

TAXONOMY, DISTRIBUTION, AND EVOLUTION OF GOLDEN PLOVERS (*PLUVIALIS DOMINICA* AND *PLUVIALIS FULVA*)

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ABSTRACT.—A discriminant function analysis of specimen measurements separates 96% of two forms of Lesser Golden Plover in breeding plumage, previously described as subspecies. The forms breed sympatrically in northwest Alaska and are not isolated by habitat, but the incidence of specimens phenotypically intermediate between the two forms is no higher there than in areas of allopatry. The absence of a cline of intergrades or of a hybrid zone indicates that the forms are reproductively isolated through assortative mating and are separate species. To explain the process of speciation in these very similar forms, I propose that the evolution of genetically controlled and markedly different migration routes (*Pluvialis dominica* to South America and *Pluvialis fulva* to the central and western Pacific and Indian oceans) during Pleistocene glacial isolation may have selected against hybrids during subsequent secondary contact of populations. This would lead to adaptations in behavior and plumage, such as the difference in male undertail coverts reported here, that would produce assortative mating and reproductive isolation in sympatry. Thus, the requirements of migration and winter range drive the process of speciation. Received 2 August 1982, accepted 28 January 1983.

Two forms of Lesser (or American) Golden Plover have been treated by almost all authors as subspecies, *Pluvialis dominica dominica* and *P. d. fulva* (for example, Peters 1934, American Ornithologists' Union 1957, Bock 1958, Johansen 1958, Bannerman 1961, Vaurie 1964, Mayr and Short 1970, Johnsgard 1981). The elucidation of their status hinges on their distribution and interactions on breeding grounds in northwest Alaska, which, in spite of several published discussions (Conover 1945, Bailey 1948, Gabrielson and Lincoln 1959), remain obscure. I have applied a multivariate statistical approach to a study of museum specimens, with the surprising result that I find no evidence of intergradation or of interbreeding in regions of sympatry. I therefore suggest that separate species status for the two forms is appropriate.

The form *dominica* breeds on arctic and subarctic tundra from Baffin Island in Canada west to northwest Alaska. *Fulva* breeds from northwest Alaska west to the Yamal Peninsula in Siberia, where its range overlaps that of the Eurasian (or Greater) Golden Plover (*Pluvialis apricaria*). Wintering ranges of the two American forms are distinct: *dominica* winters in South America, and *fulva* winters in southern Asia and on many Pacific islands south to Australia and New Zealand (American Ornithologists' Union

1957). Both forms have been collected at several localities in Alaska from Barrow to the coast of the Bering Sea. *Fulva* is more common south of Bering Strait and *dominica* predominates nearer Barrow (Conover 1945). The problem in determining ranges, and the primary reason these forms have been considered subspecies, is their close similarity in appearance, especially in breeding plumage. Published descriptions of this plumage rely on characters such as "brighter gold spotting" on the back of *fulva* and a tendency for *dominica* to "show more white, especially on forehead and sides of breast" (Prater et al. 1977). In juvenal and adult winter plumages the forms are more easily separated, primarily on the basis of the yellow-buff (*fulva*) compared with brownish-grey (*dominica*) coloration on much of the body feathering, but even these qualities will not separate all individuals.

Differences in size have long been noted, however, with wing length serving to separate a large proportion, but not all, of the Alaskan birds (Conover 1945). Bailey (1948) noted that "where the two breeding areas come together in Northern Alaska, there are many specimens which can not be satisfactorily identified subspecifically," and some authors have concluded that the two forms interbreed in this region,

resulting in intergrades where the ranges overlap (Gabrielson and Lincoln 1959, Vaurie 1964). A more thorough analysis of this problem has been stalled by the lack of clear intermediate characters to indicate hybridization, because the parent forms differ only in degree rather than presence or absence of characters.

A few authors have considered the forms as distinct species. Portenko (1939) suggested this, but subsequently (Portenko 1981) listed them as subspecies and even suggested that *P. apricaria* and *P. dominica* may not be specifically distinct. [This latter view has no apparent support among taxonomists. Mayr and Short (1970) considered *apricaria* and *dominica* to comprise a species group, or, at the closest, a superspecies.] Stresemann and Stresemann (1966) and Kinsky and Yaldwyn (1981) assigned full species status to *fulva* primarily because of apparent differences in the molt and maturation schedules of 1- and 2-yr-old birds of the two forms. Because of these differences and the distinct migrations, the Ornithological Society of New Zealand (1980) now lists *Pluvialis fulva* instead of *P. d. fulva*.

The central questions remain, however. Do *dominica* and *fulva* interbreed freely? Are the parent forms sympatric, or does a zone of intergradation connect their ranges in northwest Alaska? If they do not interbreed, what are the selective forces and isolating mechanisms that have separated these very similar forms?

METHODS

I measured 369 specimens obtained from 13 North American museums (listed in the Acknowledgments). Because I wished to establish breeding ranges in northwest Alaska from museum specimens, for which nesting information is seldom available, I considered only adult birds taken on breeding grounds in late May, June, and July. Golden plover eggs usually hatch during early and mid-July (Conover 1945, Gabrielson and Lincoln 1959), and successful breeders tend chicks for a period of days or weeks after hatching. Some movements of failed or successful breeders do occur during this time, especially in late July (Myers and Pitelka 1980); among the specimens studied, however, only 8% were collected after 20 July, with an additional 12% taken 15–20 July. Thus, the assumption of local breeding is reasonable for most of the 226 northwest Alaska specimens.

