MORPHOLOGICAL CHARACTERISTICS OF CANADA GEESE IN THE PACIFIC FLYWAY

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Abstract: The subspecific status of Canada geese (*Branta canadensis*) is a contentious matter of importance to both taxonomists and wildlife managers. In this report we consider the six subspecies that breed in Alaska. We quantitatively examine a variety of morphological measurements taken on 1,345 Canada geese believed to be sedentary on breeding or wintering areas. From this information we develop general descriptions of each subspecies. We find that various combinations of morphological characters can more reliably distinguish subspecies than can single characters, and we develop discriminant functions for this purpose. The affinities of the various subspecies, based upon our analysis, are discussed.

Canada geese have developed into various closely related subspecies. The number recognized depends upon the conservatism or liberalism of the classifier, and has varied in recent treatments from 8 (Palmer 1976) to 12 including 1 extinct subspecies (Delacour 1954, Johnsgard 1975). Generally, 11 extant subspecies are accepted (Hansen and Nelson 1964, Bellrose 1978), and this paper follows that practice.

In the West, seven subspecies of *Branta canadensis* are commonly recognized. One, *moffitti* (Great Basin Canada goose), is easily distinguished by its large size and light coloration. The remaining six are subspecies that are difficult to separate from one or more other members of that group. One subspecies, *leucopareia* (Aleutian Canada goose), has been reduced greatly in number and is classified as an endangered "species" (Springer et al. 1978). Another, *minima* (cackling Canada goose), has suffered a loss of over a third in number recorded in winter surveys during the past 24 years (J. C. Bartonek. 1978. Pacific Flyway winter waterfowl survey. U.S. Fish Wildl. Serv., Portland, Ore. Unpubl. rep. 16 p.) Several, such as *occidentalis* (dusky Canada goose), *taverneri* (Taverner's Canada goose), and *parvipes* (lesser Canada goose), have shown moderate to large population increases in recent years in the Pacific Flyway (U.S. Fish and Wildlife Service. [1978]. Washington-Oregon dusky goose counties. Migratory Bird Manage. Office, Portland, Ore. Unpubl. rep. [9 p.]; Bartonek loc. cit.), whereas *fulva* (Vancouver Canada goose), a lightly hunted subspecies, has probably remained fairly stable in number.

Because these birds may be affected differentially by environmental conditions, including land-use practices and mortality factors, within their ranges, it is essential that the various subspecies be identified correctly if management programs are to prove most effective. Usually a single character is inadequate to distinguish the six subspecies accurately; a combination of characters is necessary. Discriminant function analysis appears to offer a useful method in this regard. It may also be helpful in taxonomic studies by representing in a quantitative manner the closeness of the subspecies' affinities to one another. The purpose of the present study was to explore the efficacy of discriminant function analysis in distinguishing the individual subspecies in a reliable manner and demonstrating possible taxonomic relationships.

Description of Subspecies

All six subspecies of Canada geese included in this study are generally similar in head, neck, wing and tail coloration but differ greatly in size and in color of the upper and under parts. In order of increasing size the subspecies are:

minima -- a small goose averaging 1300-1800 g, grayish-brown above, the dark brown breast having a purplish cast; sometimes has a complete or incomplete white neckring; cheek patches often separated by a black band below.

leucopareia -- larger than *minima*, averaging 1700-2200 g, and having a browner back and a grayish-brown breast; has a conspicuous white neckring, usually bordered below by a narrow edging of dark feathers; cheek patches generally separated by a black band below.

taverneri -- similar to *leucopareia* but slightly larger, averaging 2000-2700 g, and usually having a slightly lighter breast; sometimes has a narrow or incomplete white neckring; cheek patch usually, but not always, continuous.

parvipes -- a medium-sized goose, similar to *taverneri*, but slightly larger, averaging 2200-3000 g, and lighter in color.

occidentalis -- a medium-large goose, averaging 2700-3900 g; dark brown overall.

fulva -- similar to *occidentalis*, but somewhat larger, averaging 3500-4600 g, and slightly lighter below, although breast color is more variable.

Subspecies Range in Alaska

Figure 1 depicts what we believe to be the breeding ranges of the six subspecies in Alaska. The precise delineation of these ranges will be clarified only when sufficient breeding birds are examined from all principal nesting areas. Some confusion over subspecies and their ranges has arisen because "type specimens" of non-breeding individuals belonging to one subspecies were collected within the breeding ranges of another. Only the collection of breeding specimens (birds with eggs or flightless young) permits accurate determination of breeding ranges. Non-breeding wanderers and molt migrants can occur nearly anywhere during the breeding season.

Particularly controversial is the validity of the *taverneri* and *parvipes* separation, both taxonomic and in breeding range. We concur with J. W. Aldrich (personal communications) in the distinction of breeding ranges as generally being tundra areas for *taverneri* and interior forested areas for *parvipes*. The degree of intergradation in the transition area is unknown.

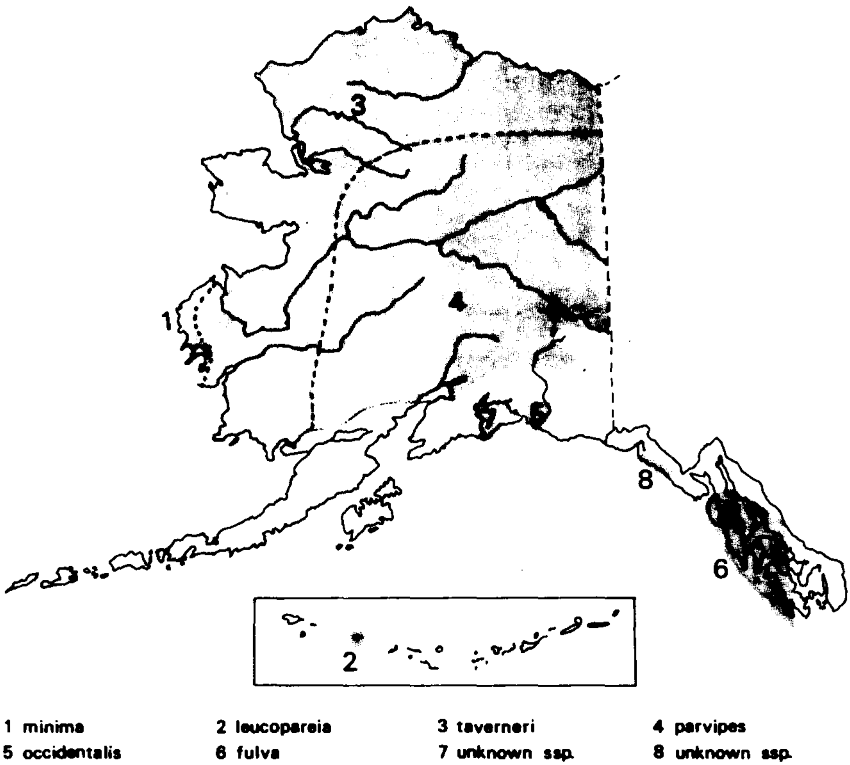

Figure 1. Breeding ranges of Canada geese in Alaska.

