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REFINED COLORIMETRY VALIDATES ENDANGERED SUBSPECIES OF THE LEAST TERN[1]

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Abstract. In contrast to the results of Thompson et al. (1992), refined colorimetry validates three subspecies of Least Tern in North America, *Sterna antillarum antillarum* (Lesson), *S. a. browni* Mearns, and *S. a. athalassos* Burleigh and Lowery. Four of nine color characters exhibited significant seasonal differences, presumably a result of plumage wear and bleaching. The sexes differed in lightness and hue of dorsum and hind neck. Males of *S. a. athalassos* differed significantly from those of both *S. a. antillarum* and *S. a. browni* in lightness of dorsum, and males of *S. a. browni* differed significantly from those of *S. a. antillarum* in lightness of hind neck. Females generally showed patterns concordant with males. Because *S. a. browni* and *S. a. athalassos* are listed as endangered, the validity of these taxa is important to conservationists and managers. Rigorous systematic methodology and scientific collections of high quality are indispensable to conservation biology.

Key words: colorimetry, conservation biology, endangered subspecies, Least Tern, Sterna antillarum, *taxonomy.*

Resumen. A diferencia de un estudio reciente (Thompson y otros 1992), la colorimetría refinada sustenta la validez de tres subespecies de golondrina marítima mínima formalmente designadas en América del Norte, *Sterna antillarum antillarum* (Lesson), *S. a. browni* Mearns y *S. a. athalassos* Burleigh y Lowery. De nueve caracteres de color, cuatro mostraron diferencias significativas temporales, presumiblemente como resultado de desgaste y blanqueamiento del plumaje. Los sexos se diferenciaron en términos del "hue" [una medida cuantitativa de color expresada en grados en un diagrama cromático] y el grado de claridad de la parte posterior del cuello y del dorso. Los machos de *S. a. athalassos* se distinguieron significativamente de los machos de *S. a. antillarum* y de *S. a. browni* en el grado de claridad del dorso, mientras que los machos de *S. a. browni* difirieron significativamente de los machos de *S. a. antillarum* en el grado de claridad de la parte posterior del cuello. Las hembras mostraron patrones generalmente concordantes con los de los machos. Debido a que *S. a. browni* y *S. a. antillarum* están consideradas en peligro de extinción, la validez de estos dos taxones como unidades evolutivas significativas es importante para conservacionistas y administradores. Una metodología sistemática rigurosa y colecciones científicas de alta calidad son indispensables para la biología de conservación.

Palabras claves: biología de conservación, colorimetría, Sterna antillarum, *subespecies en peligro de extinción, taxonomía.*

INTRODUCTION

Subspecies whose populations are threatened are more likely to receive the attention of managers and conservationists than similarly declining, non-named populations (Rojas 1992). Thus the methods by which subspecies are named and validated are of primary importance, not only for evolutionary and systematic studies but also for the assessment of units that need conservation attention.

Thompson et al. (1992) analyzed the validity of long-recognized subspecies of North American Least Terns (*Sterna antillarum*), two of which are endangered (*S. a. browni* of the Pacific Coast and *S. a. athalassos* of the Mississippi Valley). Based on a quantitative appraisal of seven morphologic features, an analysis of electrophoretic variation of proteins encoded by 50 genetic loci, and subjective comparisons of dorsal color, they found no significant differences among the named subspecies.

In describing *S. a. browni,* Mearns (1916)

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claimed that this taxon was "slightly smaller than *Sterna antillarum antillarum.*" Burleigh and Lowery (1942), the original describers of *S. a. athalassos,* found no size differences among any subspecies of North American Least Terns. Thompson et al.'s (1992) more thorough morphometric analysis clearly established the uniformity of the various populations and also provided a rigorous statistical analysis heretofore lacking. Although their allozyme results also were negative, Thompson et al.'s (1992) genetic findings provided a useful perspective not previously available.

Because North American subspecies of Least Terns were described primarily on the basis of color differences, it is in this category of characters that the subspecies should be assessed. Thompson et al's. (1992) analysis of color consisted of an assessment of the mid-region of the back which

> "was quantified by comparison with a Kodak Reflection Density Guide ... graduated in 24 steps ... that varied from white (0.0) to black (2.0). Each specimen was viewed independently by four observers under the same lighting conditions and scored by determining closest match between scale patch and specimen back reflectance (or coloration). Four scores for each specimen were averaged to produce a composite reflectance value (DENSITY)."

