GENERAL NOTES

Wilson Bull., 96(2), 1984, pp. 277–286

A morphometric comparison of Western and Semipalmated sandpipers.—Semipalmated (*Calidris pusilla*) and Western (*C. mauri*) sandpipers are common migrant shorebirds of the east and west coasts of North America, respectively. Identification of these species can be notoriously difficult. In the field this can be accomplished by behavioral differences that include call notes (Bent, U.S. Natl. Mus. Bull. 142, 1927; Wallace, Br. Birds 67:1–17, 1974), feeding microhabitat (Recher, Ecology 47:393–407, 1966; Ashmole, Auk 87:131–135, 1970), and flight posture (Palmer, pp. 143–267 *in* The Shorebirds of North America, E. Stout, ed., Viking, New York, New York, 1967). In spring plumage, these species are more readily separable, *C. mauri* shows extensive chestnut on the crown and on the dorsum, and greater amounts of spotting on the breast and flanks than does *C. pusilla* (Palmer 1967). In winter plumage, however, the two species are difficult to distinguish. Size differences are known; *C. mauri* generally has a longer bill (Ouellet et al., Can. Field-Nat. 87:291–300, 1973; Fig. 1, this study). Frequently birds in winter plumage are hard to separate by bill length alone.

Ouellet et al. (1973) found considerable overlap in bill size. They used sexed museum study-skins and graphically contrasted two bill measurements which yielded a maximum separation between the species. Because of the broad overlap *C. pusilla* and *C. mauri* seemed morphometrically inseparable.

I analyzed mensural data from museum study skins and skeletons of *C. pusilla* and *C. mauri* to determine if these species are indeed morphometrically distinct. My primary objectives were: (1) to quantify and compare the phenetic differences between the two species and their sexes; and (2) to provide species- and sex-differentiating criteria for problematic skeletal and study-skin specimens.

Methods.—I measured study skins and skeletons of *C. mauri* and *C. pusilla* taken during breeding or on migration. No juvenile birds taken from July through December were measured, because many likely do not reach full adult dimensions in this interval. I measured 22 characters on skeletons to the nearest 0.1 mm, using dial calipers (Fig. 2). I measured 49 male and 61 female *C. pusilla,* taken in autumn during migration (N = 90) from southern Canada and the northern United States and from the Arctic breeding grounds (N = 20), and 42 male and 41 female *C. mauri,* taken in autumn migration (N = 65), and from the breeding grounds (N = 18).

I measured the following variables on study skins (estimated measurement error in parentheses): exposed culmen (0.2 mm), distance from distal portion of nostril to tip of bill (0.2 mm), tarsus length (0.5 mm), and natural (unflattened) wing length (1.0 mm). Characters measured but discarded due to low measurement repeatability were: bill width (across the base of the nostrils), tail length, and phalanx length. In the study skin analyses, I measured 147 male and 107 female *C. pusilla,* and 51 male and 52 female *C. mauri,* all taken with a similar seasonal and geographic distribution as the skeletal material.

For the skeletal data set, missing values were estimated with the BMDP-AM procedure (Dixon and Brown, Biomedical Computer Programs, P-series, Univ. Calif. Press, Berkeley, California, 1979). Specimens missing more than three measurements were not used.

I used direct and stepwise discriminant functions analysis (DFA; Nie et al., Statistical Package for the Social Sciences, McGraw-Hill, New York, New York, 1975). In all analyses, except where noted, the "direct" method was used to analyze those variables with means differing between groups (species or sexes) by at least 0.1 mm (measurement error). Hence, I minimized the consideration of univariate differences attributable solely to measurement error.