The areas designated 7 and 8 in Figure 1 are Prince William Sound and Yakutat Forelands, respectively. The subspecies of Canada geese breeding in these locations are undetermined. Birds collected in Prince William Sound (D. E. Timm unpublished data) were intermediate in size between *fulva* and *occidentalis*, but their nesting and brood-rearing habits resembled *fulva* (D. J. Kurhajec. 1977. Breeding Canada geese of the Port Etches area, Hinchinbrook Island, Alaska. U.S. Fish Wildl. Serv. Unpubl. rep. 12 p.). No breeding birds have been collected in the Yakutat area, although D. W. Zimmerman (personal communications) observed two or three broods there in 1972. Hansen (1962) and D. E. Timm (unpublished data) observed molting adult geese in Yakutat Bay.

The following is a summary of recent data which helps clarify the ranges of Canada goose subspecies in Alaska and the Pacific Flyway.

minima: We generally agree with the range descriptions of *minima* provided by Nelson and Hansen (1959) and Bellrose (1978), with some refinements. C. P. Dau (personal communications) reported that large numbers of *minima* stage on Nunivak Island during September. The Pilot Point area is the primary fall use area on the Alaska Peninsula, but the Cinder River Delta is also frequented by many birds (P. A. Arneson, personal communications). These areas receive the heaviest use between October 5 and 20. Although *minima* have been reported at Izembek Lagoon and the eastern Aleutians (Bellrose 1978), D. E. Timm and J. E. Sarvis (personal communications) are unware of *minima* in these locations, despite the large numbers of birds measured and the many surveys conducted there.

leucopareia: Formerly thousands bred throughout the outer two-thirds of the Aleutian Islands and on the Commander and Kurile Islands (Springer et al. 1978). Introduction of Arctic foxes (*Alopex lagopus*) for fur-farming purposes was primarily responsible for a great reduction in numbers. Presently the only wild breeding geese known occur on Buldir Island in the outer Aleutians. The only verified records (of color-marked birds) of Aleutian Canada geese in Alaska outside of the Aleutian Islands are on St. George Island in the Pribilofs where a yearling male goose was collected in May 1978 and an immature female with two unmarked birds was sighted in June 1978 (W. E. Rodstrom personal communications). This subspecies apparently migrates to the base of the Aleutians and then makes a transoceanic flight to the northern coast of California and into the Central Valley (Springer et al. 1978).

taverneri: Up to 73,500 geese have been counted staging their fall migration in the Cold Bay area of Alaska (D. E. Timm and J. E. Sarvis unpublished data). Although yet to be confirmed, we believe that these birds nest on the Yukon-Kuskowim Delta. Birds banded on the Delta before 1969 wintered primarily in central California. Recently, however, band recoveries and observation of color-marked geese indicate that the Cold Bay population is beginning to winter in Oregon's Willamette Valley. Breeding *taverneri* from the Innoko River drainage, Kotzebue Basin, and the North Slope winter primarily in eastern Washington, eastern Oregon and near the mouth of the Columbia River (C. J. Henny unpublished data; D. E. Timm. 1974. Alaska Fish Game, Rep. Fed. Aid Wildl. Restor. Proj. W-17-6, Job 11 and 22. 54 p.; King and Hodges 1979). Our examination of measurement data from Canada geese captured in large flocks of molting non-breeders on the North Slope in the Cape Halkett area (D. V. Derksen unpublished data) indicates that a portion of the geese are *parvipes*, which probably undertake a molt migration from the south. No young have been found among the large flocks of non-breeders near Cape Halkett. We have found no records of Canada geese breeding or molting on the Alaska Peninsula.

parvipes: Contrary to the ranges described by Hansen (1962), Palmer (1976), Ogilvie (1978) and others, all of the more than 450 breeding Canada geese or their young examined since 1974 in Upper Cook Inlet were *parvipes*, not *occidentalis*. J. W. Aldrich (personal communications) examined birds from this area and concurred in our findings. Hansen (1962) reported that a small flock of Canada geese, probably subadult non-breeders, was seen several times during July in Kamishak Bay in Lower Cook Inlet. However, extensive recent ground studies in this area during the summer by P. A. Arneson (personal communications) revealed no breeding or molting birds. To our knowledge, no Canada geese currently breed or molt in Cook Inlet south of the Kustatan Peninsula. Those birds which nest in upper Cook Inlet winter in Oregon's Willamette Valley.

occidentalis: We can add little to Hansen's (1962) description of the range of dusky Canada geese, despite recoveries of about 3,000 banded geese and intensive color-marking programs in recent years. Contrary to Delacour (1954), this subspecies is a regular migrant to the Willamette Valley and to a lesser extent the Oregon coast. Band recoveries in California have totaled seven (three at Tule Lake, three near Crescent City and one in north central California). Another bird was taken in Utah. However, all eight recoveries occurred before 1966. In addition, three neck-collared birds believed to be *occidentalis* were sighted in 1978 near Crescent City, and up to 100 similar non-collared birds are seen there each winter (P. F. Springer). Individual birds of a different subspecies occasionally are captured on the Copper River Delta and until recently their capture was not noted in field records. Perhaps the banding of such wanderers accounts for some of the abberant recoveries in the past.

fulva: Recoveries of banded birds and the color-marking and subsequent sighting of Vancouver Canada geese have not markedly changed the range of *fulva* as described by Delacour (1954) and Hansen (1962). However, *fulva* apparently do not wander as far south as California (Hansen 1962, D. E. Timm unpublished data), as reported by Delacour (1954) and the American Ornithologists' Union (1957). Also, the segment of the Alaskan population that migrates is much smaller than was thought previously. Hansen (1962) reported 17 percent of the band recoveries occurred outside Alaska, but Ratti and Timm (1979) demonstrated that only about 2 percent of the population actually migrates.

METHODS

Data Sources

Measurements of geese were taken from live birds and museum specimens obtained in 16 general locations (Table 1) by numerous individuals. We tried to use only birds believed to be sedentary (on discrete breeding or wintering areas). In some instances it was necessary to subjectively classify two groups of birds obtained in the same area. For example, fall-staging geese from Nunivak Island and breeding geese from the Yukon-Kuskokwim Delta were classified as either *minima* or *taverneri* on the basis of size and color. Some measurements from *leucopareia* were obtained at Crescent City, California, the spring staging area for the subspecies (Springer et al. 1978); very few geese of other subspecies are present there during the spring.