For the following reasons, we think that Thompson et al's (1992) analysis of color skirted the rigorous requirements of modern avian systematic methodology and was prone to error: (1) human color perception is subjective and notoriously variable among individuals (Endler 1990, Mollon 1995); (2) color assessment along a white to black gradient disguises the fact that color varies and can be measured quantitatively according to three independent parameters, lightness (value), chroma (purity), and hue (dominant wavelength) (Rossotti 1983, Minolta Company 1994); and (3) Thompson et al. (1992) did not mention the strict requirement that only clean specimens are suitable for a proper color analysis. Because the majority of specimens of Least Terns in existing museum collections are discolored to varying degrees as a result of soiling, fat leakage, and other adventitious sources, we suspect that real color differences could have been obscured by failure to exclude all such specimens. Finally, (4) Thompson et al. (1992) did not comment on the need to exclude specimens taken late in the nesting season, when feather bleaching or wear could have modified colors (Cardiff and Remsen 1994). This is an especially important consideration for species such as the Least Tern, which nest in open, sunny, sandy areas, a potentially bleaching and highly abrasive environment.

We used modern colorimetry to quantitatively analyze color variation in populations of the Least Tern in North America, including *S. a. antillarum, S. a. athalassos,* and *S. a. browni.* In the absence of sufficient museum specimens, *S. a. mexicana,* which breeds along the Pacific Coast of Mexico from Sonora to Sinaloa, and *S. a. staebleri,* which breeds on the Pacific Coast of Oaxaca and Chiapas, were excluded from the study. Patten and Erickson (1996) have recently commented on the distributions and characters of all five subspecies.

METHODS

MUSEUM SPECIMENS

In view of the endangered status of *S. a. athalassos* and *S. a. browni,* we relied upon existing material in museum collections for this study. Colorimetric analysis was based upon 147 clean specimens of breeding adults taken in six regions of the United States (Fig. 1, top) as follows: *S. a. browni*—Population 1, Pacific Coast of central California ($n = 42$ [Monterey County, $n = 41$; Santa Cruz County, $n = 1$]); Population 2, Pacific Coast of southern California ($n = 15$ [Los Angeles County, $n = 2$; Ventura County, $n = 3$; Orange County, $n = 4$; San Diego County, $n = 6$]). *S. a. athalassos*—Population 3, central interior Mississippi Valley ($n = 15$ [South Dakota, $n = 1$; Kansas, $n = 13$; Missouri, $n = 1$]); Population 4, southern interior Mississippi Valley ($n = 25$ [Tennessee, $n = 5$; Texas, $n = 1$; inland Louisiana, $n = 14$; inland Mississippi, $n = 5$]). *S. a. antillarum*—Population 5, Gulf Coast ($n = 32$ [Texas, $n = 4$; Louisiana, $n = 5$; Mississippi, $n = 16$; Alabama, $n = 1$; Florida, $n = 6$]); Population 6, Atlantic Seaboard ($n = 18$ [Massachusetts, $n = 2$; New York, $n = 2$; Maryland, $n = 1$; Virginia, $n = 2$; South Carolina, $n = 2$; Georgia, $n = 4$; Florida, $n = 5$]). Because the majority of suitable specimens were males (108 vs. 39 females), the analysis of females is preliminary. The unfortunate macrogeographic scale of this analysis was unavoidable given the scarcity of museum specimens in acceptable condition from large geographic regions, a problem not likely to be overcome in the near future in view of the endangered status of many populations.

COLORIMETRY

Coloration of specimens was assessed with a Minolta CR-300 Colorimeter using the L*C*h° color space, where: "L" (value [= brightness]) is percentage lightness on a scale of 0 for black and 100 for white; "C" (chroma [= "purity"]) is percentage saturation on a scale of 0 for white and 100 for pure color; and "h°" (= hue) is expressed in degrees of a circle, starting with red (0 degrees), continuing through yellow (90 degrees), green (180 degrees), blue (270 degrees), and completing the circle at red (360 degrees). Measurements were taken from the center of the back (dorsum), the hind neck immediately posterior to the black crown, and the center of the breast. To reduce measurement error, this instrument takes three readings and computes an average. To assure that a representative average reading was taken from the body region of interest, we repositioned the colorimeter on the sample between both the first and second and the second and third readings.