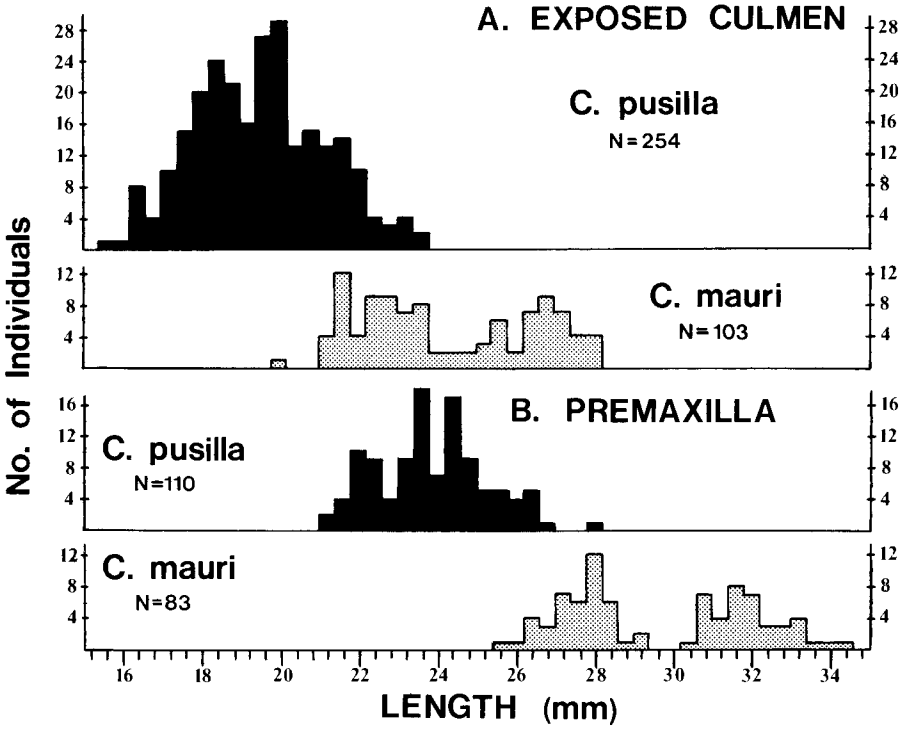

FIG. 1. Bill measurements from study skins (exposed culmen) and skeletons (premaxilla) showing the degree of overlap between the two species on this character which best discriminates between the two species. (Species identification of birds in [B] verified correct from Fig. 3.)

To establish species-discriminating criteria, I used a "known" (correctly identified) sample of birds from each species, irrespective of sex and chosen by their collecting locality and season. I assumed that a bird could correctly be identified as *C. mauri* when collected in breeding plumage (April to July, Palmer 1967), or on the west coast of the United States. Similarly, a "known" *C. pusilla* was one collected in breeding plumage (April to July, Palmer 1967), and/or in arctic or eastern Canada. To separate the species, a DFA using "knowns" only was performed. This allowed the "unknowns" to be verified. Classification of all "unknowns" (birds not conforming to the above criteria) corresponded to identity on spec-

