

# IS THE PAINTED BUNTING ACTUALLY TWO SPECIES? PROBLEMS DETERMINING SPECIES LIMITS BETWEEN ALLOPATRIC POPULATIONS<sup>1</sup>

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**Abstract.** Painted Buntings, *Passerina ciris*, breed in two allopatric eastern and western breeding ranges that differ greatly from the breeding ranges of the two currently recognized subspecies (AOU 1957). These two populations differ dramatically in their timing and pattern of molt and migration. All age and sex classes in the western population typically begin fall migration at least two months earlier than their respective age and sex classes in the eastern population. These birds subsequently interrupt their fall migration in exclusively migratory areas in southern Arizona and northwestern Mexico to begin and complete their annual flight feather molt before continuing their fall migration. In contrast, birds in the eastern population usually complete flight feather molt on the breeding grounds before beginning fall migration. Last, the eastern and western populations winter in allopatric ranges; the eastern population winters in southern Florida, the Bahamas, Cuba, Jamaica, and Haiti, and the western population winters in southern Texas, Mexico and Central America. These data strongly indicate that no significant gene flow occurs between these populations, and suggests that they represent valid phylogenetic species.

Two subspecies of Painted Buntings, *pallidior* and *ciris*, are currently recognized based on previous studies (Mearns 1911, Storer 1951) that documented variation between the eastern and western populations in winglength of adult (in definitive plumage) males and plumage color of adult males and females on the breeding ground. However, this study indicates that the patterns of variation in these characters in males and females within and between populations are inconsistent with the current subspecific geographic limits in this species, and that separating Painted Buntings into subspecies based on these criteria is not warranted.

**Key words:** *Biological species; phylogenetic species; geographic variation; clinal variation; carotenoids; plumage; color; winglength; Painted Bunting; Passerina ciris.*

## INTRODUCTION

Species concepts should achieve two primary goals of systematic biology, "namely the taxonomic recognition, description and historical analysis of all potential evolutionary units, and then the expression of this information within the context of Linnean hierarchical classifications" (Cracraft 1983). The prevailing view in ornithology is that the unit of evolution is the species and that species are defined according to the biological species concept (BSC; Mayr 1969, 1982a; Cracraft 1983; Fjeldså 1985; Haffer 1986). Species are defined by the BSC as "groups of interbreeding natural populations that are reproductively isolated from one another" (Mayr 1969). However, reproductive isolation results

from, and maintains, genetic divergence (speciation), but does not cause speciation. Thus, genetic and phenotypic divergence must precede reproductive isolation (Mayr 1982a, Donoghue 1985, Zink and Remsen 1986). This is well exemplified in North American birds in which all taxa that are currently recognized as species because they are presumed to be reproductively isolated (AOU 1983) also exhibit genetic and phenotypic divergence, that is, no species are recognized solely on the basis of reproductive isolation (Cracraft 1983). As a result, the BSC has been widely criticized in many fields including ornithology because it does not allow assignment of species status to taxa that exhibit marked, non-clinal phenotypic and genetic differences from one another but that are not reproductively isolated from one another (reviews by Cracraft 1983, Donoghue 1985, de Queiroz and Donoghue 1988, McKittrick and Zink 1988). The BSC is especially problematic for assessing the taxonomic status of allopatric populations because the requisite

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criterion of reproductive isolation cannot be tested directly (Mayr and Short 1970, Futuyma and Mayer 1980). The extent of reproductive isolation among allopatric populations is reflected only indirectly by the extent of phenotypic divergence among such populations. In addition, the correlation between inherited (versus environmentally induced) phenotypic divergence and reproductive isolation among allopatric populations may be poor (Amadon 1950, Ayala 1982). Further, the BSC can obscure phylogenetic relationships among allopatric taxa because speciation among such taxa can occur without reproductive isolation (McKittrick and Zink 1988).

As an alternative to the BSC, the phylogenetic species concept (PSC; Eldredge and Cracraft 1980, Nelson and Platnick 1981, Cracraft 1983, Donoghue 1985, McKittrick and Zink 1988) defines species as the smallest diagnosable cluster of individual organisms that are monophyletic as assessed by cladistic analysis of character variation (McKittrick and Zink 1988). The PSC has many advantages over the BSC for studying phylogenetic relationships, especially among allopatric taxa (Cracraft 1983, Donoghue 1985, McKittrick and Zink 1988). Most importantly, the PSC focuses on patterns of genetic and phenotypic variation, and not on reproductive isolation which can not be adequately determined for allopatric taxa and which may be poorly correlated with genetic and phenotypic divergence.

A good model for evaluating the potential use of the PSC is the Painted Bunting, *Passerina ciris*. Two subspecies of Painted Buntings are currently recognized based on geographic variation in winglength and plumage color (AOU 1957). *Pallidior* typically is paler red and yellow-green in plumage color on the underparts of adult males and females, respectively, in definitive plumage (terminology follows Humphrey and Parkes 1959), and is larger in winglength in males in definitive plumage than is *ciris* (Mearns 1911, Storer 1951). Painted Buntings breed in two allopatric eastern and western ranges separated by at least 550 km at their closest point. The breeding ranges of these allopatric eastern and western breeding populations differ greatly from those of *ciris* and *pallidior*, respectively. The breeding range of *ciris* comprises all of the eastern breeding population as well as the easternmost portion of the western population (hereafter referred to as the western *ciris* population). The breeding range of *pallidior* comprises the remainder of the western population (AOU 1957, Thompson 1991;

Fig. 1). In the western population, most individuals undergo flight feather molt in exclusively migratory areas in southern Arizona and northwestern Mexico, whereas in the eastern population nearly all undergo flight feather molt on the breeding grounds prior to fall migration (Thompson 1991). That Painted Buntings breed in two allopatric populations that have evolved dramatically different molt-migration strategies suggests that gene flow between these populations is limited or absent. In turn, this suggests that the currently accepted geographic ranges for subspecies of Painted Buntings are incorrect, and that the allopatric eastern and western populations are valid phylogenetic species.