STATISTICAL ANALYSES

Because feather wear during the breeding season may influence colorimetric measurements, we divided the specimens into two groups according to date of collection: April to mid-July (early season), and mid-July to early September (late season). Multivariate and one-way analyses-of-variance (SPSS 1990) were used to test for possible effects of season, sex, and geography (clusters of populations) on patterns of variation. Geographic variation in single colorimetric characters was then examined with the sums-of-squares simultaneous test procedure (SS-STP; Gabriel 1964, Gabriel and Sokal 1969), using the program from Sokal and Rohlf (1969) as modified into the program PAIRS by Bruce Krogman and Alan Stangenberger (Department of Environmental Science, Policy, and Management, University of California, Berkeley). This procedure conducts an *a posteriori* analysis-of-variance on all samples for each character in order to identify maximally homogeneous subsets of means (significantly different from other subsets at $P < 0.05$). Multivariate separation of samples was assessed using stepwise canonical discriminant function analysis (SPSS 1990). Specimens with at least one missing colorimetric measurement (males = 8, females = 2) were automatically excluded from this analysis. Groups were defined according to the three subspecies (*S. a. browni, S. a. athalassos, and S. a. antillarum*), and prior probabilities of classification were based upon the proportion of specimens in each group. Wilk's lambda and Mahalanobis' distance criteria were used to select variables entered into each step of the analysis. Discriminant scores were plotted on two functions.

RESULTS

We found a strong seasonal effect ($P < 0.05$) on four of the nine characters (dorsum-C, dorsum-h° , hind neck-C, breast-L), presumably resulting from plumage wear, and a strong interaction between geography and season (Wilks' multivariate test, $P < 0.001$). Consequently, 27 late-season specimens (17 males, 10 females) were excluded from further analysis. Of the 120 April to mid-July birds in the final sample, 104 (87%) were taken prior to 1950. The remaining 16 specimens also are relatively old (1951–1960, 5 specimens; 1961–1970, 6; 1971–1980, 4; 1987, 1). Thus, no recent specimens exist to allow the study of possible change in coloration in relation to specimen year. We note, however, that the cleanest series of specimens we encountered (in the California Academy of Sciences) were taken 90 years ago (1907) by R. H. Beck, indicating that condition does not necessarily correlate with specimen age.

Analyses-of-variance (Table 1) on specimens collected before mid-July demonstrated significant effects of geography for all characters except chroma (for dorsum and hind neck, weakly significant in one-way analysis but not significant in multivariate analysis). An unexpected sex effect also was evident for lightness and hue of both dorsum and hind neck but not for any color feature of the breast. There was no significant interaction of geography with sex (Table 1). Differences between sexes prompted us to separate them in the SS-STP and discriminant analyses.

UNIVARIATE PATTERNS OF GEOGRAPHIC VARIATION

The SS-STP analyses illustrated significant differences among samples from clusters of popu-

TABLE 1. Univariate F-statistics for multivariate (top value[a]) and one-way (bottom value[b]) analyses-of-variance on nine colorimetric characters and two factors.[c]

	Dorsum (n = 120)			Hind neck (n = 112)			Breast (n = 116)		
Factor	L	C	H	L	C	H	L	C	H
Geography	24.51***	2.11	12.76***	2.83*	1.63	11.30***	19.92***	1.11	6.77***
	34.30***	3.11*	15.21***	5.45***	2.81*	14.68***	26.60***	1.17	10.92***
Sex	25.53***	0.01	11.36**	1.93	0.18	9.68**	3.76	0.70	0.16
	25.21***	0.27	13.09***	4.67*	0.03	12.70**	1.27	1.64	0.06
Geography × Sex	1.13	0.45	2.22	0.52	1.04	1.68	1.25	2.06	0.69
	1.22	0.35	2.06	0.54	1.02	1.92	1.24	1.90	0.70

[a] Degrees of freedom (df) for univariate F-tests in multivariate analysis: Geography, $F_{5,98}$; Sex, $F_{1,98}$; Geography × sex, $F_{5,98}$.