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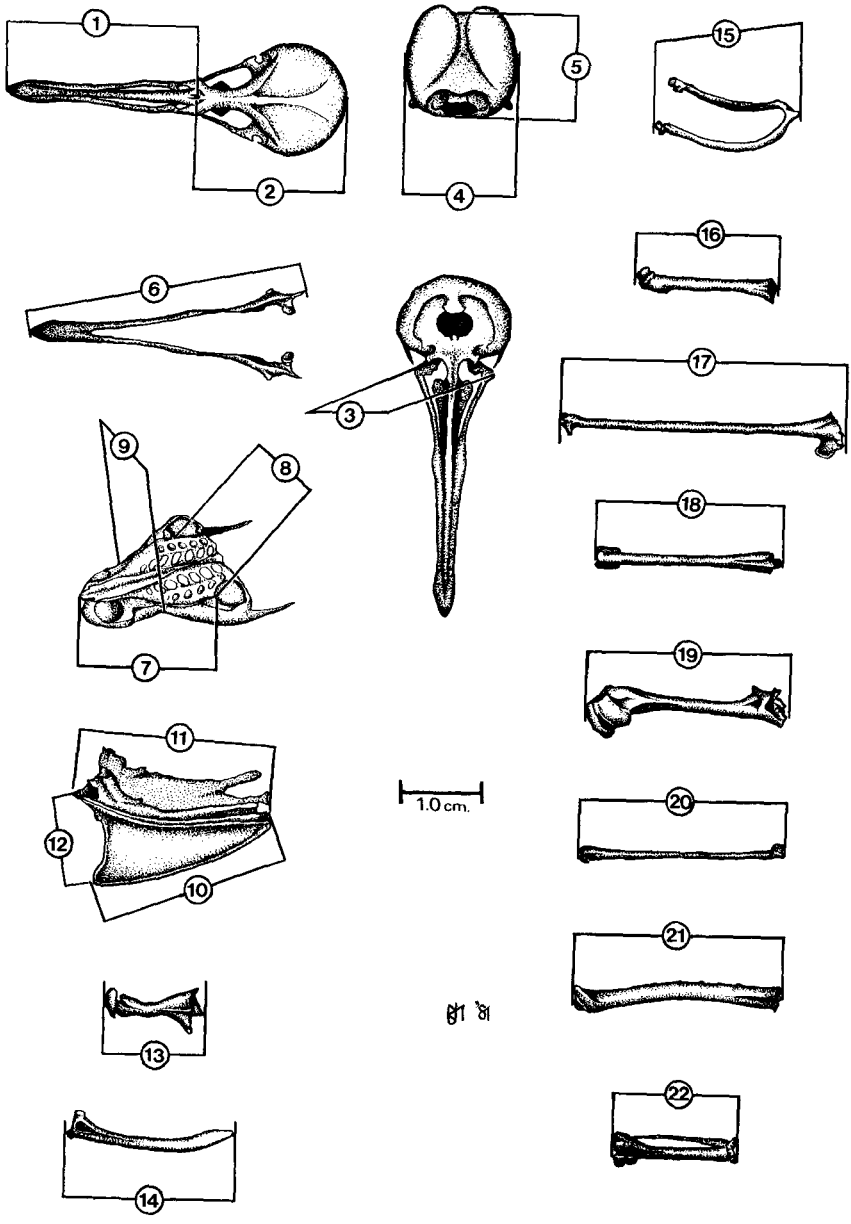
FIG. 2. Skeletal elements from *C. pusilla*, showing the 22 measurements used in this study: (1) premaxilla length (to base of depression in skull); (2) skull length; (3) quadrate length; (4) skull width; (5) skull depth; (6) mandible length; (7) anterior synsacrum length; (8) posterior synsacrum width; (9) anterior synsacrum width (across narrowest portion); (10)



keel length; (11) sternum length; (12) keel depth; (13) coracoid length; (14) scapula length; (15) furcula length; (16) femur length; (17) tibiotarsus length; (18) tarsometatarsus length; (19) humerus length; (20) radius length; (21) ulna length; (22) carpometacarpus length.