The purpose of this study was to 1) document geographic variation in winglength, plumage color and migration patterns of Painted Buntings, and 2) determine whether these data further support the view that the allopatric eastern and western populations of Painted Buntings are valid phylogenetic species.

## MATERIALS AND METHODS

### SPECIMENS

All data for this study were collected from museum specimens of definitive-plumaged male ( $n = 1,309$ ) and female ( $n = 338$ ) *P. ciris* collected in all months of the year from throughout the breeding, migratory and wintering ranges of the species.

### GEOGRAPHIC COORDINATES

Geographic coordinates of collection localities were determined from gazetteers, atlases, and maps and converted into decimal form for statistical analyses and mapping.

### VARIATION IN WINGLENGTH

Unflattened winglength (wing chord) of all specimens was measured to the nearest 0.5 mm as described and recommended for measurement of museum specimens by the British Trust for Ornithology (1984) and the U.S. Fish and Wildlife Service (1977). All winglength measurements are reported as means  $\pm$  SE.

*Summer.* Variation in winglength of definitive-plumaged (hereafter referred to as adult) males on the breeding grounds was determined by constructing a contour plot of mean winglength against latitude and longitude as calculated by a distance weighted least squares algorithm (Wilkinson 1990a). Using mensural data (e.g., winglength) measured from sampling units

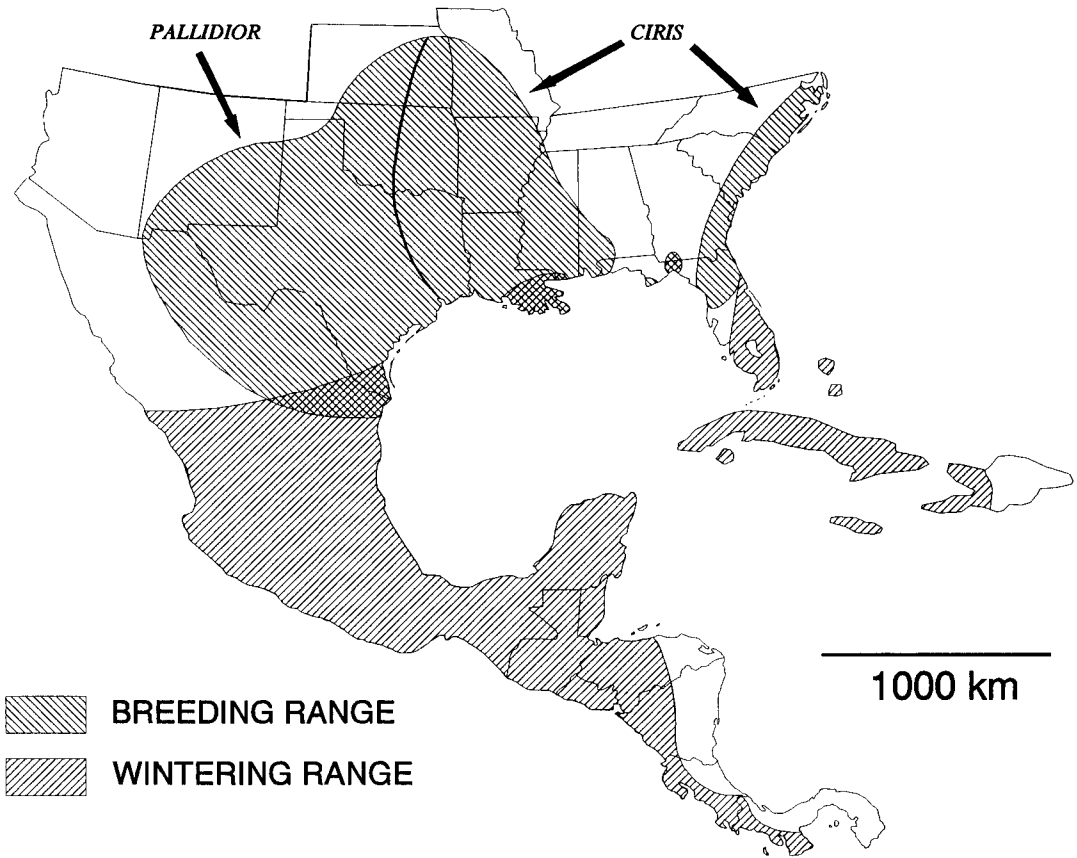


FIGURE 1. Map (stereo projection) of the breeding and wintering ranges of Painted Buntings, *Passerina ciris*. The boundary on the breeding grounds between the recognized ranges of the western subspecies, *pallidior*, and the eastern subspecies, *ciris*, is indicated by a solid curved line through eastern Kansas, Oklahoma, and Texas.

(e.g., birds) collected at known latitudinal and longitudinal coordinates, this method constructs unbiased isoclinal lines of mean values of mensural variables by an algorithm that corrects for non-uniformity in the geographic distribution of specimen collection localities and sample sizes (McLain 1974). As a result, this method is appropriate for analysis of geographic variation (Thorpe 1976, Baker 1985). To avoid inclusion in this analysis of males in migration, only males collected on the breeding grounds after spring migration and prior to fall migration were used. A conservative estimate of this period is 1 May–31 July (Figs. 2, 3).