[b] df for one-way analyses: Dorsum—Geography, $F_{5,108}$; Sex, $F_{1,108}$; Geography × sex, $F_{5,108}$. Hind Neck—Geography, $F_{5,100}$; Sex, $F_{1,100}$; Geography × sex, $F_{5,100}$. Breast—Geography, $F_{5,104}$; Sex, $F_{1,104}$; Geography × sex, $F_{5,104}$. Differences in df are due to different sample sizes for dorsum, hind neck, and breast; on some specimens, hind neck and breast were not suitable for colorimetry because of soiled or ruffled plumage.

[c] * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; others $P > 0.05$.

lations in the six geographic regions. Because the sexes varied concordantly within each set of samples for most individual color characters, only the diagrams for males are illustrated (Fig. 1–3). Results for females are discussed below. The few discrepancies in pattern between males and females are probably a result of relatively small sample sizes for females.

In lightness of dorsum of males (Fig. 1), Mississippi Valley (*S. a. athalassos)* sample means were significantly lower than those from the Pacific Coast (*S. a. browni*), which in turn were significantly lower than those from the Gulf Coast but not the Atlantic Seaboard *(S. a. antillarum*). In females, Mississippi Valley and Pacific Coast birds formed a subset of means that differed significantly from the higher mean shown by Gulf Coast–Atlantic Seaboard samples. Chroma of dorsum separated males into two subsets, with those from the central interior Mississippi Valley having significantly lower values than those from the southern California Pacific Coast; in females no subsets were discriminated. In hue of dorsum in males, Mississippi Valley birds differed significantly from Atlantic Seaboard, Gulf Coast, and southern California clusters of populations but not from central Pacific Coastal birds. Females showed two subsets in hue of dorsum, with combined samples of *S. a. antillarum* (Gulf Coast, Atlantic Seaboard) differing significantly from all samples of both *S. a. athalassos* and *S. a. browni.*

In lightness of hind neck in males, samples from the two population clusters of *S. a. antillarum* showed a strong break that distinguished them from both Mississippi Valley and Pacific Coastal birds (Fig. 2). The latter two groups were inseparable. Samples of females did not differ in this character. Two subsets of males segregated in chroma of hind neck, with central interior Mississippi Valley birds differing significantly from those along the Pacific Coast of southern California; females again showed no difference. This pattern for both males and females duplicated the findings for chroma of dorsum. High mean values for hue of hind neck separated males of *S. a. antillarum* (Gulf Coast–Atlantic Seaboard) and S. *a. athalassos* (Mississippi Valley), but the latter did not differ significantly from males of central California *S. a. browni.* In contrast, southern California *S. a. browni* were separable from both central and southern samples of *S. a. athalassos,* but did not differ significantly from either of the two sets of samples of *S. a. antillarum.* In females, combined samples of *S. a. antillarum* differed significantly in hue of hind neck from all samples representing both the Mississippi Valley and Pacific Coast, a pattern duplicated by hue of dorsum.

Lightness of breast in males paralleled lightness of dorsum in demonstrating a trenchant geographic pattern (Fig. 3), whereby low mean values along the Pacific Coast contrast with intermediate values in the Mississippi Valley and high values along the Atlantic Seaboard–Gulf Coast. *S. a. browni* differed significantly in this character from *S. a. antillarum,* but not from *S. a. athalassos.* Females showed the same pattern as males. Chroma of breast in males is noteworthy in showing an unexpectedly strong significant difference between the two Pacific Coast populations representing the same subspecies, *S. a. browni.* Means for the other four population clusters of males did not differ significantly, nor did any samples of females. For hue of breast in males, both the Gulf Coast and Atlantic samples of *S. a. antillarum* showed high mean values that contrasted with low to intermediate values in *S. a. athalassos* and *S. a. browni.* Females exhibited a similar pattern.

DISCRIMINANT ANALYSIS OF SUBSPECIES

Discriminant function analysis clearly separated the three subspecies along functions I and II (Fig. 4). Specimens of *S. a. antillarum* were especially distinct on the first axis. Males of this subspecies showed only modest overlap with *S. a. browni* and no overlap with *S. a. athalassos,* whereas females of *S. a. antillarum* were completely separate from the other two groups. Both sexes of *S. a. browni* were separated from *S. a. athalassos* along the second discriminant function, although overlap was greater in females (possibly a result of small sample sizes).

