

SPECIATION IN GOLDEN-PLOVERS, *PLUVIALIS DOMINICA* AND *P. FULVA*: EVIDENCE FROM THE BREEDING GROUNDS

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ABSTRACT. Two forms of golden-plover have long been considered subspecies, *Pluvialis dominica dominica* and *P. d. fulva*. Prior studies have shown differences between forms in breeding distributions, wintering distributions, plumage, morphology, molt, and maturation schedules. We report clear and consistent differences in breeding vocalizations and nesting habitat, and strict assortative mating in areas of sympatry in western Alaska. These results indicate a greater degree of differentiation between the forms than was previously appreciated. They are appropriately treated as separate species and should be referred to under the names *Pluvialis dominica*, for the American Golden-Plover, and *Pluvialis fulva*, for the Pacific Golden-Plover. Received 24 May 1991, accepted 18 February 1992.

TWO FORMS of golden-plover traditionally have been treated as subspecies, *Pluvialis dominica dominica* and *P. d. fulva* (e.g. Peters 1934, Bock 1958, Vaurie 1964, Mayr and Short 1970, AOU 1983). The form *dominica* breeds on arctic and subarctic tundra from Baffin Island in Canada west to western Alaska; *fulva* breeds from the Yamal Peninsula in Siberia eastward to western Alaska (AOU 1983). However, based on an analysis of almost 400 museum specimens, Connors (1983) concluded that there was no evidence of interbreeding in western Alaska where both forms had been collected during the breeding season. Employing a multivariate statistical analysis to characterize specimens, he detected no increase in intermediate phenotypes within the region of potential sympatry from Nunivak Island to Point Barrow, and he recommended full species status for the forms. The museum data, however, could not prove widespread breeding sympatry of *dominica* and *fulva*, because of the absence of breeding information accompanying most museum specimens and the possibility of distributional changes during the century of collections. Furthermore, data identifying any potential differences in ecology, breeding behavior, or vocalizations were not available. The AOU (1983), therefore, has retained subspecific status for these forms, although other authorities now consider them separate species (BOU Records Committee 1986, Hayman et al. 1986).

Ideally, taxonomic decisions to separate closely related forms should be supported by a broad spectrum of evidence, including data

showing assortative mating in regions of sympatry and clear differences in molecular genetics, plumage and morphology, biogeography, display behavior and vocalizations, and ecology. In practice, decisions often must be based on a subset of these data. Differences between the *dominica* and *fulva* forms of golden-plover have already been documented with respect to plumage and morphology (Connors 1983), migration routes and wintering areas (AOU 1983), and molt and maturation schedules (Stresemann and Stresemann 1966, Kinsky and Yaldwyn 1981, Johnson and Johnson 1983, Johnson 1985). We now provide additional evidence documenting extensive breeding sympatry in western Alaska, consistent habitat differences, species-specific breeding vocalizations, and assortative mating in the two forms. These data, bolstered by molecular genetic evidence to be presented elsewhere (F. B. Gill, P. G. Connors, J. L. Maron in prep.), unambiguously indicate that separate species status is appropriate for *Pluvialis dominica* and *Pluvialis fulva*.

STUDY AREA AND METHODS

Our observations and data were collected at many sites on the Seward Peninsula and Yukon Delta National Wildlife Refuge (YDNWR) in northwestern Alaska from 1985 through 1990 (Fig. 1). In 1988 (31 May-21 June), Connors and Maron surveyed slopes and ridges at many sites on the southern Seward Peninsula accessible along the gravel highway system emanating from Nome. The three principal roads—to Teller, Kougerok, and Council—cover more than 300 km, repeatedly passing through or near suitable