*Winter.* Variation in winglength of adult males on the wintering grounds was determined by constructing a contour plot of isoclinal variation in mean winglength as described above. To avoid inclusion in this analysis of males in migration,

only males collected on the wintering grounds after fall migration and prior to spring migration were used for this analysis. A conservative estimate of this period of time is 16 November–29 February (Figs. 2, 3).

#### VARIATION IN PLUMAGE COLOR

To avoid inclusion of males and females collected during migration and specimens with excessive feather wear in this analysis, only unworn specimens collected between 1 May–31 July were used (Figs. 2, 3). To evaluate potential differences in plumage color in adult males and females, I covered the specimen labels of all adult male and adult female specimens collected within the breeding range of *P. ciris* between 1 May–31 July, and then ordered all specimens of each sex in an array from “dullest” to “brightest” in plumage color. Males were ordered from “dullest” to

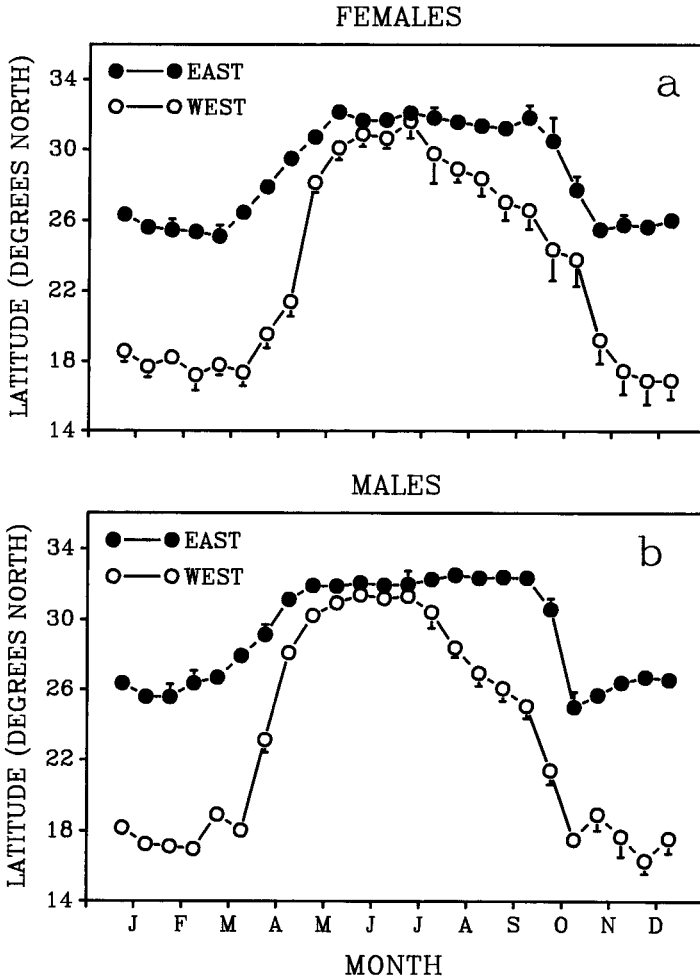


FIGURE 2. Plot of latitude (mean  $\pm$  1 SE) versus month for female (a) and male (b) Painted Buntings in definitive plumage from the allopatric eastern and western populations. Each month is represented by two means: 1) days 1–15 (1–14 for February), and 2) day 16 and thereafter.

“brightest” along a color (hue) axis from orange to red ventral plumage, regardless of variation in color intensity (saturation). Specimens of the same apparent hue were ordered by color saturation. Females were arrayed in a similar fashion from least to most yellow in ventral plumage color. The duller 50% of specimens from each array were designated as “dull,” and the brighter 50% as “bright.” In arrays that contained an uneven number of specimens, I removed the specimen at the midpoint of the array from subsequent analyses. I then uncovered the specimen label of each specimen and separated each specimen into one of three groups based on the geographic coordinates of its collection locality: (1)

those collected in the breeding range of the eastern population, (2) those collected in the breeding range of the western *ciris* population, and (3) those collected within the breeding range of *pallidior*.

STATISTICAL ANALYSES

*Variation in winglength.* Due to non-uniformity in the geographic distribution of specimen collection localities and large variation in specimen sample sizes, substantial areas of the breeding range of this species were either under- or over-represented by the specimens examined in this study (compare Fig. 4 to Fig. 1). Analysis of geographic variation in winglength by standard anal-