For males, Wilks' lambda and univariate *F*-ratios ($F_{2,80}$) were significant ($P < 0.05$) for eight of the nine colorimetric characters, the exception being chroma of breast. Colorimetric characters were entered into the stepwise discriminant function analysis in the following order: lightness of dorsum, lightness of breast, hue of breast, lightness of hind neck, and chroma of hind neck. *F*-statistics for these were highly significant ($P < 0.0001$). The remaining four variables (chroma of dorsum, hue of dorsum, chroma of breast, hue of hind neck) were excluded from the stepwise analysis of males because of low tolerance (i.e., the proportion of their within-group variance not accounted for by the other characters already in the analysis). Lightness of dorsum had the highest standardized coefficient on function I (0.854), whereas hue of breast had the highest standardized coefficient on function II (0.723); lightness of dorsum also had a relatively high coefficient (0.686) on this second axis. Classification results for males were highly successful, with 91.6% of specimens correctly classified according to subspecies (Table 2). Males of *S. a. athalassos* were most likely to be classified correctly (100.0% of specimens), followed by *S. a antillarum* (93.3%) and *S. a. browni* (86.1%). Wilks' lambda and Mahalanobis' distance criteria for stepwise entry of variables gave identical results.

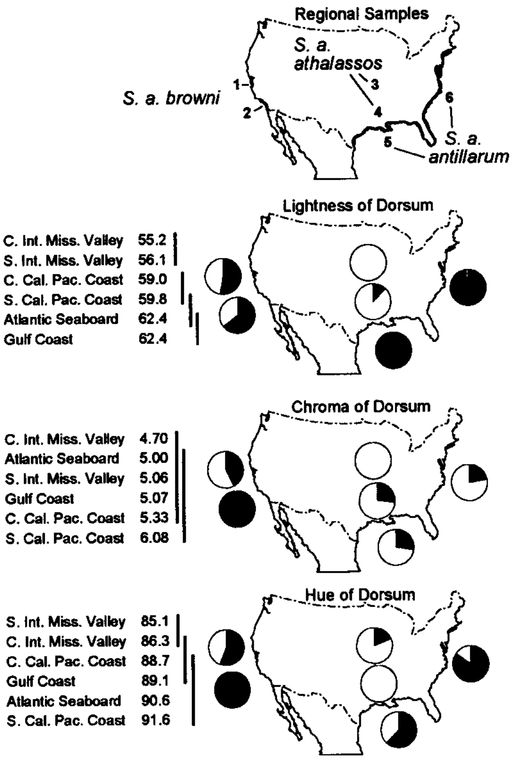

FIGURE 1. Sums-of-squares simultaneous test procedure (SS-STP) applied to variation in color of dorsum of male Least Terns. The results are presented as maps of geographic variation with accompanying lists of means, ranked in order of magnitude, and placed next to the population name of each sample. Adjacent vertical lines denote homogeneous subsets. For portrayal of the variation on each map, the total range of means for each character was converted to 100% and the pie diagrams for localities were scaled according to the relative magnitude of each mean. Because computation of homogeneous subsets was based on values for the sample mean, sample size, and standard deviation, these diagrams obviate the need to present routine statistics. Subsets are formed independently of geography; therefore, samples from widely disparate regions will be grouped together if their means do not significantly differ.

Fewer colorimetric characters were significant in the discriminant function analysis of females. Wilks' lambda and univariate *F*-ratios ($F_{2,24}$) were significant ($P < 0.05$) for lightness and hue of dorsum, lightness and hue of breast, and hue of hind neck, but not for any chroma variables nor for lightness of hind neck. Only two characters (hue of dorsum, lightness of breast) were entered into the stepwise analysis before the minimum tolerance level was reached. These two variables had high standardized coefficients on discriminant function I (0.829 and 0.909, respectively), and moderate coefficients on function II (0.666 and −0.553). Overall, 77.8% of females were classified correctly with respect to subspecies (Table 2). The best classification results were obtained for *S. a. antillarum* (100% of females correctly classified), followed by *S. a. athalassos* (71.4%), and *S. a. browni* (60.0%). As with males, identical discriminant function results were obtained using the Wilks' lambda and Mahalanobis' distance criteria.