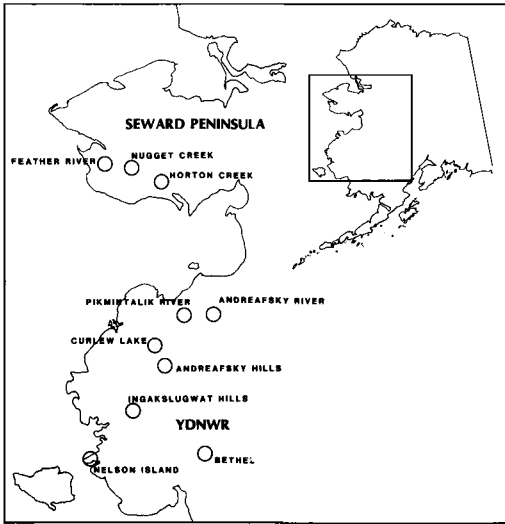


Fig. 1. Map of Seward Peninsula and Yukon Delta National Wildlife Refuge (YDNWR) study areas. Principal study sites denoted by circles.

golden-plover breeding habitat. We selected three principal study sites near: Nugget Creek, mile 31 on the Nome-Kougerok Road ($64^{\circ}54'N$, $165^{\circ}14'W$); Horton Creek, mile 58 on the Nome-Council Road ($64^{\circ}44'N$, $164^{\circ}01'W$); and Feather River, mile 37 on the Nome-Teller Road ($64^{\circ}51'N$, $166^{\circ}05'W$; Fig. 1). Other sites mentioned by name are: Cripple River, mile 19 on the Nome-Teller Road; and Crete Creek, on the road to Woolley Lagoon from mile 38 of the Nome-Teller Road.

In 1989 we attempted to revisit the three principal study sites earlier in the season (22 May–13 June). However, that spring had exceptionally heavy snowfall and late snow melt. Highway crews were delayed in opening highways because of the extensive drifted snow and the need to repair subsequent washouts during the snow melt. We were able to reach only one principal study site, Feather River, before leaving the area on 13 June. Most 1989 observations, therefore, occurred at a variety of locations within 30 km of Nome.

We spent three to six days at each of the principal study sites in 1988, locating golden-plover pairs and nests, characterizing nest habitats, and recording vocalizations. We sampled vegetation characteristics at each nest within a $50\text{ cm} \times 50\text{ cm}$ square quadrat placed at four points along each of four transects, for a total of 16 quadrat points per nest. Transects were set by compass, running in the four principal directions from the nest. Quadrat sampling points were at 2.5 m, 5 m, 10 m, and 15 m from the nest on each transect. We recorded: vegetative cover (as estimated percent of total quadrat area); maximum vegetation height within the quadrat; and vegetation richness, as indicated by the number of the eight plant species

or groups identified as present in a quadrat (i.e. *Loiseleuria procumbens*, *Empetrum nigrum*, *Betula nana*, *Ledum palustre*, *Vaccinium* spp., moss, lichen, and sedge). Data from 16 quadrats were averaged for each nest. We measured elevation change from the nest to each 15-m transect point with a sighting level, totalling these for an index of slope. We measured elevation at the nest with an altimeter and plotted nest locations on topographic maps. Using the statistical computer program SYSTAT (Wilkinson 1988), we entered these data (vegetation cover, vegetation height, vegetation richness, slope, elevation) in a discriminant-function analysis to separate the two populations statistically.

During both 1988 and 1989 we recorded golden-plover vocalizations with a Sony WM-D6C cassette recorder and an Audio-Technica AT815a directional microphone on TDK MA metallic tapes. Sonagrams were produced on a Kay Elemetrics Model 7800 digital sonograph using the wide-band filter.

On YDNWR, McCaffery observed breeding golden-plovers at the following locations (see Fig. 1): Bethel (April–May 1987), Nelson Island (May–June 1985), Andraefsky Hills and vicinity (June 1985, May–June 1986, May–July 1987), Ingaklugwat Hills (June 1988), Pikmiktalik River headwaters (June 1985), and Curlew Lake (April–July 1988–1990). In late May and early June 1987, McCaffery, Connors, and Sarah Griffin observed breeding golden-plovers at sites east of Curlew Lake. In addition, golden-plovers were observed by YDNWR personnel at several sites in the Andraefsky River watershed (June 1988, May–June 1989).