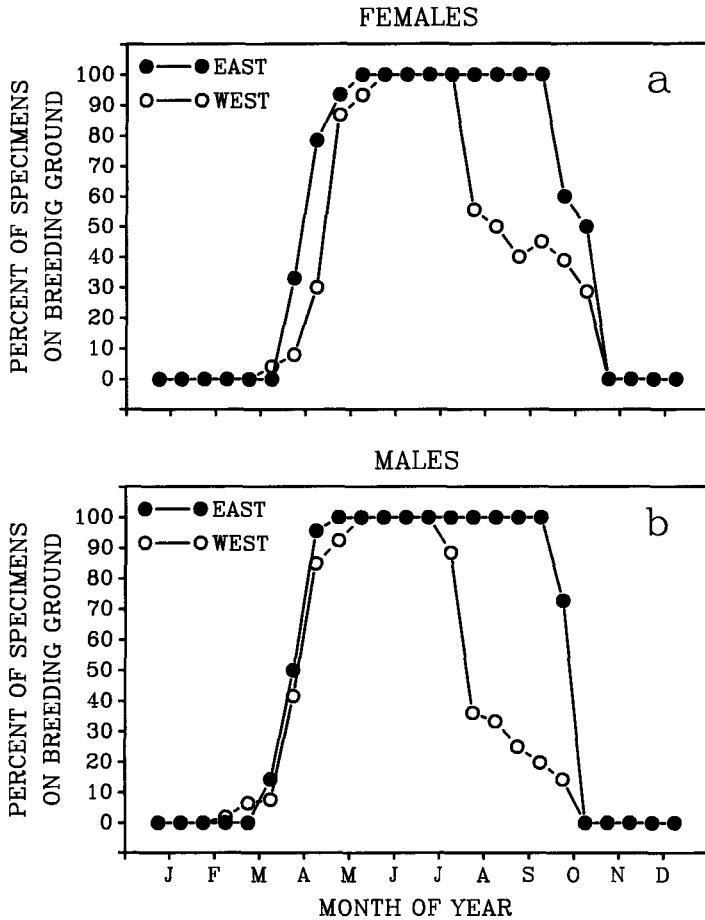


FIGURE 3. Plot of the percentage of female (a) and male (b) Painted Buntings in definitive plumage from the allopatric eastern and western populations. Each month is represented by two means: 1) days 1–15 (1–14 for February), and 2) day 16 and thereafter.

ysis of variance (ANOVA) methods was not possible because the data violated assumptions of the standard ANOVA model, especially homoscedasticity and normality of residuals. Therefore, I analyzed the data by an alternative ANOVA model: The mean winglength was calculated for all adult male specimens collected between 1 May–31 July in each 2 min × 2 min block of latitude and longitude of the breeding grounds. In cases where only one male was examined in 2 min × 2 min blocks of latitude and longitude, I omitted these blocks from statistical analyses to prevent single specimens from having a disproportionately large potential influence on these analyses. Means from each block then were treated as single data points so that all geographic areas would be represented as equally as possible

in ANOVA analyses. These data were also analyzed by Kruskal-Wallis and Mann-Whitney *U* tests.

*Variation in plumage color.* Frequency data were analyzed in all cases using the G-test with Williams' correction (Sokal and Rohlf 1981:710).

All analyses were done using SYSTAT® (Wilkinson 1990b). The level of significance was defined as  $P < 0.05$  in all tests.

**RESULTS**

**VARIATION IN ADULT MALE WINGLENGTH**

*Breeding ground.* The eastern population shows very little variation in mean winglength (Fig. 5). In contrast, the western population shows a gradual clinal increase in mean winglength with in-