To determine characteristics of parent forms where the number of specimens from breeding grounds was limited, as in the case of *fulva* in Siberia, I included some late-spring migrants as follows: breeding

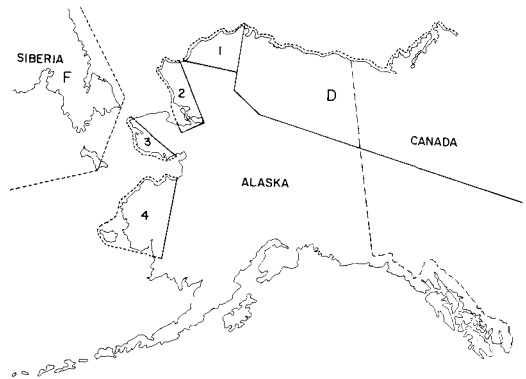


Fig. 1. Specimen collection regions in northwest Alaska (Regions 1-4) and boundaries of assumed parent populations (D and F).

grounds, Siberia and St. Lawrence Island, 11 specimens, late May–July; migration, Japan, Korea, north China, 34 specimens, 6 April–2 June; migration or winter grounds, south China and Pacific islands, 15 specimens, 6 April–30 May. The assumed parent *dominica* population was derived from: breeding grounds, northeast Alaska (east of 156°W; Fig. 1), 41 specimens, northern Canada, 29 specimens, all late May–July; migration, Alberta, 8 specimens, late May.

Five additional specimens collected in eastern Siberia (Koliutschin Bay) on one date (18 July 1909) were excluded from the *fulva* parent group in the analysis, because they appear to represent a population of *dominica*. Four of the birds are classed by the discriminant function analysis as *dominica*, and the fifth as intermediate between the two forms. The five birds are statistically separable from the 60 birds in the parent *fulva* group ($P < 0.0001$). The step of excluding these specimens is risky in view of my principal assumption that location is indicative of form in Regions D and F. It is taken only because the entire local sample of five specimens is internally consistent and clearly distinguishable from the remainder of the Region F sample. An explanation based on distribution of forms rather than on individual variation within a form therefore seems appropriate. The Koliutschin Bay sample may represent a local breeding group of *dominica* or a wandering flock from outside the area; in either case, it would be misleading to include them with the *fulva* parent group.

I made the following measurements on all 369 specimens: (1) wing chord length—average of both wings, adjusted for wear when appreciable; (2) exposed culmen length; and (3) tarsus length—average of both tarsi. Tarsi were measured from the posterior depression of the tibio-metatarsus joint to the distal end of the central process of the metatarsus (Hubbard 1970).

On all specimens not in molt (254 specimens), I

TABLE 1. Golden plover specimen measurements (mean \pm standard deviation).

	<i>n</i>	Wing	Tarsus	Culmen	W/T \times C
Region D (<i>dominica</i>)					
Males	42	177.6 \pm 4.3	43.9 \pm 1.2	22.7 \pm 1.1	0.178 \pm 0.011
Females	35	176.8 \pm 3.9	43.6 \pm 1.8	22.6 \pm 1.1	0.180 \pm 0.012
Region F (<i>fulva</i>)					
Males	44	165.1 \pm 4.2	44.3 \pm 1.5	23.6 \pm 1.0	0.158 \pm 0.010
Females	16	165.5 \pm 5.5	44.5 \pm 1.5	23.5 \pm 1.5	0.159 \pm 0.014
D vs. F, sexes combined		<i>P</i> < 0.0001	<i>P</i> < 0.03	<i>P</i> < 0.0001	<i>P</i> < 0.0001

recorded the following measurements and categorizations: (4) height, along forehead center line, of the band of black feathering from culmen to white band; (5) height of double band of black plus white feathering; (6) percentage of breast feathering that is black rather than white on a scale of less than 50% black, through 50-75%, 76-90%, and 91-97%, to 98-100%; (7) percentage of undertail coverts that is black rather than white on a scale of less than 10% black, through 10-35%, 36-65%, and 66-90%, to 91-100%; and (8) boldness of tail barring, an estimate of the contrast between light and dark bands, on a scale of faint (1) through moderate (2) to bold (3). Measurements (4) and (5) are susceptible to variation due to differences in specimen preparation techniques. No correction was made for this potential variation, but the large number of collectors responsible for these specimens makes systematic, biasing variation unlikely.

I also recorded the degree of wear of primaries for all birds, in four categories (none, light, moderate, heavy; Prater et al. 1977). Only 13% of the specimens had primaries worn sufficiently to require a correction (1-8 mm) added to the measured length to indicate original length. The correction was an estimate based on the relative width of the rachis at the feather's tip in comparisons with the unworn primaries of other birds. For wing and tarsus length, a single measurement was used when right or left member was not measurable. For four specimens no tarsus measurement was possible, and two specimens lacked culmen measurements; mean values were substituted in the analysis.

I applied step-wise discriminant function analysis (DFA) to the parent groups, region F vs. region D (Fig. 1), maximizing Rao's *V* (Nie et al. 1975). This procedure combines the measured variables, weighted with computed coefficients, to form a new linear function that maximally separates the two populations statistically. The advantage of the procedure is that it considers differences between populations in all variables simultaneously rather than addressing measurements independently. The resultant separation is therefore statistically greater than that provided by any single measurement. Rao's *V* is a generalized statistical measure of the distance between populations on the discriminant function axis and

indicates the relative contribution of each variable to the separation (Nie et al. 1975).

Analysis variables were derived from the list of measured variables. For all birds these were lengths of wing (W), tarsus (T), culmen (C), and ratios W/T, W/C, and W/T \times C. Although the ratios of normally distributed variates are not normally distributed, I judged the deviation to be slight in these cases, because a comparison of ratios of population means of measured variables with population means of individually computed ratios gives an estimate of the non-normality of ratios, and the differences between these means for three ratios and two groups (*fulva* and *dominica*) were less than 0.4% in all cases.

A discriminant function analysis was repeated for birds not in molt. I used the same six mensural variables plus six plumage variables—height of black forehead band (BBAND), height of white forehead band (WBAND), difference in the percentage of black feathering between breast and undertail coverts (BUDIF)—and three variables derived from the three categories of tail barring—each variable (T_1 , T_2 , T_3) had the value 1 or 0 depending on whether the tail barring was (1) or was not (0) faint (T_1), moderate (T_2) or bold (T_3). This last conversion is necessary to satisfy statistical assumptions of discriminant function analysis. The difference in breast and undertail covert blackness, rather than the original measurements, is used to avoid potential confusion arising from birds beginning to molt but not recognized as such, or from individual differences in overall blackness arising from age or other factors. The transformation emphasizes the relative coloration of the two plumage areas.