RESULTS

Of areas surveyed to date, we have located large numbers of both forms on breeding territories only on the Seward Peninsula. Seward Peninsula sites, therefore, have presented the most useful and revealing comparisons, and provide the data we emphasize here. Observations from other sites are presented mainly as comparisons with the Seward Peninsula situation.

Identification.—With practice in the field, we found that both sexes of *fulva* and *dominica* were easier to identify on the basis of breeding-plumage differences than indicated in previous reports (Conover 1945, Gabrielson and Lincoln 1959), or by examination of museum specimens (Connors 1983). Most males in breeding plumage are easily separable by the pattern of white on the undersides. In *dominica*, white at the forehead and sides of the face continues only as far as the upper breast, where it terminates, usually in a widened, bulbous patch on each side of the breast. Flanks and undertail coverts are black,

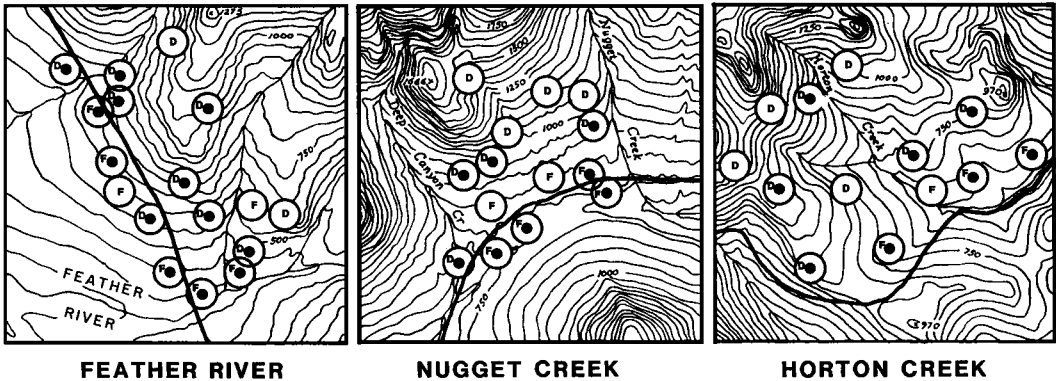


Fig. 2. Golden-plover breeding distributions at Seward Peninsula study sites. Map dimensions are 3.6 km \times 3.6 km (F = *fulva*; D = *dominica*). Circles are schematic, and do not indicate territory-boundary locations; circle diameter is 350 m. Dark circle centers indicate nest locations. Open circles indicate areas of nesting activity with probable nests. Location of gravel road at each site shown as a bold line. Peripheral areas of each site map were not searched.

rarely with some white mixed in undertail coverts. In *fulva*, the white shows little or no broadening at the upper breast, and almost always continues in an irregular streak past the breast and along the flanks to the undertail coverts, which are predominantly white (see illustrations in Hayman et al. 1986:100-101). Female *dominica* show a pattern of white on black or dark brown underparts similar to that of males, but with additional white flecks scattered throughout the black area. Terminal white bulbous patches are usually evident at the upper breast, as in male *dominica*. Many female *dominica* are almost as uniformly dark on face and breast as are males. Female *fulva*, in contrast, are much lighter than males throughout the face and breast, and are almost always lighter than female *dominica* in full breeding plumage. Many female *fulva* have underparts mainly white, with only scattered dark feathers on the face and breast, often forming an irregular, dark, triangular patch near each eye. When postnuptial molt begins in late June or July, pale feathers appear on the face and breast of all adults, and distinctions between forms and sexes blur.