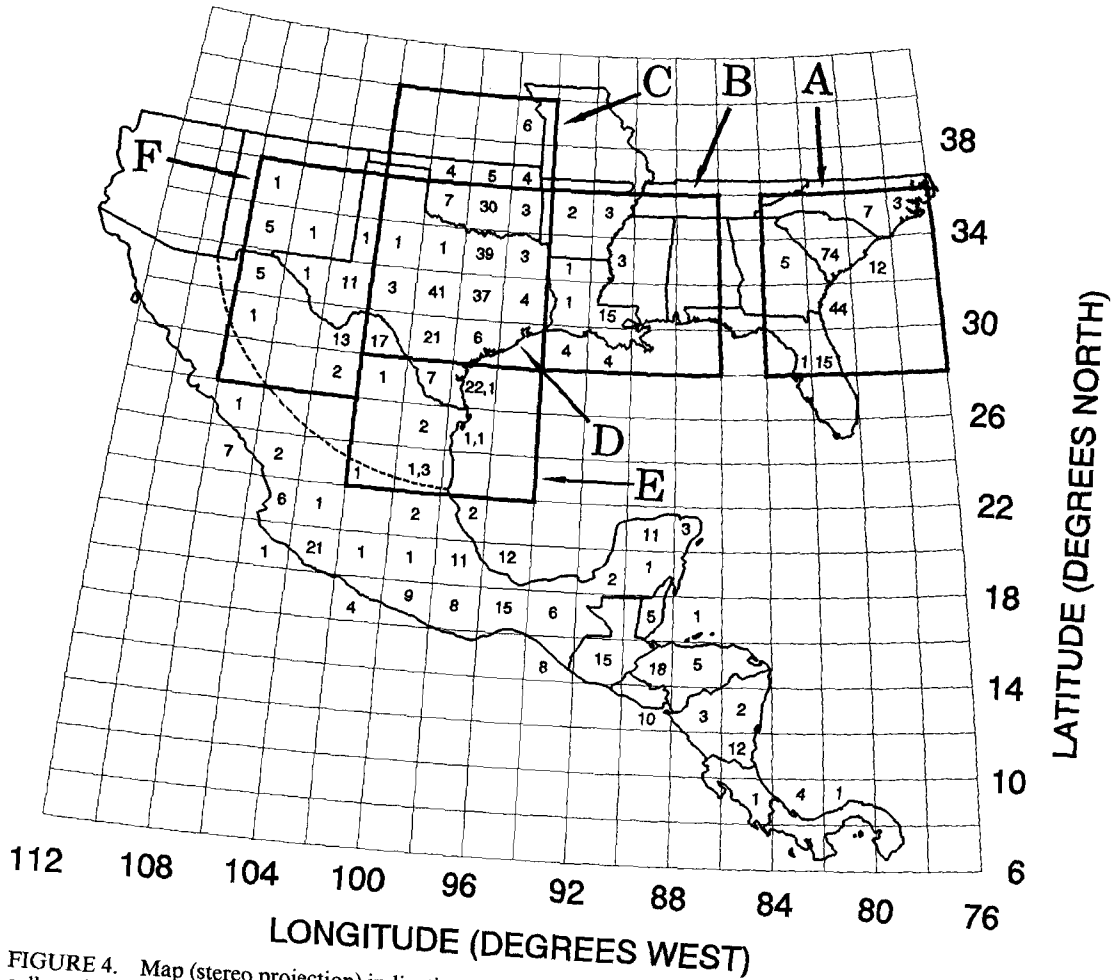


FIGURE 4. Map (stereo projection) indicating the sample size of male Painted Buntings in definitive plumage collected in each  $2 \times 2$  min block of latitude and longitude that were used in analyses of geographic variation in winglength. Specimens collected in each of the large blocks labelled A through F were treated as separate treatment groups for statistical analyses (see discussion of statistical methods in methods section). The  $2 \times 2$  min blocks above the dashed line in Mexico that contain two numbers represent the sample size of breeding specimens followed by the sample size of wintering specimens. Specimens were collected on the breeding and wintering grounds (above and below the dashed line in Mexico, respectively) from May 1–31 July and from 16 November–29 February, respectively.

creasing longitude and increasing latitude. For statistical analyses, the breeding range was divided into six large blocks of latitude and longitude (labelled A through F in Fig. 4). Analysis by ANOVA indicates highly significant differences in winglength among blocks ( $F = 13.755$ ,  $df = 5, 31$ ,  $P < 0.001$ ). Post-hoc multiple comparisons using Tukey's Honestly Significant Difference method (see Sokal and Rohlf 1981:244–245 for explanation) indicate that the eastern population (block A) is significantly smaller than the western *ciris* population (block B) which, in

turn, is significantly smaller than the *pallidior* population (blocks C–F) (Tables 1a and 1b). Analogous nonparametric comparisons between the eastern, western *ciris*, and *pallidior* populations yielded similar results (Mann-Whitney  $U$  test,  $U > 3.5$ ,  $df = 1$ ,  $P < 0.01$ ). However, the four blocks comprising the *pallidior* population did not differ significantly from one another (Tables 1a and 1b, Kruskal-Wallis test,  $K-W = 3.633$ ,  $df = 1$ ,  $P = 0.304$ ). In addition, there is no indication of a larger rate of increase (i.e., a stepped cline) in mean winglength at the interface be-

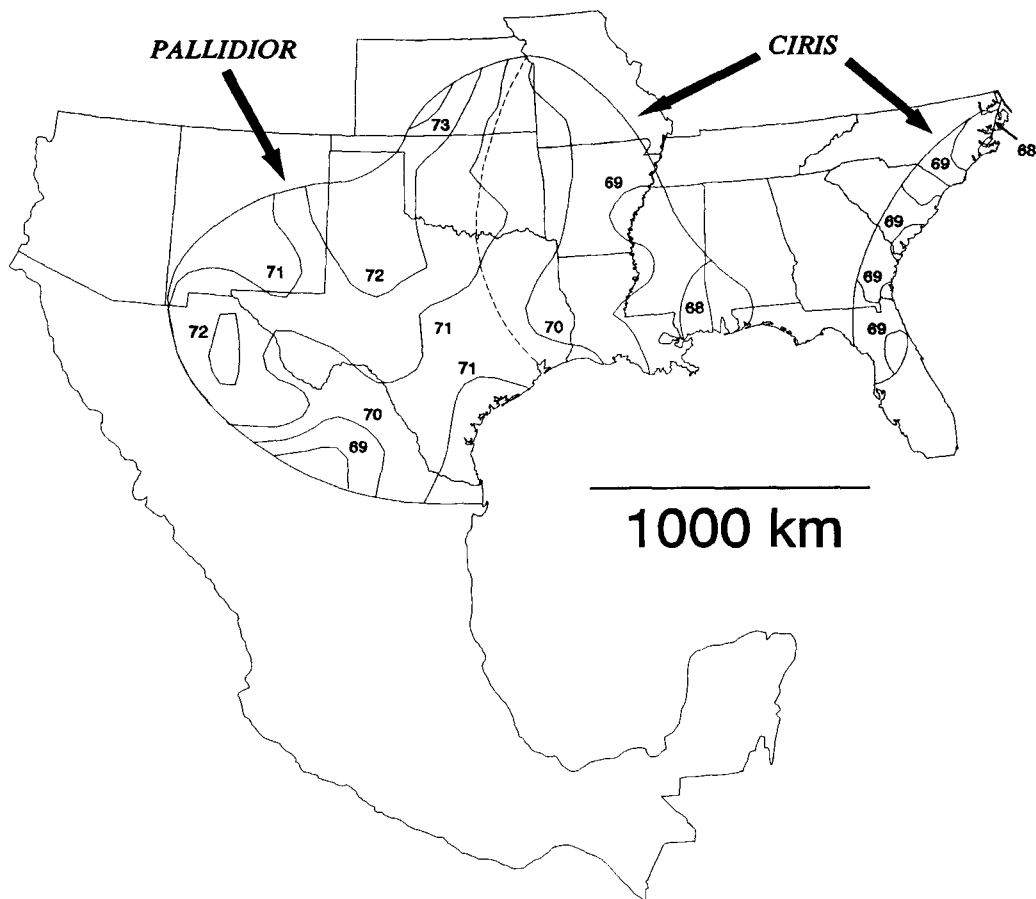


FIGURE 5. Clinal variation in winglength of male Painted Buntings in definitive plumage collected on the breeding grounds between 1 May–31 July is indicated by isoclinial lines. Numbers associated with isoclinial lines indicate mean winglength in mm. The boundary between the breeding ranges of the two currently recognized subspecies, *pallidior* and *ciris* (AOU 1957), is indicated by a dashed curved line through Kansas, Oklahoma, and Texas.