After deriving the discriminant function that maximally separated the parent groups, I classified all individuals collected in northwest Alaska as *fulva* or *dominica* on the basis of their discriminant scores, and I computed the probabilities of these classifications.

RESULTS AND DISCUSSION

Sexual differences.—There are no significant differences between sexes in any of the length measurements (Table 1). Size dimorphism is common in Scolopacidae (sandpipers), females

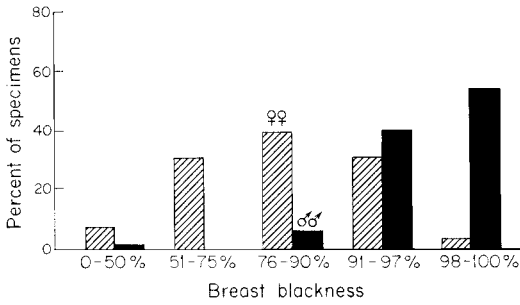


Fig. 2. Sexual dimorphism in blackness of breast in breeding plumage, *fulva* and *dominica* combined. June specimens only. Females, $n = 43$. Males, $n = 89$.

being larger in most species, but in the Family Charadriidae (plovers) most species show little or no dimorphism (Prater et al. 1977). Weights of female *dominica* at Barrow exceed weights of males throughout the summer, however, by 14% in May and June, decreasing to 6% in July and August, as weights of both sexes increase (t -test: May-June, $n = 26$, $P < 0.001$; July-August, $n = 35$, $P = 0.17$; unpublished data of F. A. Pitelka). In view of this, the close agreement in size within both groups shown in Table 1 is surprising. Breeding plumages, of course, are quite different, most males having essentially uniform black breasts and females typically including scattered light feathers on the breast and face (Fig. 2).

Differences between fulva and dominica.—The close similarity of size between sexes permits combining sexes for comparisons between forms. Population means of wing, tarsus, and culmen lengths all differ significantly between *fulva* and *dominica*, with means of wing length showing the greatest difference (*dominica* 7% greater). Note, however, that tarsus and culmen lengths are greater in *fulva*, producing an

average difference of 13% in the ratios of wing to tarsus times culmen. The two forms differ in proportion even more than in wing length.

The plumage difference most widely presented in the ornithological literature to distinguish *fulva* from *dominica* in breeding dress is the brightness of gold spotting on the back. I found this qualitative character to be highly variable and broadly overlapping between forms. Both forms have yellow spots and white spots, with intensity, size, and relative numbers of spots variable among individuals. Many *fulva* do appear brighter than many *dominica*, but the difference is not easily quantifiable and seems too inconsistent to be useful.

None of the measured plumage characters is significantly different between females of *fulva* and *dominica*, but males differ in several respects (Table 2). The difference in the percentage of black feathering between breast and undertail coverts is sharp. Males of both forms have almost completely black breasts and faces, but undertail coverts of *dominica* are black, lightly spotted or banded with white, whereas those of *fulva* are predominantly white with variable black markings (Fig. 3). The height of the black forehead band is also significantly different between forms, but the white-band height, frequently mentioned in published descriptions, is less different in these samples. Male *fulva* frequently have more boldly barred tails than do *dominica*, but this difference is also quite variable. Additionally, Portenko (1981) pointed out that *fulva* in breeding plumage have a narrow white band interrupted by black patches along the flanks, whereas *dominica* have completely black flanks. I did not quantify this characteristic on all specimens, but among male specimens in breeding plumage at the Museum of Vertebrate Zoology it is highly correlated with coloration of undertail coverts: male *fulva*

TABLE 2. Differences in male breeding plumages of *dominica* and *fulva*.

	n	BUDIF ^a	BBAND ^b	WBAND ^c	TAIL ^d
Region D (<i>dominica</i>)	36	16.1 ± 17.0	2.41 ± 0.78	8.07 ± 1.62	2.36 ± 0.68
Region F (<i>fulva</i>)	25	69.4 ± 19.9	1.42 ± 0.82	7.28 ± 1.55	2.68 ± 0.56
		$P < 0.0001$	$P < 0.0001$	n.s.	n.s.

^a Percentage blackness of breast minus percentage blackness of undertail coverts.

^b Height of black forehead band (mm).

^c Height of white forehead band (mm).

^d Mean of category values for boldness of tail barring: 1 = faint, 2 = moderate, 3 = bold.

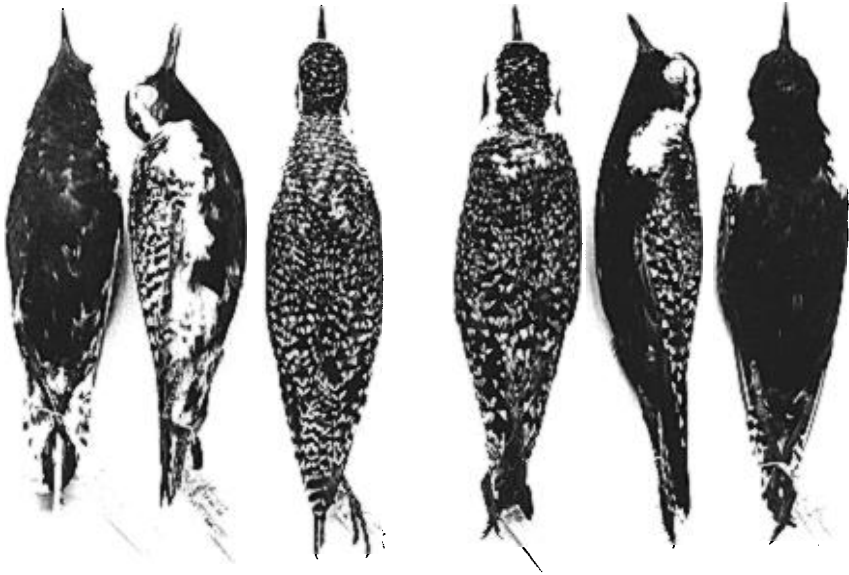


Fig. 3. Typical male breeding plumages showing similar dorsal spotting and differences in amount of white on flanks and undertail coverts. *Fulva*, 3 birds on left; *dominica*, 3 birds on right.

have white undertail coverts and white along flanks; *dominica* are predominantly black in both these areas.