Geese were measured at Cold Bay during September and October and were classified as *taverneri* on the basis of size and color. Although 23.3 percent of the birds had a complete white neckring, suggestive of *leucopareia*, we believe that none was, because the presence of *leucopareia* has not been confirmed in the Cold Bay area by color-marked birds.

Table 1. Source of 1345 Canada geese used in the study, months they were measured, and sample size.

Subspecies	Source	When measured	Number
minima	outer Yukon-Kuskokwim Delta	June-August	287
(304)	Nunivak Island	September	17
leucopareia	Crescent City, California	March-April	151
(242)	Aleutian Islands	July	91
taverneri	Cold Bay area	September-October	62
(121)	Nunivak Island	September	21
	North Slope	June	19
	outer Yukon-Kuskokwim Delta	July	13
	Brooks Range	June	10
	Bristol Bay	June	3
	Seward Peninsula	June	3
parvipes	Cook Inlet	July	38
(47)	forested NW Territories and Yukon	June-July	7
	interior Alaska	July	2
occidentalis (261)	Copper River Delta	June-August	261
fulva	Glacier Bay	July	309
(370)	other SE Alaska	January-March, June-August	57
	British Columbia	August	4

Measurements and Mensuration Techniques

Most of the measurements taken -- Culmen (exposed culmen length), Tarsus (diagonal tarsus length), Midtoe (middle toe without nail length), Bill Nail length, Wing (wing chord length), Bill width at Base, and Bill width at posterior edge of Nail -- are standard according to methods of Baldwin et al. (1931). The Total Tarsus measurement refers to the distance from the distal end of the tarsometatarsus to the posterior condyle of the distal end of the tibiotarsus with the tarsometatarsus placed perpendicularly to the tibiotarsus. The Bill width at Nares is the perpendicular distance across the bill (lateral edge to lateral edge) at the proximal end of the nares. Neckring measurements were taken mid-ventral. A Vernier caliper was used to take all measurements to the nearest 0.1 mm.

Weights of *minima* and *occidentalis* were obtained during molt. The weights of *leucopareia* were taken both during summer molt on Buldir Island and during March and April at Crescent City, California. The weights of *taverneri* were taken from mid-September through October at Cold Bay, Alaska.

Unfortunately, not all standard taxonomic measurements were taken on each bird in the study. In fact, only Culmen, Tarsus and Total Tarsus were recorded fairly consistently. Midtoe, Bill Nail length, and Weight were taken regularly for some subspecies, but not for others. The remaining measurements were taken on many individuals of certain subspecies but on few individuals of other subspecies. The non-uniformity of mensural data influenced the kinds of analyses that could be performed, as will be described later.

Except for the Neckring measurement obtained on fair numbers of *leucopareia*, *taverneri* and *parvipes*, no plumage variables were recorded or used in the present study. Because plumage characteristics are recognized as distinguishing features of certain subspecies, the inclusion of such information might enhance the power of discriminatory techniques.

Statistical Procedures

Three basic types of statistical procedures were used in the study: error-checking, descriptive statistics, and discriminant function analysis. Errors in measurement were sought by listing data and looking for suspiciously extreme values, and by plotting one variable against another (e.g. Tarsus against Culmen) for each subspecies and sex and then searching for observations that lay outside the swarm of points associated with that group. In these ways apparently deviant observations were identified for closer examination for errors in recording, transcription, or keypunching.

Descriptive statistics computed were sample size, mean, standard deviation, minimum, maximum, and coefficient of variation. Separate values for all variables were obtained for each subspecies, sex, and age. No appreciable differences were found in values for adult birds and fledged immature birds, except for weight, which was not used in any discriminant function. Accordingly, the age classes were combined. The descriptive statistics served to define the basic parameters of each subspecies, and to suggest variables that might be useful discriminators between subspecies.

The discriminant function (DF) analysis proceeded in two steps. The first involved constructing an initial DF that would classify a bird into one of the six subspecies. If the results of the initial DF were conclusive, the classification process could terminate. If the initial DF was not definitive, because it suggested that the goose had a reasonable probability of belonging to either of two subspecies, then the second step would be invoked. For this, DFs for classifying birds into one of two subspecies are required. For example, suppose that the initial DF indicated that a bird was likely a member of *leucopareia* or *taverneri*, but was probably not a member of any of the other subspecies. Then a secondary DF is employed to distinguish only between these two candidate subspecies. The major advantage of this two-step approach is that more variables may be brought into play. The initial DF can use only Culmen, Tarsus and Total Tarsus, because no other variables were recorded regularly on all subspecies. But by restricting attention to only two subspecies, more variables may be used in a secondary DF. For example, a DF for *leucopareia* and *taverneri* could use, in addition to the three variables just mentioned, Midtoe, Bill at Base, Bill at Nares, Bill at Nail, and Neckring. All these variables were recorded for appreciable numbers of both subspecies.

Two criteria were used to select DFs. The first was that the DF should, when applied to the observations from which it was formed, classify a large proportion of them into correct subspecies. The second was the use of as few variables as possible; large numbers of variables, especially highly correlated ones, may result in unstable DFs. It is well known that the error rate of a DF applied to the data on which it was based will be smaller than that

Table 2. Means and standard deviations of selected morphological characters of six subspecies of Canada geese -- males.

Character	*minima*	*leucopareia*	*taverneri*	*parvipes*	*occidentalis*	*fulva*
Exposed Culmen	29.7 2.1	35.6 2.0	37.8 2.3	43.0 2.6	46.3 2.4	51.3 3.0
Bill width at Nares	17.1 .6	18.5 .7	19.0 .9	20.0 .8	21.3 .8	-
Tarsus (diagonal)	70.2 2.9	76.7 3.1	75.8 3.4	80.8 3.3	88.6 3.5	93.9 3.2
Total Tarsus	83.2 3.1	91.4 3.2	92.8 3.9	97.0 2.8	106.2 3.9	111.9 3.7
Midtoe	56.2 5.2	61.1 3.0	62.3 3.5	68.2 2.5	80.8 7.4	80.3 2.8
Bill Nail length	11.3 .8	12.6 .8	12.4 .9	13.4 .7	14.8 1.0	15.3 1.1
Wing chord	361.2 10.9	-	402.6 14.9	-	-	-
Neckring	-	15.9 6.1	0.8 1.8	0.5 1.4	-	-
Weight	1546.1 199.5	1945.6[a/] 136.3 2109.7[b/] 224.1	2606.5 267.4	-	3232.5 260.7	-

[a/] Summer weights -- Buldir Island.
[b/] Spring weights -- California.

Table 3. Means and standard deviations of selected morphological characters of six subspecies of Canada geese -- females.