TABLE 1a. Matrix of pairwise mean differences in winglength (in mm) among male Painted Buntings in definitive plumage collected from 1 May–31 July from six geographic subdivisions of their breeding range (labelled A through F and corresponding to blocks A through F in Fig. 4). The mean winglength of adult males in block A is 68.56 mm.

	A	B	C	D	E	F
A	0.00					
B	1.08	0.00				
C	2.97	1.88	0.00			
D	2.34	1.26	-0.62	0.00		
E	1.78	0.70	-1.18	-0.56	0.00	
F	2.30	1.22	-0.67	-0.04	0.51	0.00

TABLE 1b. Matrix of probabilities that the two populations of adult males represented in each of the pairwise comparisons in Table 1a do not differ in mean winglength. Probabilities were calculated using Tukey's Honestly Significant Difference method (Wilkinson 1990b). Populations A through F correspond to blocks A through F in Fig. 4.

	A	B	C	D	E	F
A	1.00					
B	0.003	1.000				
C	0.000	0.002	1.000			
D	0.000	0.017	0.667	1.000		
E	0.013	0.739	0.291	0.834	1.000	
F	0.000	0.086	0.738	1.000	0.922	1.000

TABLE 2. Number of males and females in definitive plumage collected within the breeding ranges of *Passerina ciris ciris* and *P. c. pallidior* between 1 May–31 July.

Date	Males			Females		
	<i>pallidior</i>	<i>ciris</i> (west)	<i>ciris</i> (east)	<i>pallidior</i>	<i>ciris</i> (west)	<i>ciris</i> (east)
May 1–15	107	23	71	22	14	27
May 16–31	66	13	26	15	7	4
June 1–15	25	8	28	12	5	3
June 16–30	46	4	16	11	4	8
July 1–15	30	0	7	8	4	4
July 16–31	15	3	12	3	6	2

tween *ciris* and *pallidior* compared to elsewhere within the western breeding range of Painted Buntings to justify a demarcation between subspecies in this area (Fig. 5).

*Wintering ground.* On the wintering grounds in Mexico and Central America, the pattern of clinal variation in mean winglength of adult males is essentially opposite to that exhibited on the breeding ground, i.e., mean winglength increases from north to south. Adult males are smaller, on average, in southern Texas, Tamaulipas and the northern Yucatan Peninsula than elsewhere in Mexico and Central America. This suggests 1) that the western *ciris* population either migrates south around the Gulf of Mexico to southern Texas and Tamaulipas or across the Gulf of Mexico to the Yucatan Peninsula, and 2) that Painted Buntings from the northern breeding grounds of *pallidior* “leap-frog” migrate to the southern part of their wintering grounds.

#### VARIATION IN PLUMAGE COLOR

If Painted Buntings within the breeding range of the western *ciris* population are phylogenetically sister taxa to the eastern population rather than to *pallidior*, then the proportion of “bright” adult males and females in the western *ciris* population should be more similar to the proportion of “bright” adult males and females in the eastern population than in the *pallidior* population. However, the proportion of “bright” adult males and females in the breeding range of the western *ciris* population is similar to that of the adult males and females in the breeding range of *pallidior* (males:  $G_{adj} = 0.562$ ,  $df = 1$ ,  $P > 0.25$ ; females:  $G_{adj} = 0.75$ ,  $df = 1$ ,  $P > 0.25$ , Table 3), but differs significantly from that of adult males and females in the breeding range of the eastern population (males:  $G_{adj} = 9.292$ ,  $df = 1$ ,  $P < 0.005$ ; females:  $G_{adj} = 8.178$ ,  $df = 1$ ,  $P < 0.005$ , Table 3). In these comparisons, expected fre-

quencies in Table 3 were calculated from data in Table 2.

In addition, for a proposed character such as plumage color to be useful for subspecific identification, assignment of subspecies to individual specimens should be repeatable among investigators. Therefore, when individual specimens are assigned to subspecies independently by each of two investigators, their subspecies designations should agree with one another more often than not. However, of 48 adult males that were collected on the wintering grounds and assigned to subspecies independently by each of two investigators, only 20 males were given the same subspecies designation by both investigators. These results do not differ from that expected by random subspecies assignment ( $\chi^2 = 0.182$ ,  $df = 1$ ,  $P = 0.669$ ) and, therefore, suggest that variation in plumage color is not sufficiently greater between than within eastern and western populations to permit investigators to independently assign subspecies in a reproducible fashion to individuals or populations of Painted Buntings.

#### VARIATION IN PATTERN AND TIMING OF MIGRATION

*Pattern.* Three lines of evidence indicate that the eastern and western populations winter allopatrically, the eastern population wintering exclu-

TABLE 3. Frequency of males and females in definitive plumage collected within the breeding ranges of *Passerina ciris ciris* and *P. c. pallidior* between 1 May–31 July that exhibited “bright” plumage color.