TABLE 1

SKELETAL MEASUREMENT STATISTICS FOR *C. PUSILLA* AND *C. MAURI*

Character	*C. pusilla*		*C. mauri*	
	Males (N=49) $\bar{x} \pm SD$	Females (N=61) $\bar{x} \pm SD$	Males (N=42) $\bar{x} \pm SD$	Females (N=41) $\bar{x} \pm SD$
Premaxilla length	23.2 ± 1.13	24.3 ± 1.37	28.0 ± 1.56	31.4 ± 1.64
Skull length	16.4 ± 0.36	16.4 ± 0.34	16.7 ± 0.23	16.7 ± 0.21
Quadrate length	9.8 ± 0.23	9.9 ± 0.24	10.3 ± 0.27	10.4 ± 0.22
Skull width	12.3 ± 0.20	12.3 ± 0.20	12.7 ± 0.20	12.7 ± 0.21
Skull depth	10.8 ± 0.19	10.8 ± 0.20	11.1 ± 0.14	11.1 ± 0.18
Mandible length	30.3 ± 1.15	31.6 ± 1.31	34.6 ± 1.55	37.6 ± 1.74
Anterior synsacrum length	12.2 ± 0.33	12.6 ± 0.44	12.2 ± 0.41	12.7 ± 0.38
Posterior synsacrum width	12.6 ± 0.36	12.7 ± 0.41	12.9 ± 0.34	13.3 ± 0.36
Anterior synsacrum width	8.3 ± 0.31	8.5 ± 0.41	8.6 ± 0.29	9.0 ± 0.30
Keel length	24.3 ± 0.65	24.4 ± 0.71	23.5 ± 0.71	24.2 ± 0.65
Sternum length	25.4 ± 0.65	25.8 ± 0.74	25.3 ± 0.64	26.1 ± 0.57
Keel depth	12.7 ± 0.32	12.9 ± 0.49	13.4 ± 0.39	13.7 ± 0.37
Coracoid length	12.1 ± 0.25	12.3 ± 0.35	12.1 ± 0.35	12.5 ± 0.24
Scapula length	19.9 ± 0.55	20.3 ± 0.72	19.8 ± 0.53	20.4 ± 0.53
Furcula length	15.5 ± 0.48	15.9 ± 0.51	16.2 ± 0.47	16.5 ± 0.51
Femur length	16.9 ± 0.40	17.4 ± 0.58	17.1 ± 0.41	17.6 ± 0.51
Tibiotarsus length	35.4 ± 1.03	36.2 ± 1.16	36.3 ± 1.00	37.9 ± 1.07
Tarsometatarsus length	21.8 ± 0.74	22.2 ± 0.84	22.5 ± 0.71	23.7 ± 0.75
Humerus length	24.0 ± 0.55	24.6 ± 0.76	24.2 ± 0.61	25.0 ± 0.55
Radius length	24.3 ± 0.61	24.9 ± 0.75	24.2 ± 0.62	25.1 ± 0.61
Ulna length	25.3 ± 0.73	26.0 ± 0.77	25.3 ± 0.59	26.1 ± 0.64
Carpometacarpus length	14.8 ± 0.39	15.2 ± 0.50	15.0 ± 0.37	15.5 ± 0.41

imen labels, consequently data for "knowns" and "unknowns" were pooled and tested again. A DFA was performed between sexes for each species separately to contrast sexual differences between the species.

Results.—All DFA's presented were highly significant ($P < 0.001$). Box's M was used to test for equality of expected covariance matrices (Nie et al. 1975). Only that DFA discriminating *C. mauri* sexes had non-equal covariance matrices ($P = 0.28$). This latter analysis, however, was performed on large nearly equal sample sizes, therefore the DFA is likely sufficiently robust to allow a departure from this assumption (see Ito and Schull, Biometrica 51:71–82, 1964).

(1) Skeletal analyses.—The DFA for species separation based on 16 variables (Table 1) shows a complete separation of the species (Table 2, col. 1; Fig. 3). There were, however, two apparently misidentified "knowns" (Fig. 3): a female identified as a *C. mauri* collected on 23 March 1953 in Washington (Univ. Washington, WSM 14177), which falls into the range of *C. pusilla,* but probably is a Least Sandpiper (*C. minutilla*) (S. Rohwer, pers. comm.); and a male identified as a *C. pusilla* collected on 21 April 1976 in Kansas (KU 70344), which probably is a *C. mauri.* These questionable specimens were subsequently excluded from all DFAs.

TABLE 2

STANDARDIZED AND UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS FOR SKELETAL ANALYSES[a]

