, we would expect to note the following adaptations to living in places with high air temperatures: (1) exposure of the bucco-gular skin by gaping when heat-loaded; (2) increase in body temperature (occurrence of hyperthermia) when heat-loaded; (3) sleeking of feathers or exposure of apteria when heat-loaded; (4) relative increase in plumage pallor in populations in which individuals are regularly exposed to heat-loading; (5) relative reduction in size of body in populations in which individuals are regularly exposed to heat-loading. All these phenomena related to heat flow between the body and the ambient air seem to be used or to have been evolved by martins. It is here suggested that it is owing to the several means of regulating heat flow that any one of the lesser factors, such as pale plumage, can be eliminated from adult males in the face of otherwise heavy selection for ritual aggressive display.

#### SUMMARY

Geographic variation in morphology in the Purple Martin (*Progne subis*) involves both size and color, with the exception that adult males show no color variation. Martins from the southwestern North American deserts are pale and small; martins from the mountains and the north and east are darker and larger.

Color of the feather coats of females and first-year males is thought to be both cryptic and of value in regulating heat flow between the bird and its environment. The uniform color of adult males from all sectors of the range of the species presumably reflects selection for display plumage in accord with Darwinian sexual selection.

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