DISCUSSION

We found that males of *Sterna antillarum browni* Mearns (1916), *S. a. athalassos* Burleigh and Lowery (1942), and *S. a. antillarum* (Lesson) are clearly distinguishable on the basis of color. Females of these three taxa also are separable from each other, with *S. a. antillarum* being most distinctive compared to the other two forms. Therefore, counter to the conclusions of Thompson et al. (1992), *S. a. browni, S. a. athalassos,* and *S. a. antillarum* constitute valid subspecies. The occupancy of profoundly different nesting environments by *S. a. athalassos* and *S. a. browni,* i.e., continental lakeshores and riverine gravel bars (Hardy 1957) versus maritime sandy beaches, respectively, also may be relevant to their systematic and evolutionary status. Because *S. a. browni* and *S. a. athalassos* remain endangered, they deserve recognition by managers and conservationists.

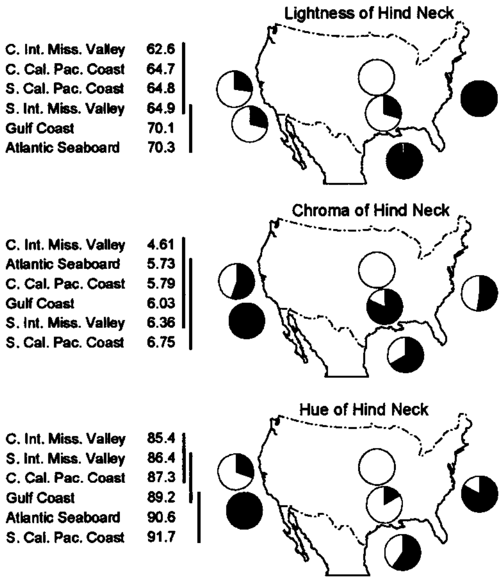

FIGURE 2. SS-STP applied to population variation in color of hind neck in male Least Terns. The analysis and presentation of geographic variation in these three characters are the same as for the three characters of dorsal color (see legend to Fig. 1).

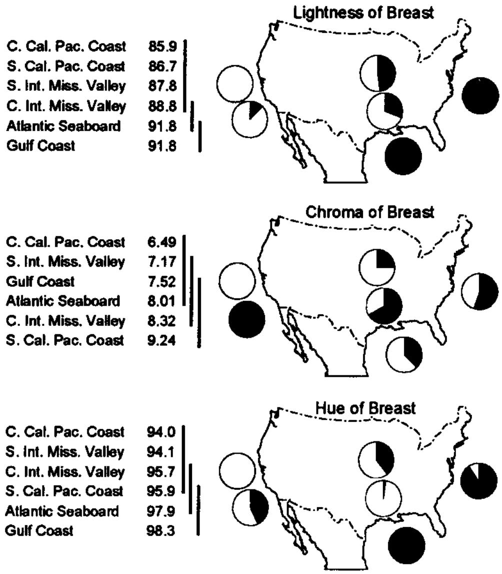

FIGURE 3. SS-STP applied to population variation in color of breast in male Least Terns. The analysis and presentation of geographic variation in these three characters are the same as for the three characters of dorsal color (see legend to Fig. 1).

A surprising finding was the distinction of central from southern populations along the coast of California, which are currently included within *S. a. browni.* Males from these two populations differed significantly in hue of hind neck and chroma of breast. For the latter character, the means occurred at the extremes of the six population clusters studied. One possible explanation is that southern populations of *S. a. browni* in California are influenced by gene flow from the (supposedly) darker *S. a. mexicana* that breeds along the northwest coast of Mexico. Investigation of this possibility will require the examination of larger samples of specimens from southern California and Mexico to clarify patterns of color differentiation in this region.

Whereas genetic differences among the three forms of Least Tern would support our view based on colorimetry that they are recognizable, Thompson et al.'s (1992) finding of allozymic similarity should not be interpreted to mean that subspecies designations are unwarranted. Birds in general demonstrate low protein differentiation, often even at the species level (Avise and Aquadro 1982), and allozymic studies of other members of the Laridae have similarly shown low levels of variation (e.g., Karl et al. 1987 for disjunct subspecies of *Larus californicus*; Hackett 1989 for *Sterna hirundo* versus *S. vittata;* Snell 1991 for large species of *Larus*). As Thompson et al. (1992) recognized, however, more sensitive molecular techniques might yield greater resolution and we encourage their use in future studies. Given the difficulty of collecting new material of endangered taxa, the application of PCR-based DNA techniques to museum skins of Least Terns would be especially promising (see Leeton et al. 1993, DeGusta and White 1996, Mundy et al. 1997).