Character	*minima*	*leucopareia*	*taverneri*	*parvipes*	*occidentalis*	*fulva*
Exposed Culmen	28.1 1.7	34.1 1.8	36.1 2.2	40.2 2.1	43.5 2.4	47.9 2.5
Bill width at Nares	16.6 .5	17.7 .8	17.8 1.2	19.0 .6	20.0 .9	-
Tarsus (diagonal)	65.6 3.0	72.0 3.4	71.4 3.2	75.3 3.3	81.3 3.0	87.2 4.0
Total Tarsus	77.9 2.8	85.8 3.7	87.1 3.4	88.7 3.7	97.3 3.4	103.7 3.9
Midtoe	53.9 5.4	58.1 3.2	59.4 3.3	62.6 2.8	74.6 6.5	77.3 3.7
Bill Nail length	10.7 .8	12.1 .7	11.8 .9	12.6 1.0	13.8 .9	14.3 .9
Wing chord	353.2 10.9	-	388.4 12.6	-	-	-
Neckring	-	15.5 5.7	1.2 2.7	1.1 3.7	-	-
Weight	1311.5 199.6	1703.0[a/] 154.9 1863.1[b/] 193.1	2420.7 238.2	-	2640.1 201.5	-

[a/] Summer weights -- Buldir Island.
[b/] Spring weights -- California.

expected from a fresh data set. Methods exist for unbiasedly estimating the error rates, but we believed that they were not necessary here inasmuch as the sample sizes were large relative to the number of variables used.

RESULTS

General Description of Subspecies

Means and standard deviations of selected morphological characters for the six subspecies are shown in Table 2 (males) and Table 3 (females). Most characters increase in average measurement in the order: *minima*, *leucopareia*, *taverneri*, *parvipes*, *occidentalis* and *fulva*. There are exceptions. Both male and female *leucopareia* average longer (diagonal) Tarsus than do *taverneri*, but this does not hold for Total Tarsus. The same two subspecies also exhibit a reversal in average length of Bill Nail, again consistently for both sexes. The only other reversal is that *occidentalis* average a longer Midtoe than *fulva* among males, but not among females.

We illustrate these differences in average measurements by developing a profile for each subspecies. We first calculate, for each of the five characters fairly regularly measured on each subspecies, the character average (the average of the six subspecies' means) and the character standard deviation (the square root of the average variance within subspecies). A score for each subspecies is the difference between its average on a character and the average for all six subspecies, divided by the character standard deviation. Consider, for example, Culmen among males. The character average from Table 2 is $(29.7 + 35.6 + 37.8 + 43.0 + 46.3 + 51.3)/6 = 40.6$. The character standard deviation is the square root of $(2.1^2 + 2.0^2 + 2.3^2 + 2.6^2 + 2.4^2 + 3.0^2)/6 = \sqrt{5.87} = 2.4$. Thus the score for *minima* males on Culmen is $(29.7 - 40.6)/2.4 = -4.5$. The profile for a subspecies is the graph of these scores.

The relationships among subspecies averages is readily apparent from the profiles (Fig. 2). The smallest subspecies, *minima*, is clearly separated from the rest. The next two, *leucopareia* and *taverneri*, are close on all five of these characters. Averages for *parvipes* are in the center. The two large subspecies, *occidentalis* and *fulva*, are separated from all others and fairly well separated from each other.

The profiles also depict the characters likely to be most useful separators. Of the five characters profiled, Culmen shows the widest separation among all subspecies (the range of scores is the greatest), and is a candidate for the best single discriminator. The second most separated character is Total Tarsus, followed by (diagonal) Tarsus. Midtoe and Bill Nail length display less separation among the six subspecies.

Some characters that were not measured on adequate numbers of each subspecies may still aid in distinguishing between a pair of subspecies. For example, although *leucopareia* and *taverneri* are close on the five characters used in the profile, they differ appreciably in Neckring width and the taper of the bill. Neckrings of *leucopareia* averaged 15.9 mm in width among males and 15.5 mm in width among females, compared to only 0.8 and 1.2, respectively, for *taverneri*. Bill taper, as measured by the ratio of Bill width at Nail to Bill width at Base, averaged 0.718 and 0.712 among *leucopareia* males and females, as opposed to 0.776 and 0.776 among *taverneri* males and females. All differences between subspecies were highly significant ($P < 0.01$; t test).

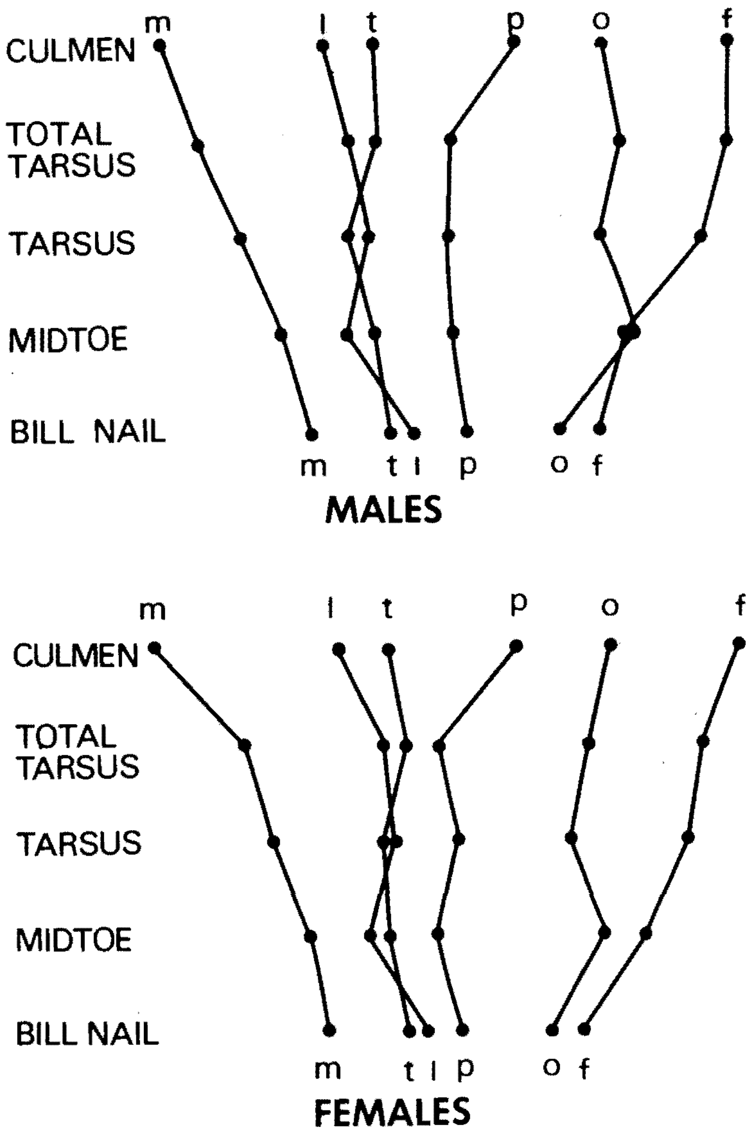

Figure 2. Profiles of Canada geese.
m=*minima* l=*leucopareia* t=*taverneri*
p=*parvipes* o=*occidentalis* f=*fulva*

Table 4. Performance of initial discriminant functions for males. Upper number is percent classified by DF employing Culmen, Tarsus, and Total Tarsus. Lower number is percent classified by DF employing only Culmen and Tarsus.