Character	Standardized DF coefficients				Unstandardized DF coefficients			
	Species	Species (min. no.)	*C. pusilla* sexes	*C. mauri* sexes	Species	Species (min. no.)	*C. pusilla* sexes	*C. mauri* sexes
Premaxilla length	0.771	0.942	−0.085	−1.28	0.4544	0.5079	−0.0672	−0.8021
Skull length	0.004	—	—	—	0.0140	—	—	—
Quadrate width	0.179	—	—	—	0.7143	—	—	—
Skull width	0.384	0.502	—	—	1.9248	2.5134	—	—
Skull depth	0.213	—	—	—	1.2020	—	—	—
Mandible length	0.210	—	0.707	0.489	0.1173	—	0.5693	0.2978
Anterior synsacrum length	—	—	—	0.101	—	—	—	0.2571
Posterior synsacrum width	−0.158	—	—	0.245	−0.4015	—	—	0.6970
Anterior synsacrum width	0.065	—	—	−0.305	0.1783	—	—	−1.0318
Keel length	−0.447	−0.439	—	−0.257	−0.6131	−0.6020	—	−0.3757
Sternum length	—	—	−0.212	−0.224	—	—	−0.3005	−0.3683
Keel depth	0.422	0.390	—	—	1.0397	0.9599	—	—
Coracoid length	—	—	—	−0.134	—	—	—	−0.4507
Scapula length	—	—	—	0.281	—	—	—	0.5299
Furcula length	−1.68	—	0.269	−0.0496	−0.0496	—	1.1660	0.5563
Femur length	−0.027	—	0.590	0.258	−0.0496	—	0.5449	0.559
Tibiotarsus length	−0.317	—	−0.063	−0.350	−0.2509	—	−0.0572	−0.3383
Tarsometatarsus length	0.243	—	−0.199	−0.209	0.2723	—	−0.2512	−0.2866
Humerus length	−0.382	−0.544	−0.131	−0.057	−0.5391	−0.7677	−0.1934	−0.0983
Radius length	—	—	−0.084	1.097	—	—	−0.1257	1.7986
Ulna length	—	—	−0.051	−0.461	—	—	−0.0688	−0.7503
Carpometacarpus length	−0.043	—	0.433	−0.290	−0.0882	—	0.9849	−0.7447
Wilk's Lambda	0.1306	0.1448	0.3722	0.7042	—	—	—	—
Constant	—	—	—	—	−31.0569	−24.0063	−34.5717	21.4317

[a] $P < 0.001$ in all cases.

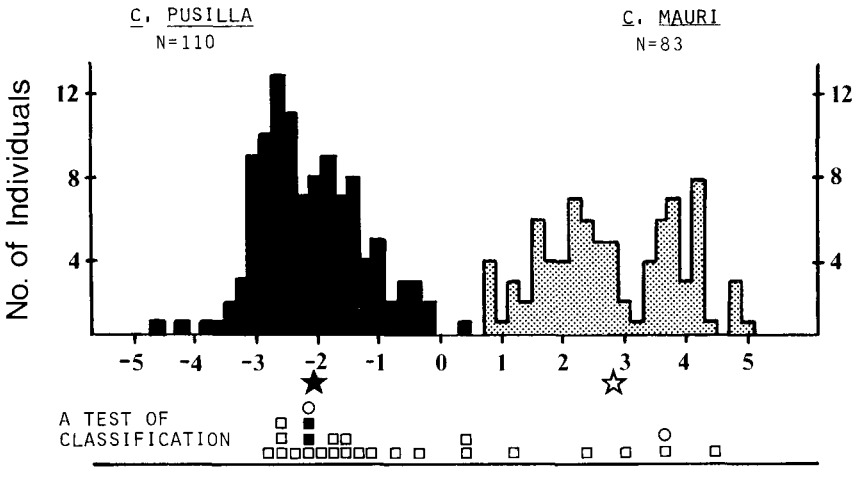


FIG. 3. Species discrimination based on five skeletal characters. The discriminant function axis is in standard deviation units. The mean (★) of *C. pusilla* is −2.1 and that of *C. mauri* (☆) is 2.8. The 95% confidence limits for individual values spans two discriminant function units either side of the mean. A test of the accuracy of the classification function is provided (○ = mis-classified "known," ■ = mis-classified "unknown," and □ = correctly classified "known").

As shown by standardized discriminant function coefficients (SDFCs), species were separated most by skull measurements, especially premaxilla length (Table 2, col. 1).

A stepwise DFA showed total separation between species can be achieved with only five characters. Relatively long wings and long keel in *C. pusilla* are contrasted with a large skull and deep keel in *C. mauri* (Table 2, col. 2). These results were tested by classifying 22 "knowns" previously excluded because each had at least four missing values, but all had values for the five species-separating variables. All 22 were correctly classified based on label identity (Fig. 3).

Sexes of *C. pusilla* overlap broadly in morphometric characters (Fig. 4, overlap = 84.5%). DFA correctly classified the sex in only 74.8% of the individuals (81% of females, 66.7% of males). Lengths of mandible, femur, and carpometacarpus were the most important discriminating characters (Table 2, col. 3). Sexual dimorphism in *C. mauri* (Fig. 5, overlap = 65.8%) is stronger than in *C. pusilla,* with premaxilla and radius lengths most important in discriminating between males and females (Table 2, col. 4). DFA correctly classified to sex 88.6% of the individuals (87.2% of females, 90% of males).