Discriminant function analysis.—Wing length, the first variable selected by the DFA, produced the greatest contribution to separation of region F and region D samples, as indicated by Rao's V (Table 3). The three variables subsequently selected improved the separation. The quality of separation can be tested by reclassifying all region F and region D individuals with the discriminant function already derived. This procedure correctly classified 94.2% of the 138 individuals as belonging to their region of origin, that is, as *fulva* or *dominica*. Adding plumage variables for males not in molt (a subset of

61) and repeating the DFA brings the total correctly classified to 96.4%. This is a very good separation, but it remains slightly overlapping, indicating that almost 4% of individuals from our assumed parent populations would still be identified as the other form. These birds are represented by the overlapping tails in the distributions of discriminant scores based on mensural characters for regions D and F (Fig. 4). The distributions are normal, and they define the individual variation expected in populations of *fulva* or *dominica*.

The bottom plot in Fig. 4 presents the distribution of discriminant scores for all 226 individuals from northwest Alaska, regions 1-4 (see Fig. 1). This distribution is bimodal and can be

TABLE 3. Discriminant function analysis of *dominica* (Region D) vs. *fulva* (Region F).

Step entered	Variable	Rao's V	Significance of added variable	Function coefficients
1	Wing	266	$P < 0.0001$	-0.2058
2	Wing/(tarsus × culmen)	358	$P < 0.0001$	229.3
3	Culmen	362	$P < 0.05$	2.137
4	Wing/tarsus	387	$P < 0.0001$	-11.38
	Constant			-8.405

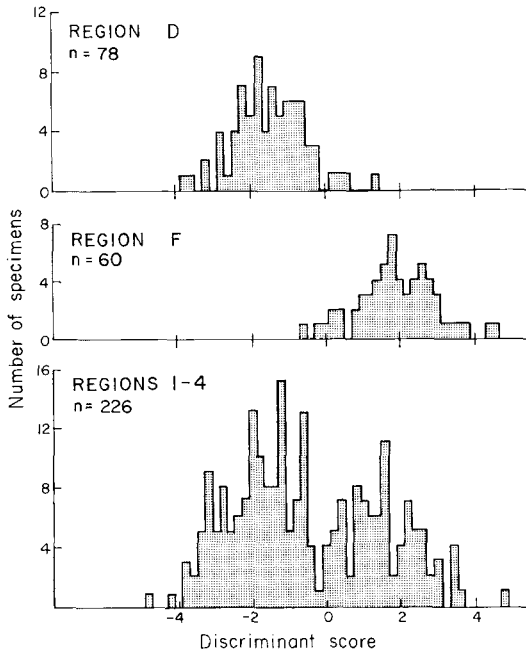


Fig. 4. Distributions of discriminant function scores of golden plover specimens. Region D, *dominica*; Region F, *fulva*; Regions 1-4, northwest Alaska. See Fig. 1.

generated from the two parent distributions, slightly shifted toward negative discriminant scores. I have tested for this shift by splitting the region 1-4 distribution into two unimodal portions, separated at the discriminant value (0.221) indicating equal probabilities of belonging to distribution D or distribution F. These half-distributions then test as significantly different from the comparable D and F distributions (Mann-Whitney and *t*-tests: $P < 0.04$). The amount of shift along the discriminant function axis is approximately -0.325 , 9% of the separation between *fulva* and *dominica* means. This value was calculated by comparing corresponding distribution means and is the average of *fulva* ($= -0.312$) and *dominica* ($= -0.338$). A graphic method gives similar values. This test for a shift is conservative, because the dividing value chosen was based on the absence of a shift; this has the effect of including intermediate scores in the *dominica* half and excluding intermediate scores from the *fulva* half. To the extent that a shift is real, this arbitrary division will tend to obscure the shift. If we accept the shift and divide the bimodal

TABLE 4. Relative abundance of golden plover forms in northwest Alaska (see Fig. 1).

Species	Region			
	1	2	3	4
<i>fulva</i>	8.0%	19.2%	83.9%	73.5%
<i>dominica</i>	92.0%	80.8%	16.1%	26.5%
<i>n</i>	100	26	62	38

distribution accordingly at -0.104 , the *P* value of significance of the shift improves by an order of magnitude.

The combination of variables used in the discriminant function makes interpretation of the measured shift difficult, but it seems to indicate that birds of both forms are longer-winged in northwest Alaska. Reasons for such a pattern are not apparent. If both forms shifted closer together on the discriminant function axis, character convergence, clinal variation, or intergradation between interbreeding populations would be suggested; if, on the other hand, the distributions shifted apart in opposite directions on the axis, the likely interpretation would be character displacement arising from competition between noninterbreeding populations. Instead, the parallel shift in both forms may suggest ecotypic variation, with both *fulva* and *dominica* responding similarly to requirements of breeding in northwest Alaska (climate, habitats, migration distances, etc.).

Distribution of fulva and dominica.—Applying the observed shift to the discriminant classification procedure based on mensural characters and supplementing these results with the classification based on plumage characters, I identified 93% of all 369 specimens as *fulva* or *dominica* (probability of at least 0.90, and agreement between mensural and plumage classification). An additional 5% of specimens can be classed as “probably” one form or the other, and 2% of specimens are impossible to assign to either form. I divided northwest Alaska specimens into four groups based on regions shown in Fig. 1. The groups were arbitrarily chosen but were based on the availability of collected specimens. Proportions of *fulva* and *dominica* in different regions varied widely, but both forms occurred throughout northwest Alaska (Table 4). Both sexes of both forms have been collected in each region during early June, the period when local breeding is most prob-

able. The general pattern shows an increase in the proportion of *fulva* toward the Bering Strait, with *dominica* more common in the northernmost regions. There is a slightly higher incidence of *dominica* in region 4, the southernmost, than in region 3, but this may partly reflect a larger component of possibly migrating birds from late July in the region 4 sample. No region contained equal numbers of *fulva* and *dominica*, but there were no available collections from the most likely area, between the Bering Strait and Kotzebue, a distance of about 260 km. Four birds identified as *dominica* were also collected on a single date at a site in eastern Siberia, but whether these represent breeding or migrating birds is unknown (see Methods). Portenko (1981) reported a nesting bird identified as *dominica* from Wrangel Island and states that *dominica* was an uncommon nesting bird in northeast Siberia at the end of the last century and beginning of the present century.