	Males		Females	
	Observed	Expected	Observed	Expected
<i>pallidior</i>	105	144	26	35
<i>ciris</i> (west)	14	25	10	20
<i>ciris</i> (east)	131	80	43	24



sively in southern Florida, the Bahamas, Cuba, Jamaica, and Haiti, and the western population in southern Texas, Mexico and Central America. First, banding recovery data indicate that Painted Buntings in the eastern population winter exclusively in southern Florida and the Caribbean. All birds recovered in the breeding range of the eastern population ( $n = 5$ ) were initially banded in southern Florida or the Caribbean. Similarly, all birds recovered in the wintering range of the eastern population ( $n = 5$ ) were initially banded on the breeding grounds of the eastern population (United States Fish and Wildlife Service, Office of Migratory Bird Management, unpubl. banding recovery data). Second, adult males collected on the wintering grounds in southern Florida and the Caribbean are very similar in mean winglength ( $69.01 \pm 0.22$ ,  $n = 46$ ) to that of adult males collected on the eastern breeding grounds ( $69.08 \pm 0.07$ ,  $n = 314$ ; two sample  $t$ -test with separate variances,  $t = 0.281$ ,  $df = 56.3$ ,  $P = 0.78$ ; see also Fig. 5). Third, if some birds from the western population winter in southern Florida or the Caribbean, or from the eastern population winter in southern Texas, Mexico or Central America, then some of these individuals should be identifiable on the wintering grounds by their unusually large and small winglengths, respectively. I tested this prediction using adult males because use of this age and sex class yielded greater statistical power than use of other age and sex classes. Fourteen percent of adult males in the western breeding range have winglengths greater than 72.5 mm, the upper limit of the ninety-nine percent confidence interval (mean + 2.576 SD) for winglength of adult males in the eastern breeding range. However, no males with winglengths greater than 72.5 mm were found in southern Florida or the Caribbean ( $n = 46$ ). Similarly, three percent of adult males in the eastern population have winglengths less than 66.5 mm, the lower limit of the ninety-nine percent confidence interval for winglength of adult males in the western breeding range. However, no males with winglengths less than 66.5 mm were found in southern Texas, Mexico or Central America ( $n = 456$ ).

*Timing.* Because the eastern and western breeding populations winter allopatrically, timing of migration was analyzed separately for each population. Adult males and females undergo spring migration at about the same time in both populations, but undergo fall migration at least

two months later in the western population than in the eastern population (Figs. 2, 3).

## DISCUSSION

### VALIDITY OF *CIRIS* AND *PALLIDIOR* AS BIOLOGICAL SUBSPECIES

The subspecies concept is incompatible with the PSC in most if not all cases (Cracraft 1983, McKittrick and Zink 1988). Even within the BSC, the use of subspecies has been and continues to be controversial in many fields including ornithology (e.g., Barrowclough 1982, Gill 1982, Johnson 1982, Lanyon 1982, Mayr 1982b, Monroe 1982, O'Neill 1982, Parkes 1982, Phillips 1982, Storer 1982, Weins 1982, Zusi 1982). Optimally, if biological subspecies designations are to reflect meaningful phylogenetic relationships, then variation among subspecies should be discrete rather than continuous (e.g., clinal) in those characters used to discriminate among subspecies (O'Brien and Mayr 1991). This is most frequently the case when "members of a subspecies share a unique geographic range or habitat, a group of phylogenetically concordant phenotypic characters, and a unique natural history relative to other subdivisions of the species . . . . They will normally be allopatric and they will exhibit recognizable phylogenetic partitioning, because of the time-dependent accumulation of genetic difference in the absence of gene flow" (O'Brien and Mayr 1991).

Two lines of data presented above indicate that the patterns of geographic variation in adult male winglength and adult male and female plumage color do not warrant separating *P. ciris* into biological subspecies based on these criteria, and that the current subspecific geographic boundaries of the breeding distribution of *P. ciris* are not biologically meaningful.

First, clinal variation in winglength of adult males does not exhibit a stepped increase anywhere within the breeding range of *P. ciris*, including at the interface between the currently accepted breeding ranges of *ciris* and *pallidior* (Fig. 5). In addition, variation in winglength may result from environmental influences rather than heritable variation (James 1983). When this is the case, the use of such characters for systematic purposes is invalid.

Second, adult males and females collected within the breeding range of the western *ciris* population are more similar in plumage bright-

ness to specimens collected within the breeding range of *pallidior* than they are to specimens collected within the breeding range of the eastern population. If variation in adult plumage color is caused predominantly by heritable versus environmentally induced variation, then these results suggest that the western *ciris* population is more closely related to the *pallidior* population than to the eastern population. Although this supports my view that the subspecific boundaries of *pallidior* and *ciris* are inappropriate, the use of variation in adult plumage color as a taxonomic character in Painted Buntings is probably inappropriate for two reasons: (a) Although my results indicate that the eastern breeding range has a larger proportion of "bright" adult birds than does the western breeding range, variation in adult plumage color within each of these populations exceeds that between these populations. This has been commented on by many renowned ornithologists (e.g., Sutton 1967, Blake 1950). In addition, as discussed above, when individual specimens are assigned to subspecies by independent investigators, their subspecies designations do not agree with one another more often than expected by chance. This suggests that variation in plumage color is not significantly greater between than within eastern and western populations of Painted Buntings. (b) Red plumage color in Painted Buntings is produced by carotenoids (Thompson, unpubl. data) which must be ingested in the diet (Brush 1978). Aside from feather wear, variation in red plumage color probably results from variation in carotenoid composition in their plumage. Variation in carotenoid composition can occur due to differential absorption, transport and/or metabolic processing of ingested carotenoids and differential intake of carotenoids. Species that differ in absorption, transport or metabolism of ingested carotenoids usually exhibit substantial qualitative differences in plumage color (Brush 1981, 1990, pers. comm.). However, small quantitative differences in plumage color usually result from differential intake of carotenoids (e.g., Brush and Power 1976, Hill 1990, but see Hudon and Brush 1989). Because adult male and adult female Painted Buntings exhibit only small quantitative variation in plumage color, I speculate that this variation is due to differential intake of carotenoids rather than to heritable differences, but this remains to be tested.