Skeletal material can easily be identified by using unstandardized discriminant function coefficients (UDFCs, see Table 2). Determination of species or sex of an unknown specimen requires summing of the products of all raw measurements with their UDFCs, and adding of the constant. The resultant value (the discriminant score) can then be used to assign the specimen in question to the most likely group, through comparison with the appropriate figure (Figs. 3, 4, 5).

(2) Study-skin analyses.—Combination of study-skin variables (in a DFA) was better than univariate measures in differentiating between sexes only for *C. pusilla.* Improvements in discrimination for bill length alone were: 1.4% for species separation, 1.0% for *C. mauri*

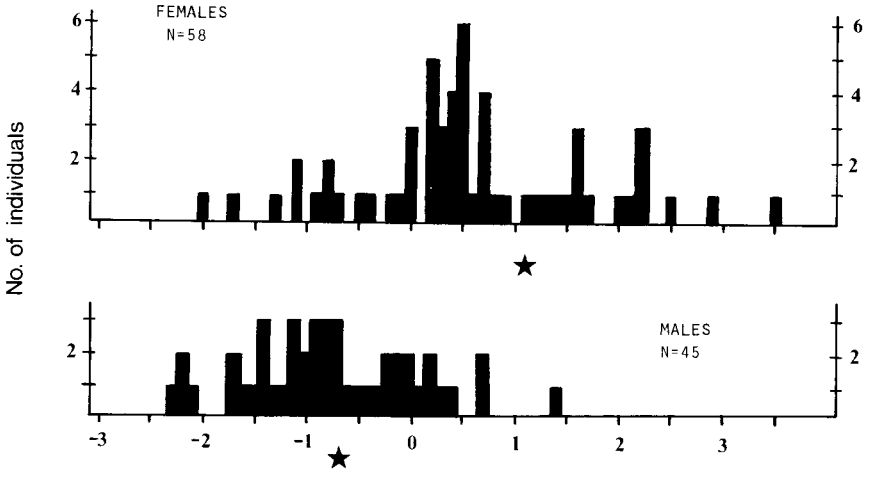


FIG. 4. Discriminant function for sexes of *C. pusilla,* based on 11 skeletal variables. The mean (★) for males is −0.7 and that for females is 1.1. The 95% confidence limits for individual values spans two discriminant function units on either side of the mean.

sexual separation, and 9.8% for *C. pusilla* sexual discrimination. Hence only univariate information is provided for the former two, while SDFCs and UDFCs are provided for *C. pusilla* sexual discrimination (Table 3). This DFA correctly separated 83.1% of the 254 individuals (78% of females, 87% of males). In comparison, Harrington and Taylor (J. Field Orn. 53:174–177, 1982) were only able to sex 40% of their 45 *C. pusilla,* by contrasting wing and bill lengths and constructing 95% confidence ellipses.

Bill lengths of *C. mauri* fall into two discrete groups (Fig. 2), corroborating the studies of Page and Fearis (Bird-Banding 42:297–298, 1972) and Phillips (Am. Birds 299:799–806, 1975), in which 91% and 98%, respectively, of individuals were correctly sexed by bill length. Each group actually contains an assortment of both sexes, raising the possibility that if these groups are subdivided according to sex, some mis-sexed specimens must have been included. I have accepted all sex identifications because there is no way now of ascertaining their correctness. The extreme outliers in Figs. 4 and 5, however, may be attributable to mis-sexed specimens.