The region of sympatry, from Barrow to Nunivak Island at least, covers a distance of over 1,300 km, but the specimen collection dates ranged over a century (1877–1980). It is quite possible that the ranges of one or both forms have varied over time, in unison or independently. At an extreme, an apparent pattern of sympatry in museum specimens might result from allopatric populations whose ranges have shifted over the entire region of collection. We know this is not the case, because both forms have been collected at several sites within single years, and my own collections include *fulva* and *dominica* defending adjacent territories at Cape Krusenstern in region 2. Range shifts may, however, explain some of the apparent sympatry.

The relative population densities of the two forms have probably changed independently during the past century as a result of heavy sport and market gunning of *dominica* during migration, which occurred in eastern and central North America in the late 19th century (Bent 1929). Numerous published reports indicate that American Golden Plovers were among the most abundant of all North American migrants before that period, and by the early 1900's most authors were lamenting the disappearance or drastic decline in numbers of this species at all localities. Audubon (1840) described a spring hunt near New Orleans in 1821 in which 200 gunners shot an estimated 48,000 golden plovers in one day. A century later, Ob-

erholser (1938) described golden plovers in Louisiana as rare transient visitors. Bent (1929) estimated that the species population reached a low point about 1900, when "it had become scarce where it once abounded; no more big flights occurred; and in many places it was rarely seen." Changes in game laws occurred in time, however, and the species proved capable of a strong increase in population after a reduction of the artificially high mortality rate. Today the species is widespread and common in suitable habitat throughout the North American arctic.

Because of differences in migration routes, the heavy shooting in eastern North America devastated only *dominica* (probably including Alaskan birds), while Alaskan *fulva* migrating to Pacific islands were less drastically affected. *Fulva* have probably been taken for food for centuries by Pacific island natives, and heavy sport gunning occurred in Hawaii considerably later than in eastern North America (Munro 1945), but the overall impact on *fulva* populations is unlikely to compare with the impact of market gunning of *dominica* in the late 19th century. We might have learned a great deal about population interactions of the two forms if we had density estimates before and after this period. Museum specimens indicate that the proportion of *dominica* compared to *fulva* in regions 1 and 2 combined and in regions 3 and 4 combined has been higher, but not significantly so, since 1930 than it was in the preceding half century ($P < 0.06$, two-tailed χ^2 test). Such a change would be expected for *dominica* recovering from a depressed population level. Of course, the museum collections do not sample all times and places equally; some collecting bias may affect this comparison. No marked range changes are indicated: both forms were collected over the same range of sympatry during both periods, and comparison of discriminant score distributions between early and late periods for all four regions does not indicate any range shifts. Thus, the conclusion of widespread sympatry seems inescapable.

Lack of evidence of fulva-dominica hybrids.—Because the two forms lack distinctive plumage characters, hybrids cannot be identified by the presence of clear hybrid characters. Unless the differences in size, proportion, and plumage are controlled by an extremely simple gene system [such as a single switching gene as proposed by Smith (1969) to explain the lack of inter-

TABLE 5. Incidence of phenotypically intermediate golden plovers in northwest Alaska, Regions 1-4.

	<i>n</i>	Percentage of sample within interval	
		A	B
Expected, if no hybridization		10.0%	20.0%
Expected, if free hybridization		27-39%	45-64%
Observed, Regions 1-4	226	9.7%	20.8%

mediates between the small ringed plovers *Charadrius semipalmatus* and *C. hiaticula* on Baffin Island], we can expect hybrids to exhibit intermediate characteristics within the range of continuous phenotypic variation in the two parent populations. On the discriminant function axis, the most probable distribution for hybrids would be unimodal and intermediate between the peaks of *fulva* and *dominica* distributions (Schueler and Rising 1976, Neff and Smith 1978). Because of the similarity of parent forms, however, some presumed pure parent types occur in this intermediate range. Thus, individual hybrids cannot be distinguished phenotypically. To circumvent this limitation, I measured the incidence of these phenotypically intermediate plovers in samples from different regions in the following manner. The parent distributions, regions D and F, can be fit with normal curves. From these theoretical curves, I calculated the interval on the discriminant function axis that contains 10% of each distribution. There exists one, but only one, interval that satisfies this requirement, and it contains the overlapping tails of both distributions.

This approach carries a significant benefit: any mixture of samples taken from pure parent populations should include the same 10% of individuals within the specified interval, whether the mixture contains all *fulva*, all *dominica*, or any proportion between these extremes. Thus, we need not identify birds before we look for intermediates. After shifting the interval by -0.325 on the discriminant function axis (to account for the distributional shift described above), we can identify intermediate phenotypes in samples from northwest Alaska. If the population in regions 1-4 is a mixture of interbreeding *fulva* and *dominica*, the resultant genetic intermediates should contribute to a greater than 10% portion of phenotypes in the intermediate zone. In the absence of inter-

breeding, the incidence of intermediates should be the same as that calculated for the parent populations (10%).

I repeated this test for a wider interval containing 20% of the parent populations. Table 5 presents expected percentages of sample distributions included in each of these intervals for assumptions of (1) no hybridization or (2) free hybridization forming a hybrid zone encompassing the sample area (Short 1969). Two sets of values for free hybridization reflect different assumptions of heterogeneity and are meant to provide a range of expected values: the larger number in each interval assumes the same hybrid or intergrade distribution width as observed for parent distributions; the smaller number indicates a distribution with standard deviation 50% greater than parent populations, indicating increased heterogeneity due to backcrossing of hybrids (Schueler and Rising 1976). The actual incidence of intermediates in the combined regions 1-4 is almost precisely that expected on the assumption of no hybridization and differs significantly from either assumption of free hybridization ($P < 0.001$, χ^2 test). With this result, the shift of -0.325 applied to the interval used to test specimens from regions 1-4 is seen to be conservative, because an unwarranted shift would place the interval closer to a peak of the bimodal distribution, incorrectly increasing the number of intermediates within the interval. Because the number recorded equals the minimum expectation, we can be confident that the shift does not introduce such an error.