Classified from subspecies	Classified into subspecies *minima*	*leucopareia*	*taverneri*	*parvipes*	*occidentalis*	*fulva*
minima	95.8	4.2				
	94.3	5.7				
leucopareia	3.1	77.3	17.5	2.1	0	
	4.2	70.3	23.7	0.8	0.8	
taverneri	4.8	14.3	66.7	14.3		
	3.3	26.2	59.0	11.5		
parvipes		4.5	9.1	77.3	9.1	
		3.6	3.6	78.6	14.3	
occidentalis				8.4	79.8	11.8
				11.5	76.2	12.3
fulva					12.6	87.4
					13.7	86.3

Initial Discriminant Functions

The initial DFs, used to assign geese to one of the six subspecies, performed as shown in Table 4 (males) and Table 5 (females). Results for males will be discussed; those for females were similar. Two DFs were established, one employing Culmen and Tarsus, the other including Total Tarsus as well. Slightly better accuracy was achieved with the latter DF, but sample sizes were somewhat smaller. Overall, 82.9 percent of 1156 geese were classified correctly with three measurements, and 79.8 percent of 1289 geese were classified correctly with two measurements.

The purpose of the initial DF is not necessarily to assign a goose to the correct subspecies, but simply to eliminate all but two subspecies as likely candidates for membership so that the secondary DFs could be employed. The initial DFs performed their function well. Coefficients of the initial DFs will be found in Table A0 of the Appendix.

Secondary Discriminant Functions

Some subspecies are so widely separated that confusion between them is unlikely. For example, the distinction between *minima* and *occidentalis* is clear. Subspecies that are adjacent on the gradient of overall size, however, do exhibit considerable overlap in many measurements. The following pairs of

Table 5. Performance of initial discriminant functions for females. Upper number is percent classified by DF employing Culmen, Tarsus, and Total Tarsus. Lower number is percent classified by DF employing only Culmen and Tarsus.

	Classified into subspecies					
	minima	*leucopareia*	*taverneri*	*parvipes*	*occidentalis*	*fulva*
Classified from subspecies						
minima	96.6 96.8	3.4 3.2				
leucopareia	5.2 4.1	67.0 66.9	24.3 25.6	3.5 3.3		
taverneri	2.4 1.8	21.4 26.3	64.3 56.1	11.9 15.8		
parvipes			18.8 5.9	75.0 82.4	6.2 11.8	
occidentalis				8.3 14.7	79.7 72.8	12.0 12.5
fulva					11.6 13.4	88.4 86.6

subspecies could not adequately be distinguished on the basis of Culmen, Tarsus, and Total Tarsus alone, and therefore required additional effort to discriminate between them: (1) *minima* - *leucopareia*, (2) *leucopareia* - *taverneri*, (3) *leucopareia* - *parvipes*, (4) *taverneri* - *parvipes*, (5) *parvipes* - *occidentalis*, (6) *occidentalis* - *fulva*.

We established secondary DFs for each such pair of subspecies, with two considerations. First, a secondary DF may employ more than the three basic measurements, Culmen, Tarsus, and Total Tarsus, if other characters were measured on a majority of the birds of both subspecies. Second, these DFs should include characters that appear particularly useful as discriminators between the subspecies, e.g. Neckring for distinguishing *leucopareia* and *taverneri*.

For most secondary DFs we assumed that a goose had an equal chance of belonging to either subspecies. This is termed the "equal prior" assumption, which implies that assignment is based strictly on the measurements, not on prior knowledge. In the DFs for distinguishing *leucopareia* and *taverneri*, however, we separated the data into two groups depending on whether or not the Neckring measurement exceeded 5 mm. It was then no longer appropriate to consider the two subspecies as equally likely to occur within each group; 95.8 percent of *leucopareia* have neckrings greater than 5 mm, but only 4.9 percent of *taverneri* do so. To incorporate this information in the DFs, we assigned priors to each subspecies, not equally, but in proportion to their occurrence in the group. This is termed the "proportional prior" assumption.

The performance of DFs for the various pairs of subspecies is shown in Table 6. Coefficients of the secondary DFs are given in Appendix Tables A1-A7. *Minima* and *leucopareia* were well distinguished simply by Tarsus and Culmen measurements (DF 1a), although Total Tarsus (DF 1b) aided further. Neckring measurements would perhaps clinch matters, but we have none for *minima*.

Distinguishing *leucopareia* and *taverneri* was primarily a function of the Neckring measurement. A simple classification rule (DF 2a): assign individual to *leucopareia* if Neckring > 5 mm, *taverneri* if Neckring $\leq$ 5 mm, performed nearly as well as any DF which includes additional measurements (DF 2b-2f). Less than 5 percent of the birds were misclassified. Other characters that aided in distinguishing these two subspecies were Bill at Nares, Bill at Nail, the ratio of Bill at Nail to Bill at Base (a measure of bill taper), and the ratio of Tarsus to Bill at Nares.

Individuals belonging to *leucopareia* or *parvipes* were distinguished easily by using only Culmen, Tarsus, and Neckring data (DF 3a). If Neckring is not recorded, adequate discrimination can be made by using Culmen, Midtoe, Bill at Nares, and Bill at Nail measurements (DF 3b).

This study found no highly reliable method of segregating *taverneri* and *parvipes*. A DF (DF 4a) based on Culmen and Tarsus misclassified about 10 percent of the birds. The addition of Bill at Nail (DF 4b) pared the error rate to about 7 percent, but the sample of birds was substantially reduced. Further research, including the examination of more *parvipes* specimens from the primary breeding range, could perhaps uncover additional discriminatory characters.

Distinguishing between *parvipes* and *occidentalis* was also difficult from our samples. The error rate based on Culmen, Tarsus, and Total Tarsus (DF 5a) was 9 percent and was reduced only slightly by the addition of Midtoe to the DF (DF 5b).

The two large subspecies, *occidentalis* and *fulva*, were not easily separable on the basis of available measurements. A DF (DF 6a) based on Culmen and Tarsus misclassified 12.6 percent of the birds.

Example -- Using Discriminant Functions

We illustrate how a set of discriminant functions is used, by examining Bird # 1151, a male *leucopareia*. The measurements for the initial DF are Culmen = 37.4 mm, Tarsus = 81.1 mm, and Total Tarsus = 93.7 mm. We first calculate the initial DF. Applying the male DF for *minima* (Table A0), we obtain: -302.821 + 1.719 (37.4) + 3.015 (81.1) + 4.110 (93.7) = 391.09. The DFs for the other subspecies are evaluated similarly, resulting in the following values:

minima	391.09
leucopareia	398.09
taverneri	396.73
parvipes	395.73
occidentalis	389.76
fulva	377.89.