Inter-sexual differences are considerably greater in *C. mauri* (Fig. 5) than in *C. pusilla* (Figs. 1, 4). Geographic variation might explain the relative lack of dimorphism found for *C. pusilla* in this study. Palmer (1967) speculates on the existence of three possibly disjunct populations: eastern, central, and western. Harrington and Morrison (Stud. Avian Biol. 2: 83–100, 1979) document a cline of decreasing bill and wing size from east to west. I compared degree of sexual dimorphism in three groups of *C. pusilla* taken on the breeding grounds with the dimorphism in the total sample. The three samples represented western (northern Yukon Terr. to western Victoria Island and south to Fort Thompson, N.W.T.; 14 females, 27 males), central (eastern Victoria Island to Melville Peninsula and south to the NW shore of Hudson Bay; 8 females, 26 males), and eastern (Baffin Island through Ungava to the Belcher Islands; 13 females, 27 males) breeding populations (Palmer 1967), and as such they do not necessarily represent discrete populations. When the four study-skin variables were standardized (to remove the effect of absolute size), the Euclidean distances between

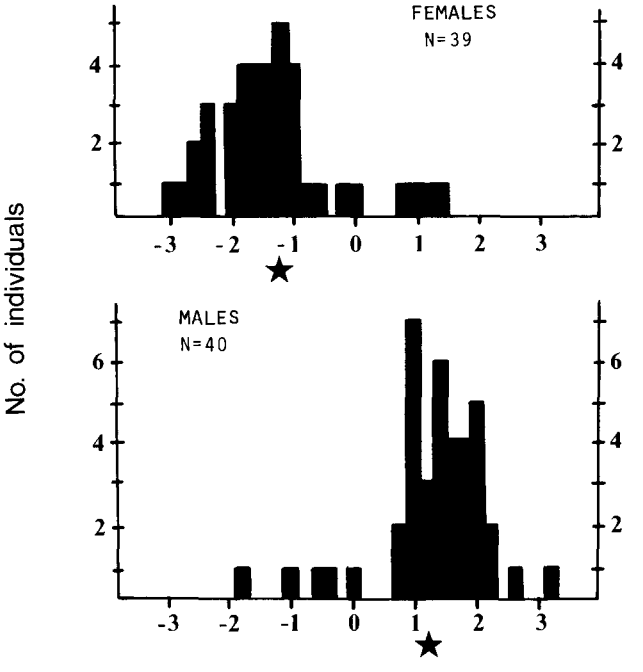


FIG. 5. Discriminant function for sexes of *C. mauri,* based on 16 skeletal characters. The mean (★) for males is 1.3 and that for females is −1.3. The 95% confidence limits for individual values spans two discriminant function units on either side of the mean.

means for males and females in each geographic group were calculated as: *C. pusilla*—western, 2.575; central, 2.100; eastern, 2.553; *C. mauri*—3.039. Even when treated as above, *C. pusilla* is less dimorphic than *C. mauri.*

Discussion.—I have here reaffirmed the phenetic distinctiveness of *C. pusilla* and *C. mauri.* However, because analyses of study-skin measurement characters produced no strong separation between species, perhaps these species cannot be completely separated by measurements alone. Results from my geographic variation and sexual dimorphism assays suggest two questions for future study: (1) Why is *C. mauri* more sexually dimorphic than *C. pusilla*? (2) Why are the two species most dissimilar in sympatry, and most similar where they are farthest apart?

One hypothesis to account for the differing degrees of sexual dimorphism in these species is that latitudinally different wintering regions for *C. mauri* sexes (Page et al., Calif. Birds 299:799–806, 1972) selectively favor different bill lengths. Recent work on the importance of mortality on the wintering grounds (e.g., Page and Whitacre, Condor 77:73–83, 1975) supports this speculation.

That *C. pusilla* and *C. mauri* are most dissimilar in sympatry and most similar in allopatry suggests character displacement. Indeed, recent behavioral work (Connors, A.O.U. annual meeting scientific paper abstract, 1983) has found that sympatric territorial males of *C. pusilla* and *C. mauri* spent almost as much time chasing males of the other species as they did chasing conspecifics.