If, however, a very narrow hybrid zone were to exist, the effect of combining large samples of pure parent phenotypes taken from outside the area of contact would be to mask the existence of the expected hybrid intermediates. Distributions of discriminant scores for regions 1-4 are shown by region in Fig. 5, with interval A (the 10% interval) indicated. These depict a

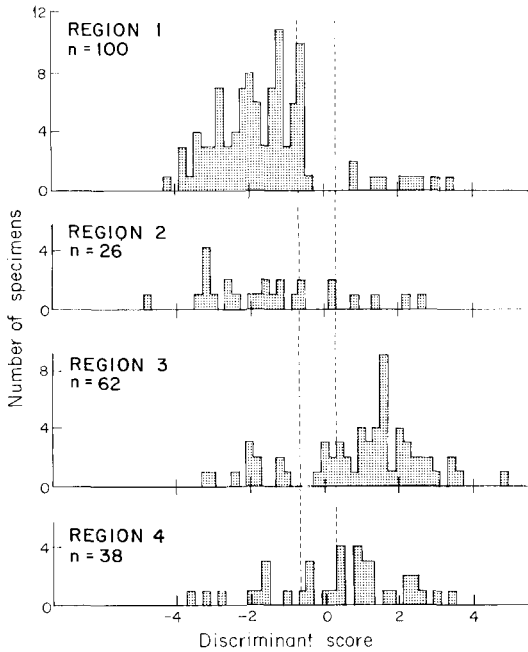


Fig. 5. Distributions of discriminant function scores of golden plover specimens from northwest Alaska. See Fig. 1. Interval A, containing 10% of parent phenotypes, is indicated.

rather broad zone of sympatry, as described above. None of these smaller regions is suggestive of a hybrid zone. In Table 6, the actual incidence of intermediates in each region shows no significant difference from that expected in the absence of any hybridization between parent forms. Only in Region 4, with a small sample size, is the incidence of intermediates higher than expected in both intervals (5 vs. 3.8, 11 vs. 7.6); this difference remains nonsignificant and does not approach expected results for a hybrid zone (Table 5). I conclude that these data show no pattern of elevated incidence of phenotypic intermediates in regions of sympatry, indicating strongly assortative mating. If hybrids occur at all, they are much less common than would be expected if *fulva* and *dominica* were freely interbreeding. Field data sufficient to deny or support assortative mating in these forms are lacking, but I have collected three pairs of plovers on their breeding territories in region 2: two *dominica-dominica* pairs at Cape Krusenstern, and one *fulva-fulva* pair at Kotzebue, 60 km distant.

Habitat isolation does not appear to be im-

TABLE 6. Incidence of phenotypically intermediate golden plovers in each region (see Fig. 1).

Region	n	Percentage of sample within interval		
		A	B	
D	78	7.7%	17.9%	n.s.
F	60	10.0	18.3	n.s.
1	100	7.0	20.0	n.s.
2	26	11.5	19.2	n.s.
3	62	11.3	17.7	n.s.
4	38	13.2	28.9	n.s.
Expected, if no hybridization		10.0	20.0	

portant. Both forms nest on well-drained tundra on slopes and uplands or on ridges and high polygons in lowland tundra (Drury 1961, Sauer 1962, Johnsgard 1981, Portenko 1981). At Cape Krusenstern, I found both forms nesting in an area of parallel former beach ridges. Both *fulva* and *dominica* territories included sections of the same few adjacent ridges. No habitat distinctions were apparent to me, and birds of both forms must have been in contact repeatedly during the season. More extensive observations or collections are needed, especially if these can include a large sample size at a single locality during a single season. Nevertheless, with present information, the conclusion of substantial reproductive isolation through assortative mating seems unavoidable.

Taxonomic status.—Because of the large region of sympatry and the strong indication of assortative mating, the prevailing treatment of these forms as subspecies is inappropriate. They satisfy the accepted central requirement for biologically distinct species, the occurrence of sympatry without interbreeding (Mayr 1969). Short (1969) presented a hierarchical classification of avian subspecies groups, superspecies, and related species on the basis of hybridization interactions. The apparent interaction of *fulva* and *dominica* places them well beyond Short's "taxonomic species border," to be classified as allospecies of a superspecies (Amadon 1966) or as related, but not allospecific, species.

Initially, this conclusion may seem surprising, primarily because of the extremely similar appearance of the two forms. Short (1969), in fact, alludes to the expected distinctness of even subspecies as being sufficient to permit recognition of hybrids; yet these forms fail that test.

He argues rightly that "the often considerable morphological differences between forms interbreeding in a hybrid zone is no reason for reluctance to merge them," because the two forms apparently "accept each other as conspecific." Conversely, the absence of prominent morphological differences between sympatric forms assortatively mating is no reason to merge them, when the two forms themselves show such a reluctance to merge. We must not confuse our own ability to distinguish forms with the ability of the birds themselves. At present, analyses of behavioral repertoires of the two species are unavailable; in future these may show important differences.