Table 6. Performance of various discriminant functions. The "error rate" is the percentage of birds classified incorrectly.

Number	Subspecies	Measurements	Sample Size Males	Sample Size Females	Error Rate
1a	*minima-leucopareia*	Culmen Tarsus	223	277	4.2%
1b	*minima-leucopareia*	same as 1a + Total Tarsus	193	260	3.3
2a	*leucopareia-taverneri*	Neckring $\lessgtr$ 5 mm	133	140	4.4
2b	*leucopareia-taverneri* (Neckring > 5 mm)	Bill at Nares Bill at Nail Tarsus/Bill at Nares Neckring	72	85	3.8[a] 3.2[b]
2c	*leucopareia-taverneri* (Neckring > 5 mm)	same as 2b + Bill at Nail/Bill at Base	59	65	2.4[a] 2.4[b]
2d	*leucopareia-taverneri* (Neckring > 5 mm)	Bill at Nares Bill at Nail Tarsus/Bill at Nares	72	85	4.5[a] 2.5[b]
2e	*leucopareia-taverneri* (Neckring ≤ 5 mm)	same as 2b	40	44	10.7[a] 2.4[b]
2f	*leucopareia-taverneri* (Neckring ≤ 5 mm)	same as 2c	30	34	6.2[a] 6.2[b]
3a	*leucopareia-parvipes*	Culmen Tarsus Neckring	107	109	0.9

Table 6. Continued

Number	Subspecies	Measurements	Sample Size		Error Rate
			Males	Females	
3b	*leucopareia-parvipes*	Culmen Midtoe Bill at Nares Bill at Nail	107	120	3.1
4a	*taverneri-parvipes*	Culmen Tarsus	89	74	9.8
4b	*taverneri-parvipes*	same as 4a + Bill at Nail	58	55	7.1
5a	*parvipes-occidentalis*	Culmen Tarsus Total Tarsus	141	149	9.0
5b	*parvipes-occidentalis*	same as 5a + Midtoe	134	144	7.9
6a	*occidentalis-fulva*	Culmen Tarsus	326	300	12.6

a/ Prior probabilities assumed equal for each subspecies.
b/ Prior probabilities assumed proportional to the number of each subspecies in the sample.

The value for *leucopareia* is highest, so Bird # 1151 would be assigned (correctly in fact) to this subspecies. Since the value for *taverneri* is somewhat close, however, we should examine the secondary DFs for distinguishing these two subspecies.

Bird # 1151 has Neckring = 12.0 mm, so we could use DF 2a and assign the bird to *leucopareia* because its Neckring exceeded 5 mm. Alternatively, we could employ the measurements: Bill at Nares = 18.8 mm, Bill at Nail = 15.6 mm, Tarsus/Bill at Nares = 81.1 mm/18.8 mm = 4.31, and apply DF 2d (Table A2), to obtain values 1538.84 for *leucopareia*, and 1535.16 for *taverneri*. Again, because the value for *leucopareia* is greatest, Bird # 1151 would be assigned to that subspecies.

Plumage Characteristics

Plumage characters were not quantified in this analysis, except that the presence and width of white neckrings was noted for some subspecies. This was done in recognition of the special interest in *leucopareia*. Delacour (1951, 1954), Gabrielson and Lincoln (1959) and Palmer (1976) provided general plumage descriptions for the six subspecies of Canada geese addressed here. From examinations of numerous geese in Alaska and California, we are able to make the following refinements of Delacour's (1951, 1954) accounts of plumage characteristics:

minima: If present, neckrings were usually narrow and incomplete, but some adult birds had a complete solid white neckring, up to 25 mm wide and frequently over 10 mm wide (P. G. Mickelson personal communications).

leucopareia and *taverneri:* Breast color of *leucopareia* generally ranged from grayish brown to brownish gray, and adults were usually darker than immatures. Breast color of *taverneri* was typically grayish, but quite variable among birds, and frequently lighter among young birds. All adult *leucopareia* had a complete white neckring, which averaged 20 mm in width; 97.5 percent of the immature birds had a neckring, which averaged 14 mm wide. Among *taverneri* 40.6 percent of the adults had a complete white neckring, which averaged 5 mm wide. An additional 31.2 percent of the adults examined had an incomplete or trace neckring (individual white feathers). Nearly 10 percent of immature *taverneri* had a complete neckring, averaging 3 mm wide, and an additional 19.5 percent of the young birds had a trace neckring. Neckrings on most *leucopareia* consist of completely white feathers; those of *taverneri* typically include white feathers edged with black.

parvipes: Only birds from Cook Inlet were examined by the authors and these geese had a light-colored breast. Breast feathers were sandy colored rather than brownish or grayish, as in *leucopareia* and *taverneri*. Among 38 adult birds, 8 percent had a complete white neckring averaging 8 mm wide, and an additional 30 percent had trace neckrings.

occidentalis and *fulva:* Among adult *occidentalis*, 6.5 percent had a complete neckring averaging 5 mm wide and an additional 14 percent had a trace neckring. Although the presence or absence of neckrings on *fulva* was not recorded, we believe that 5 percent or less of the birds had a complete neckring with an average width less than 5 mm.

DISCUSSION

Taxonomic Implications

Palmer (1976:188) stated that "Despite more than 60 years of sometimes acrimonious debate, the allocation of Canada Geese to subspecies has remained both logically and heuristically unsatisfactory." He and Delacour (1951, 1954) identified a number of factors contributing to this confusion, including: scarcity of breeding specimens from a number of remote but critically important areas, lack of banding in many breeding areas, great variation in size and color of birds, confusion caused by wandering of non-breeders or molt migrants to nesting areas of other subspecies, egging and capture of flightless birds by Natives, shooting, local extinction by introduction of predators such as foxes on islands, escape of captives or deliberate stocking and transplanting of birds of non-endemic or questionable origin, establishment of refuges, and other changes in land use. These factors have modified breeding, migrating and wintering traditions and have caused subspecies to mix. The net effect has been to alter and occasionally to obscure forever the former population status and distribution patterns.

Most authorities consider *minima* to be a valid entity (subspecies or higher level), and our findings support this conclusion. Palmer (1976) pointed out, however, that *minima* probably overlapped greatly in all characteristics with *leucopareia* when the latter was numerous and had many breeding places, and we did note a degree of relationship.