TABLE 3

MEASUREMENT STATISTICS FOR STUDY SKINS

Variable	*C. pusilla* Males (N = 147) $\bar{x} \pm SD$	Range	*C. pusilla* Females (N = 107) $\bar{x} \pm SD$	Range	SDFC[a,b]	UDFC	*C. mauri* Males (N = 51) $\bar{x} \pm SD$	Range	*C. mauri* Females (N = 52) $\bar{x} \pm SD$	Range
Exposed culmen	18.6 ± 1.36	15.5–23.0	20.5 ± 1.38	17.5–23.7	−0.623	−0.4555	22.6 ± 1.08	20.5–26.5	25.9 ± 1.84	21.0–29.0
Nostril to bill tip	15.2 ± 1.17	12.8–18.1	16.9 ± 1.28	13.2–19.9	0.073	0.0602	18.8 ± 0.97	17.2–22.9	22.0 ± 1.68	17.1–24.6
Tarsus length	21.2 ± 0.74	19.4–23.4	22.1 ± 0.63	20.0–23.9	−0.535	−0.7674	21.7 ± 0.71	19.8–22.7	23.2 ± 0.88	21.4–25.1
Wing length	93.6 ± 2.10	87.5–98.5	96.1 ± 2.40	90.0–101.0	−0.326	−0.1470	93.0 ± 1.80	89.5–97.0	96.1 ± 2.80	90.0–101.0
Constant						38.3385				

[a] Wilk's Lambda = 0.5584 ($P < 0.001$).
[b] 95% confidence limits for SDFCs: males: −1.2–2.8 ($\bar{x} = 0.8$); females: −3.0–1.0 ($\bar{x} = -1.0$).

The measurements provided here are of use to workers attempting to identify species and sex of problematic museum specimens for these two sandpipers. This species-separating information must be applied with caution, since the possibility of confusion with other sandpiper species, especially Palearctic ones, exists. For North America, though, only the skull of *C. minutilla* is likely to be similar in size to *C. pusilla,* and this species has a distinctive bill shape (Prater et al., Guide to the Identification and Ageing of Holarctic Waders, Maud and Irvine, Tring, Herts., England, 1977).

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Macrohabitat use, microhabitat use, and foraging behavior of the Hermit Thrush and Veery in a northern Wisconsin forest.—*Catharus* is one of several genera of North American passerines (e.g., *Dendroica, Empidonax, Parus, Toxostoma, Vireo*) that has received particular attention from ecologists (Grinnell, Auk 34:427–433, 1917; MacArthur, Ecology 39: 599–619, 1958; Lack, Am. Nat. 103:43–49, 1969; Beaver and Baldwin, Condor 77:1–13, 1975; James, Wilson Bull. 88:62–75, 1976). These researchers addressed the question of how series of congenerics differ ecologically to promote sympatric coexistence. Dilger (Auk 73:313–353, 1956a; Wilson Bull. 68:170–199, 1956b; Syst. Zool. 5:174–182, 1956c) arranged the four *Catharus* thrushes and the related *Hylocichla mustelina* along a synthetic gradient based on morphology, behavior, macrohabitat use, and geographical and elevational distributions. Of these factors, subsequent studies of interspecific interactions focused on macrohabitat use (Morse, Wilson Bull. 83:57–65, 1971; 84:206–208, 1972; Sealy, Condor 76:350–351, 1974; Bertin, Condor 79:303–311, 1977; Noon, Ecol. Monogr. 51:105–124, 1981). Relatively little information exists on the behavioral mechanisms behind the observed patterns.

To examine the relationship of *Catharus* thrushes to their habitat, I chose two sympatric species occupying adjacent, intermediate positions on Dilger's morphological-ecological gradient, the Hermit Thrush (*C. guttatus*) and the Veery (*C. fuscescens*). Data were collected for interspecific comparisons of habitat relationships at three levels of detail: (1) the structure of the two species' habitats (macrohabitat use); (2) species' use patterns for vegetation types and height strata within these habitats (microhabitat use); and (3) movement rates and lengths and prey capture methods (foraging behavior).

Based on the observations of earlier workers (Bent, U.S. Natl. Mus. Bull. 196, 1949; Dilger, 1956b, c; Morse 1971; Eckhardt, Ecol. Monogr. 49:129–149, 1979; Noon 1981), I made the following predictions. (1) Hermit Thrushes would occupy available sites dominated by coniferous vegetation, while Veeries would occupy sites dominated by deciduous vegetation. (2) Hermit Thrushes would be active primarily on the ground, whereas Veeries would