Two other distinctions between *fulva* and *dominica* have occasionally been proposed as evidence of sufficient distinctness to convey separate species status. The forms differ markedly in migration routes and wintering areas, and they may differ in schedules of molt and maturation among young birds on winter grounds. Kinsky and Yaldwyn (1981) interpret plumages of birds found on South Pacific wintering grounds during the boreal summer as indicating that young *fulva* remain in winter quarters longer (1.5 or 2.5 yr) than young *dominica* (0.5 yr, Stresemann and Stresemann 1966). Their results differ in several respects from those of Johnson and Johnson (unpubl.) on molt and migration of *fulva* in Hawaiian winter quarters, however, and the situation with wintering *dominica* remains poorly defined. My own examination of breeding specimens does not support their contention. Some almost 1-yr-old *fulva* can be identified among Alaskan specimens in breeding plumage by their distinctive juvenile rectrices (see Kinsky and Yaldwyn 1981), but I could not confidently distinguish all young birds of both forms in breeding dress. The condition of primaries provides a useful indicator, however: first-year birds in June have primaries acquired as juveniles 10 months earlier, and these usually show considerable wear compared to those of older birds, whose primaries are nearer 5 months old (Prater et al. 1977) or 7 months old (Johnson and Johnson unpubl.). Figure 6 compares primary wear between *fulva* and *dominica* among birds collected in spring migration (57 specimens) and on breeding grounds (311 specimens). The same criteria were applied to all specimens. The distributions differ ($P < 0.001$, χ^2 test) primarily in moderate and heavy wear classes. If these

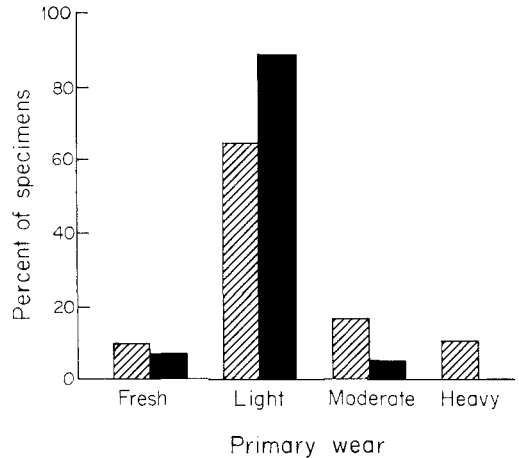


Fig. 6. Difference in frequency of primary wear classes in specimens of *P. dominica* (shaded portion, $n = 220$) and *P. fulva* (striped portion, $n = 148$).

correspond to 1-yr-old birds (as suggested by Johnson and Johnson unpubl.), the data indicate that many more *fulva* than *dominica* return to breeding grounds during their first spring. This is the opposite of the situation described by Kinsky and Yaldwyn and Stresemann and Stresemann, although it, too, suggests a distinction between the forms.

Nomenclature.—The appropriate species designations *Pluvialis dominica* (Muller) and *Pluvialis fulva* (Gmelin) are obvious, but several common names are possible. The dichotomy of Greater (*P. apricaria*) and Lesser (*P. dominica*, including *P. fulva*) Golden Plovers (Palmer 1967, Johnsgard 1981) becomes inappropriate when we must treat three species. Other common name adjectives for *apricaria* in English include Golden (Bannerman 1961), European Golden (Bent 1929), and Eurasian Golden (A.O.U. 1957). Names used recently for *dominica* (excluding *fulva*) include American Golden (Bent 1929, Bailey 1948) and Eastern American Golden (Gabrielson and Lincoln 1959). For *fulva*, at least seven names exist: Pacific Golden (Bent 1929, Bailey 1948), Western American Golden (Gabrielson and Lincoln 1959), Asiatic Golden (Bannerman 1961, Vaurie 1964), Eastern Golden (Royal Australasian Ornithologist's Union 1968), Least Golden (Ornithological Society of New Zealand 1980), Siberian (Portenko 1981), and Asian Lesser Golden (Johnsgard 1981). I suggest that all three species be given names consisting of a single adjective preceding gold-

en plover and that this adjective reflect their obvious differences in range rather than the more subtle differences of size. This eliminates some names but still leaves choices. Eurasian best describes the breeding range of *apricaria*, and American is clearly the choice for *dominica*. Three regional possibilities for *fulva*, Asiatic, Asian, and Siberian, are somewhat ambiguous in view of the occurrence of *apricaria* in those regions. Western American ignores the major portion of the species' range, and Eastern is ambiguous or misleading over a large portion of the globe. The remaining name, Pacific, fails to account for that portion of the wintering area in the Indian Ocean, but it is unambiguous and informative. I suggest the names Eurasian Golden Plover (*P. apricaria*), Pacific Golden Plover (*P. fulva*), and American Golden Plover (*P. dominica*).

Speciation of fulva and dominica: a hypothesis.—These results present us with a puzzle: what factors in the evolution of these two tundra-breeding birds, so similar in appearance and ecology, have produced the present reproductive isolation? I suggest an explanation that depends not on the conditions on the breeding grounds but rather on the migratory requirements of the two forms. This is a purely speculative suggestion that I offer because it is plausible and because it focuses attention on the importance of migration in the evolution of these and many other taxa of migrant birds.

Speciation of the three species representing the almost circumpolar golden plover complex probably occurred during glacial periods of the Pleistocene. Larson (1957) proposed that the forms were isolated during the warmest interglacial period in cold tundra refugia in northern Greenland (*apricaria*) and the highlands east and west of the Bering Strait (*dominica-fulva*) and were also isolated during the last glacial period in tundra refugia in Europe and western Siberia (*apricaria*), the Bering Sea area (*fulva*), and eastern North America (*dominica*). Johansen (1958) postulated a similar history, with *apricaria* moving westward from an ancestral Siberian form and *dominica* moving eastward at a later date. *Fulva* would have remained in the eastern Siberian and Bering Sea area during the last glaciation. A comparison with the evolutionary histories given by Ploeger (1968) for pairs such as White-fronted Geese (*Anser albifrons frontalis* and *A. a. gambelli*) and Western and Semipalmated sandpipers (*Calidris mauri*

and *C. pusilla*) suggests that *dominica* might have been isolated during the last glaciation in a tundra refuge in the northwest Canadian archipelago (Banks Island), while *fulva* bred in refuges around the Bering Sea and in eastern Siberia. Precise locations and sequences of isolation periods are disputable, but a general pattern of glacial isolation into three regions associated with present breeding ranges is probable.