All authorities regard *leucopareia* as a distinct subspecies. Morgan et al. (1977) analyzed the serum proteins of nine subspecies of *Branta canadensis* (not including *parvipes*). However, they classified as *taverneri* birds from Cook Inlet, which would be termed *parvipes* by the classification we adopted. They concluded that *leucopareia* was the most distinct qualitatively, because of its present restricted distribution and presumed long isolation and lack of gene exchange with other Alaskan populations. Delacour (1951, 1954) mentioned a close resemblance between *leucopareia* and *taverneri* but observed that the latter is generally larger, has a bill less high at the base and broader toward the tip, possesses a smaller and more rounded nail, and often lacks the white neckring. We too noted a close relationship between *leucopareia* and *taverneri*, but found that the broad neckring of the former and other characteristics such as bill taper and ratio of Tarsus to Bill at Nares provided nearly complete separation of the two subspecies.

Morgan et al. (1977) concluded that *taverneri* and *minima* were clearly separated. Delacour (1951, 1954) and Ogilvie (1978), however, believed that intergradation takes place and we found a slight degree of overlap.

Parvipes is considered by most recent authorities to be a valid subspecies, but many point out its great variability. Delacour (1951, 1954) separated *taverneri* from *parvipes*, and recent writers such as Johnsgard (1975) and Bellrose (1978) followed his practice. The American Ornithologists' Union (1957) and Palmer (1976), however did not recognize *taverneri*. Our findings revealed that separation of *parvipes* and *taverneri* on the basis of the morphometric criteria available produced a higher error rate (7.1 percent) than for most other pairs. Our samples of *parvipes* were limited, however.

In our study *parvipes* proved difficult to separate from *occidentalis* (error rate 7.9 percent), but use of body color, which was not measured, would have reduced the overlap greatly.

Occidentalis is generally accepted as a distinct subspecies. Delacour (1951, 1954) separated *fulva* from *occidentalis*, and the American Ornithologists' Union (1957) and many other workers have followed this practice. Contrariwise, Dickinson (1953) and most recently Palmer (1976) and Ogilvie (1978) considered the two to be similar enough to remain as a single entity, and Morgan et al. (1977) found them to be a very similar pair. Their *fulva* were birds from Prince William Sound, an area where we are unable to classify birds as to subspecies (Fig. 1). Our study showed that the two were not easily separable on the basis of available measurements (error rate 12.6 percent).

Delacour (1951, 1954) conjectured that at one time *leucopareia* and *occidentalis* may have intergraded on the Alaskan peninsula. Also, *leucopareia* and *fulva* were considered by Morgan et al. (1977) to be a very similar pair. We encountered little or no overlap between *leucopareia* and the much larger *fulva* and a few birds with most of the characteristics of *leucopareia* but having dark plumage typical of *occidentalis* or *fulva*, which may be intergrades, have been seen at Crescent City (P. F. Springer).

Ogilvie (1978) suggested that a clinal relationship exists between *taverneri* and *occidentalis*. We encountered no difficulty distinguishing between these two subspecies, but did find a fair degree of overlap between *parvipes* and *occidentalis*.

Fulva and *leucopareia* were considered by Morgan et al. (1977) to be a very similar pair, but we did not encounter any difficulty in separating these subspecies because of their great size disparity.

Our study has shown that discriminant function analysis provides a quantitative representation of observed differences in various features of the *Branta canadensis* subspecies studied. Accordingly, it serves as an additional tool to the systematist in objectively discerning the degree of similarity or difference among a group of birds. Availability of other measurements, particularly color, would have provided additional criteria for consideration of subspecies relationships and separation. While the use of discriminant function analysis is of definite assistance in taxonomic work and can remove much personal bias, the investigator will still have to establish at least partly subjective limits in developing subspecies criteria.

Management Implications

For the waterfowl manager, as opposed to the systematist, information gained from banding and color marking geese is usually more valuable than that gained by simply determining their subspecies. Most management situations require more precise data than the subspecies of geese in consideration, because one subspecies often consists of several populations distributed over a wide geographic range; accordingly, a delineation based on population rather than subspecies is desirable. Such a delineation requires knowledge of the breeding areas of geese banded. Ideally, geese should be banded as local young or known breeders in an area; the usual practice of banding molting birds allows the possibility that they may have originated from distant breeding areas.

When banding data are absent or inadequate, the determination of subspecies can nonetheless be beneficial. For example, although it would be desirable to have all *leucopareia* marked so that positive identification could be made of individuals outside of their breeding area, this is virtually impossible. In this situation discriminant function analysis provides an alternative objective method for identifying these geese. The refinement of knowledge about the range of these birds will aid in restoring the subspecies to a secure status.

In Alaska and Arctic Canada it is often difficult and expensive to band geese. For those instances in which banded geese are not available, the determination of subspecies could be useful in identifying areas where banding efforts might most profitably be directed (e.g. interior forested versus tundra areas).

Needs for Further Research

From our study we are led to several recommendations for research that could further clarify the relationships among the six subspecies of Canada geese that breed in Alaska. The most important need is for systematic collections of geese throughout the ranges of all subspecies. Care should be taken to obtain geese known to be breeding in the area, to insure that nonbreeding vagrants do not distort the picture. Systematic collections could confirm the validity of each subspecies, assess the degree of separation between pairs of subspecies, and determine the extent of intergradation. They would also enable the ranges of each to be more clearly defined.

For each goose collected, a complete set of measurements should be taken, in a consistent manner. In addition, plumage characteristics should be measured on some quantitative scale. We have little doubt that a wider array of measurements, particularly of plumage features, could enhance our ability to distinguish subspecies. In addition, we suggest that various ways of combining measurements be considered. In the present study only linear combinations of measurements (discriminant functions) were employed, with the exception that the ratios, Tarsus/Bill at Nares and Bill at Nail/Bill at Base, were included.

Finally, we recommend that additional information on the behavior, ecology, and habitat of each subspecies be gathered and used to compare and contrast them. While it is not routine to include such information in a discriminant function for taxonomic purposes, it may well be that two subspecies differ primarily in a behavioral or ecological adaptation, and the methodology should be flexible enough to fit the situation.

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Table A0. Coefficients of initial discriminant functions used to assign individual to one of six subspecies (*m*=*minima*, *l*=*leucopareia*, *t*=*taverneri*, *p*=*parvipes*, *o*=*occidentalis* *f*=*fulva*).

Variable	Subspecies (males)					
	m	*l*	*t*	*p*	*o*	*f*
Constant	-302.821	-370.224	-380.841	-431.032	-513.728	-582.195
Culmen	1.719	2.504	2.889	3.664	3.822	4.496
Tarsus	3.015	3.144	2.726	3.205	3.549	3.831
Total Tarsus	4.110	4.479	4.786	4.587	5.045	5.136

Variable	Subspecies (females)					
	m	*l*	*t*	*p*	*o*	*f*
Constant	-299.317	-379.412	-396.910	-435.173	-518.916	-600.684
Culmen	4.154	5.375	5.880	6.688	7.260	8.054
Tarsus	2.234	2.410	2.092	2.567	2.654	2.864
Total Tarsus	4.312	4.679	4.939	4.627	5.198	5.476

Table A1. Coefficients of discriminant functions used to assign individual to *minima* or *leucopareia*.