#### GENE FLOW BETWEEN POPULATIONS

Five lines of evidence strongly suggest that there is little if any gene flow between eastern and western populations of Painted Buntings: (1) No birds initially banded in the breeding range of the eastern population were subsequently recovered in the breeding or wintering range of the western population or vice-versa; (2) If birds from the eastern population migrated in spring or fall across the hiatus between the breeding ranges of the eastern and western populations, then numerous sight and specimen records should exist for at least part of this hiatus, probably along the Gulf Coast. However, very few sight, banding or specimen records exist for these areas including the Gulf Coast (Birdlore 1899–1940, Audubon Magazine 1940–1946, Audubon Field Notes 1947–1970, American Birds 1971–1991, Sharpe 1888, Ridgway 1901, Hellmayr 1938, Ogden and Chapman 1967, Taylor et al. 1989; see also refs. cited in Thompson 1991); (3) Similarly, if Painted Buntings from the eastern population winter in Mexico and Central America, then many must pass through Cuba en route to and from the Yucatan Peninsula. As a result, Painted Buntings should be fairly common in Cuba during fall, winter and spring, especially during migration. However, records of Painted Buntings in Cuba are rare: (a) Cuba constitutes about 8.3% of their wintering grounds. However, only 15 (0.6%) of more than 2,600 museum specimens collected on the wintering ground (Thompson 1991, Orlando, pers. comm.) were collected in Cuba; (b) Only four (of 8,834) Painted Buntings have been banded ( $n = 2$ ) or recovered ( $n = 2$ ) in Cuba (Bird Banding Laboratory, unpubl. data) through 1983; four Painted Buntings also were banded in Cuba in October 1990 (Orlando, pers. comm.); (c) In the major works on the birds of Cuba (e.g., D'Orbigny 1839; Poey 1848; Lembeye 1850; Poey y Aloy 1851–1858; Gundlach and Cabanis 1854–1857; Gundlach 1861–1862, 1865–1866, 1871–1875, 1873, 1873–1876; Salvin and Godman 1879–1904; Cory 1886; Chapman 1892; Bangs and Zappey 1905; Todd 1916; Barbour 1923, 1943; Wetmore 1932; Bond 1950, 1956; Garrido and Schwartz 1969; Varona and Garrido 1970; Garrido 1973a, 1973b, 1980, 1988; Garrido and García-Montaña 1975; Garrido et al. 1986; Buden and Olson 1989; Alonso et al. 1990), Painted Buntings either are not mentioned or are

reported to be rare. In addition, most of these references do not indicate any apparent increase in frequency of Painted Buntings in fall or spring compared to winter that might indicate that Painted Buntings migrate through Cuba in spring or fall. However, Garrido and García-Montaña (1975) and Garrido (1988) report that Painted Buntings are "common" and "not rare," respectively, during migration; (4) No adult males collected on the wintering grounds in southern Texas, Mexico or Central America could be identified by winglength as eastern males. Similarly, no adult males collected on the wintering grounds in southern Florida or the Caribbean could be identified by winglength as western males; (5) The different molt-migration strategies exhibited by Painted Buntings in the eastern versus western population possibly evolved as adaptive responses to different resource availability in the eastern versus western United States in fall when Painted Buntings undergo flight feather molt (Thompson 1991). Assuming that the different molt-migration strategies are heritable characters, hybrid offspring from crosses between populations would surely be less well adapted, on average, relative to either of their parental genotypes (Rohwer and Manning 1990). As a result, hybrids must be strongly selected against, thereby favoring the evolution of reproductive isolation between these populations. That molt-migration strategies differ so dramatically between populations strongly suggests that significant gene flow does not occur between these populations.

#### TAXONOMIC IMPLICATIONS

In recent years, many former species that exhibit little morphological variation and that breed in two allopatric geographic ranges have been found to be separate species, e.g., Black-tailed, *Poliophtila melanura*, and California, *P. californica*, gnatcatchers (Atwood 1988), Canyon, *Pipilo fuscus*, and California, *P. crissalis*, towhees (Zink 1988, Zink and Dittmann 1991), Red-eyed, *Vireo olivaceus*, and Yellow-green, *V. flavoviridis*, vireos (Johnson and Zink 1985), and Cordilleran, *Empidonax occidentalis*, and Pacific Slope, *E. difficilis*, flycatchers (Johnson and Marten 1988). Such pairs of species often exhibit different vocalizations and allozyme frequencies (e.g., Zink 1988, Zink and Dittmann 1991).

The data presented above indicate that there is little if any gene flow between the eastern and

western populations of Painted Buntings. In addition, variation in song structure in Painted Buntings is significantly greater between eastern and western populations than it is within these populations, e.g., at least some males in each population sing songs that are unique to their own population (Thompson 1968, pers. comm.). These results suggest that eastern and western populations of Painted Buntings probably represent separate phylogenetic species. This possibility should be investigated by comparison of other character systems (e.g., song structure, allozyme frequencies) between eastern and western populations of Painted Buntings.

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