I propose that, during these periods of isolation, separate wintering areas and migratory pathways evolved in each of the three groups. For arctic, tundra-breeding precursors of *fulva* and *dominica*, these involved long-distance migrations to areas south of their breeding ranges—southeast Asian and western Pacific areas for *fulva*, South American for *dominica*. These developments entailed a significant encoding of different genetic information in the two forms. Evidence for genetic control of migration comes from studies of orientation behavior in many avian species, including *Pluvialis fulva* (Sauer 1963), and from the widespread observation that juveniles of golden plovers and many other shorebirds migrate southward to their first wintering grounds several weeks after adults have left the breeding grounds. A detailed map of wintering areas may not be the inheritance of young plovers, but at least a direction, and probably a distance, must be included, as in the vector navigation hypothesis of Schmidt-Koenig (1973) and as shown for Sylviid warblers (Berthold 1978).

During the period of geographic isolation, only small changes in breeding behavior, plumage, size, or breeding habitat may have evolved. As the ranges of both forms expanded post-glacially, bringing *fulva* and *dominica* populations into secondary contact, these may have allowed some recognition of forms but would not, in themselves, have provided the selective force for isolation of the forms. For example, differences in size may provide a basis for some mate selection. Other species of shorebirds have been shown to choose mates according to size (Jehl 1970), and, if the present differences in size and proportion existed at initial secondary contact and individuals of the two forms chose mates on a basis of matching winglength (the single measurement that differs most between forms), then 15–20% of the populations would have chosen mates of the opposite form (Table 1). If individuals could integrate the differ-

ences in size and proportion of several measurements as well as our discriminant function and chose on a strict size-matching basis without errors, then 6% of the populations would still be mismatched (Fig. 3 and Discussion). This may be a small enough proportion to maintain breeding stocks as distinct as the museum data indicate (J. R. Jehl, Jr. pers. comm.). Size-based mating, however, provides no selective disadvantage to these hybrids; in fact, at the edges of the zone of sympatry there would be a selective advantage to individuals of the rare form that either were of a size similar to the common form or would be willing to mate with little regard for size matching. Both these advantages would operate to produce more hybrids and more intermediate-sized birds in the zone of sympatry. Thus, size differences that may have evolved during geographic isolation can provide an important basis for mate selection, but they must be coupled with selective forces to maintain reproductive isolation in sympatry.

The differences in migration and winter ranges between the two forms may have provided such a selective force. Requirements of juvenile migration might exert severe selection pressures against hybrid offspring. I do not insist that the result of hybridizing an Argentine migrant with a Samoan migrant would necessarily be a bird that migrates midway between these two locations and expires at sea, but the result of this cross might function poorly in some respect. There may be no way to combine the information for two very different migratory routes into a single plan that is also successful. Not only might the direction be inappropriate (western Pacific Ocean), but distance, timing, or even motivation to migrate might be altered. Shorebirds of many species are known to wander widely from their normal migratory ranges, but we do not know whether or not they return to nest successfully on breeding grounds in subsequent years.

If the result of unsuccessful migration is loss of reproduction for any reason, selection against hybrids would be extremely powerful. In this situation, behavioral isolating mechanisms would be likely to evolve in regions of sympatry, building on initial differences in size, plumage, or behavior that permit at least partial recognition of forms. These behavioral isolating mechanisms might include (1) differences in timing of nesting (but this is not suggested by published nest dates from many

sources, nor is timing a very flexible factor in view of the short summer period in high latitudes); (2) differences in vocalizations, a possibility that has not yet been fully analyzed; or (3) differences in pairing displays or in plumage features used in pairing displays. My specimen studies do indicate a few plumage differences in these otherwise very similar species. As noted earlier, the least ambiguous difference is color of undertail coverts in males. These feathers in *dominica* males are usually black with some white markings; in *fulva* males, undertail coverts are mainly white with some black markings. In view of my conclusion that assortative mating occurs in these two species where they are sympatric, we might expect that the undertail coverts of males figure prominently in a breeding ground display of at least one of the species and that this display should occur early in the season, for example in early pair-bond formation or preceding copulation. Such a display has been observed by F. A. Pitelka (pers. comm.) at Barrow, Alaska. The difference in color of the flanks of males (mostly white in *fulva*; black in *dominica*) would be apparent in raised wing displays (Drury 1961, Sauer 1962). Less emphatic plumage differences (boldness of tail barring, width of forehead bands, brightness of gold spotting) may also play a role, but published descriptions of breeding displays have not been exhaustive, and no such explanation has yet emerged.

I considered and rejected an alternative method of assortative mating that depends on pair formation occurring in winter or during spring migration. In this case hybrid pairs would be effectively excluded, as both species migrate in allopatry. Sauer (1962) reported that *fulva* arrived on breeding grounds on St. Lawrence Island, Alaska, in 1960 already paired, but this is a difficult observation to make with certainty. F. A. Pitelka and J. P. Myers (pers. comm.) interpret their early-season observations of golden plovers (mainly *dominica*) at Barrow over many years as indicating that birds arrive unpaired, and Jehl (1968) presented several arguments against the assumption of early pairing in shorebirds.

This proposal for the speciation process in *dominica* and *fulva* remains entirely speculative. Its interest lies in its recognition of the potential importance of migration and winter features in the life cycle of migratory birds, such as recently discussed by Myers (1981) concern-

ing the evolution of sandpiper breeding social systems. Whereas most discussions of bird speciation revolve around diverging adaptations to breeding conditions, my proposal accepts that breeding-ground adaptations may have remained similar for both forms. The range expansion on breeding grounds following geographic isolation during the glacial period would have been a continuous process of small steps as the range of suitable breeding tundra changed. No corresponding continuous change of winter range toward *fulva* is possible for *dominica*, however. The winter ranges cannot become sympatric without enormous discrete changes in wintering areas. Thus, geographic isolation of breeding populations permits speciation, but geographic isolation of winter populations drives speciation. This approach may also be pertinent to analyses of speciation in other migrant charadrii, for example Ringed Plover (*Charadrius hiaticula*) and Semipalmated Plover (*C. semipalmatus*) (Wynne-Edwards 1952, Smith 1969) and several pairs of other closely related shorebird taxa separated or overlapping in the Bering Strait region (Jehl 1973). I recognize that support for this theory will be difficult to gather; I offer it for its heuristic value.

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