DF	Variable	Males		Females	
		minima	*leucopareia*	*minima*	*leucopareia*
1a	Constant	-316.767	-398.726	-278.464	-365.253
	Culmen	4.854	6.202	7.136	9.185
	Tarsus	6.991	7.510	5.452	5.790
1b	Constant	-418.504	-519.966	-336.011	-431.587
	Culmen	4.333	5.584	5.954	7.891
	Tarsus	2.495	2.552	1.369	1.415
	Total Tarsus	6.401	7.047	5.336	5.729

Table A2. Coefficients of discriminant functions used to assign individual to *leucopareia* and *taverneri*.

DF	Variable	Males		Females	
		leucopareia	*taverneri*	*leucopareia*	*taverneri*
2b	Constant	-981.841	-954.259	-1190.536	-1197.469
	Bill at Nares	44.857	43.427	61.060	60.630
	Bill at Nail	22.493	25.329	7.400	9.144
	Tarsus/Bill at Nares	180.590	172.340	295.004	293.366
	Neckring	-4.026	-7.074	0.501	-0.560
2c	Constant	-1463.866	-1556.343	-959.969	-1018.527
	Bill at Nares	96.814	98.584	47.385	45.954
	Bill at Nail	-3.827	-0.712	16.803	20.345
	Tarsus/Bill at Nares	288.237	289.013	205.138	211.176
2d	Constant	-1473.456	-1561.310	-960.799	-1018.567
	Bill at Nares	96.615	98.440	47.247	45.924
	Bill at Nail	-2.744	0.069	16.941	20.375
	Tarsus/Bill at Nares	286.462	287.734	204.712	211.083
	Neckring	0.860	0.620	0.239	0.053
2e	Constant	-1778.523	-1850.614	-1112.790	-1204.396
	Bill at Nares	131.327	132.977	57.137	58.714
	Bill at Nail	-35.464	-34.133	5.590	3.998
	Tarsus/Bill at Nares	332.363	330.711	203.182	206.393
	Neckring	1.571	1.307	0.590	0.375
	Bill at Nail/ Bill at Base	352.767	384.635	400.296	493.489
2f	Constant	-1962.872	-1958.812	-1720.603	-1803.115
	Bill at Nares	97.311	97.956	108.028	110.847
	Bill at Nail	-13.523	-15.570	-51.161	-53.189
	Tarsus/Bill at Nares	267.990	258.098	357.019	360.753
	Neckring	5.254	-0.357	-3.486	-5.033
	Bill at Nail/ Bill at Base	1542.435	1639.692	1198.065	1269.261

Table A3. Coefficients of discriminant functions used to assign individual to *leucopareia* or *parvipes*.

DF	Variable	Males		Females	
		leucopareia	*parvipes*	*leucopareia*	*parvipes*
3a	Constant	-541.188	-658.156	-472.687	-592.234
	Culmen	3.787	4.905	8.413	9.950
	Midtoe	5.940	6.315	4.281	4.571
	Bill at Nares	34.742	35.347	17.606	17.657
	Bill at Nail	-3.929	-1.656	6.711	9.500
3b	Constant	-400.762	-480.019	-385.654	-476.438
	Culmen	8.024	9.848	10.368	12.558
	Tarsus	6.560	6.710	5.775	5.955
	Neckring	0.854	0.403	0.146	-0.337

Table A4. Coefficients of discriminant functions used to assign individual to *taverneri* or *parvipes*.

DF	Variable	Males		Females	
		taverneri	*parvipes*	*taverneri*	*parvipes*
4a	Constant	-291.088	-342.057	-319.794	-369.988
	Culmen	3.949	4.711	5.590	6.400
	Tarsus	5.713	5.972	6.142	6.405
4b	Constant	-354.369	-419.011	-441.002	-515.251
	Culmen	3.406	3.925	5.528	6.317
	Tarsus	4.425	4.612	6.425	6.597
	Bill at Nail	15.288	17.032	14.696	16.654

Table A5. Coefficients of discriminant functions used to assign individual to *parvipes* or *occidentalis*.

DF	Variable	Males		Females	
		parvipes	*occidentalis*	*parvipes*	*occidentalis*
5a	Constant	-390.526	-464.203	-465.676	-553.759
	Culmen	4.255	4.463	6.247	6.782
	Tarsus	1.708	1.926	4.823	4.998
	Total Tarsus	4.735	5.187	3.607	4.168
5b	Constant	-403.520	-481.084	-455.743	-538.713
	Culmen	4.892	5.280	6.453	6.789
	Tarsus	2.805	2.810	5.222	5.086
	Total Tarsus	4.615	5.146	3.967	4.137
	Midtoe	-1.048	-0.965	-0.623	-0.465

Table A6. Coefficients of discriminant functions used to assign individual to *occidentalis* or *fulva*.

DF	Variable	Males		Females	
		occidentalis	*fulva*	*occidentalis*	*fulva*
6a	Constant	-395.832	-451.758	-361.116	-423.221
	Culmen	3.011	3.529	5.844	6.476
	Tarsus	7.361	7.696	5.753	6.147

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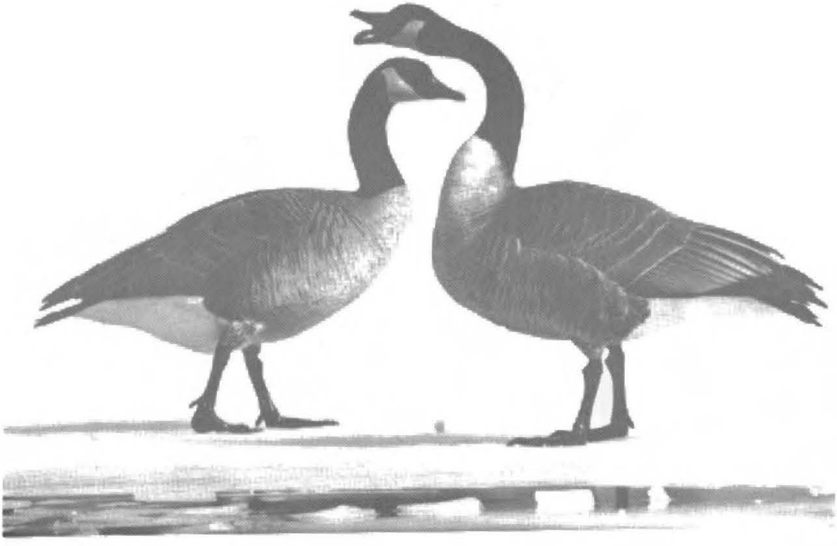

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