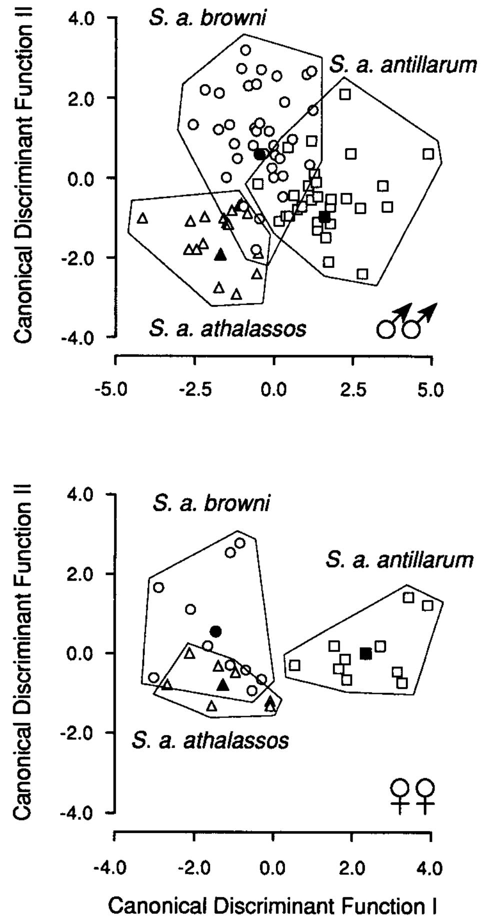

FIGURE 4. Discriminant scores of male and female Least Terns, plotted on two functions and grouped by subspecies. Solid symbols indicate group centroids.

TABLE 2. Discriminant function classification of Least Tern specimens into three subspecies groups. The overall percentage of specimens correctly classified is 91.6% for males and 77.8% for females.

			Predicted group membership (%)		
Actual group	Sex	*n*	*S. a. browni*	*S. a. athalassos*	*S. a. antillarum*
S. a. browni	Males	36	86.1	8.3	6.7
	Females	10	60.0	40.0	0.0
S. a. athalassos	Males	17	0.0	100.0	0.0
	Females	7	28.6	71.4	0.0
S. a. antillarum	Males	30	6.7	0.0	93.3
	Females	10	0.0	0.0	100.0

The lack of morphometric differences among the forms of Least Tern (Thompson et al. 1992) likewise should not influence their recognition as subspecies. Many valid geographic forms of birds are distinguishable only by features of color, and even species may not be diagnosable with complete certainty on the basis of size measurements (Rising and Schueler 1980, Connors 1983).

We have no information on possible differences in voice or breeding displays that could serve as reproductive isolating mechanisms and would therefore indicate biologic species status for the named taxa of North American Least Terns. Nor are we aware of any taxa of *Sterna* which differ *only* in minor features of plumage but are treated as species.

Cracraft (1983) recommended that diagnosable taxa, such as the three forms of terns discussed here, be recognized as "phylogenetic species." Barrowclough and Flesness (1996) further advocated that traditional subspecies be considered equivalent to such phylogenetic species when selecting units for conservation management. Although units for conservation can and should be chosen from any taxonomic rank, to use the term "species" for the three geographic forms of Least Terns would both falsely accentuate their minor differences and inflate their status in the eyes of nonsystematists and others unfamiliar with the philosophical basis of species concepts, perhaps resulting in the siphoning of scarce resources away from efforts to save more divergent taxa.

Our data underscore the importance to conservation biology of rigorous systematic methodology (Rojas 1992) and scientific collections of high-quality (Remsen 1995). Furthermore, these results reaffirm the utility of the subspecies concept in Least Terns and, by extension, in many other taxa. Named geographic segments of species flag patterns of morphology, coloration, habitat selection, and behavior, thereby attracting attention and stimulating research. Even if a significant number of geographic forms cannot stand the scrutiny of modern analytic techniques, leading to their abandonment, other such entities will turn out to be full species (Johnson 1982, Prum 1994, Cicero 1996).

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