Both sexes in *fulva* and *dominica* can also be separated by a difference in number of primaries that extend past the tertials of birds standing with wings folded; *dominica* has a longer primary extension, with four or five primary tips exposed, whereas *fulva* shows only three or fewer primary tips (Dunn et al. 1986). Use of all these characteristics permitted us to assign an identity to every bird seen clearly at Seward

Peninsula study sites ($n = 165$ in 1988, $n = 140$ in 1989). Additional differences in color, size, and distribution of spots on wings and mantle may assist in identification of both sexes in breeding plumage (Dunn et al. 1986, Kevin J. Zimmer pers. comm.). Ingvar Byrkjedal (pers. comm.) also has noted differences in body shape, with *dominica* being more slender-bodied and having a shorter naked portion of tibia.

Breeding sympatry.—Our 1988 observations on Seward Peninsula demonstrated close and consistent breeding sympatry throughout an area in which both species are common and widely distributed. We found adjacent *fulva* and *dominica* territories repeatedly in suitable habitat throughout the areas surveyed. At the three principal study sites, both forms nested in close contact at relatively high densities (Fig. 2). With only moderate searching of these sites, we located 29 nests (12 *fulva*, 17 *dominica*) and 15 additional territories probably with nests (5 *fulva*, 10 *dominica*); we also found nests of both species elsewhere in areas accessible along the roads. Territory sizes and display areas, which were very roughly estimated by observing displaying birds, were sufficiently large in comparison with the closest interspecific distances that both sexes of both species certainly had opportunities for interaction throughout the nesting season at these and other sites. Because of the wide-ranging aerial displays and aerial chases, the infrequency of territorial defense on the ground, and the frequent absence of non-incubating birds from the territory, determining the loca-

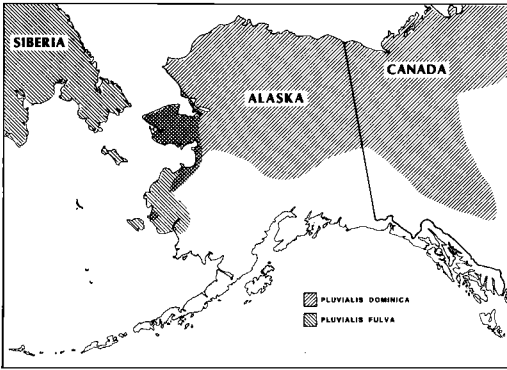


Fig. 3. Breeding distributions of *dominica* and *fulva* in Alaska and adjacent regions.

tion of territory boundaries would have required more time than we could commit to that task. Therefore, we are unable to state whether golden-plovers of either form were more strictly territorial intraspecifically than interspecifically. We did observe frequent interspecific interactions, some of which are discussed below.

We believe that the area of breeding sympatry extends far beyond the study sites and highway system of the southern Seward Peninsula. Both forms probably breed at most Seward Peninsula sites where suitable habitats occur. During June 1988, U.S. Fish and Wildlife Service personnel observed displaying or calling birds of both species at nine widely separated areas north and east of our study sites (Robert E. Gill and Shelli Vacca pers. comm.). On YDNWR, breeding *fulva* were common at all study sites; breeding *dominica* were limited to Nelson Island, the Pikmiktalik River, and the Andreafsky River watershed. North of the Seward Peninsula, there may be additional areas of breeding sympatry. In that region, *dominica* is the common form, but specimens of *fulva* have been collected as far north as Barrow during early June, and both McCaffery and Frank A. Pitelka (pers. comm.) have seen displaying male *fulva* at Barrow. The northernmost known breeding record of *fulva*, however, is from Cape Krusenstern (67°08'N, 163°43'W), where *dominica* is the more common form (P. G. Connors unpubl. data).

These records lead us to construct the distribution map in Figure 3. The areas of sympatry shown necessarily involve assumption and interpolation, but we believe that both forms probably breed at least occasionally throughout these areas wherever suitable habitat occurs.

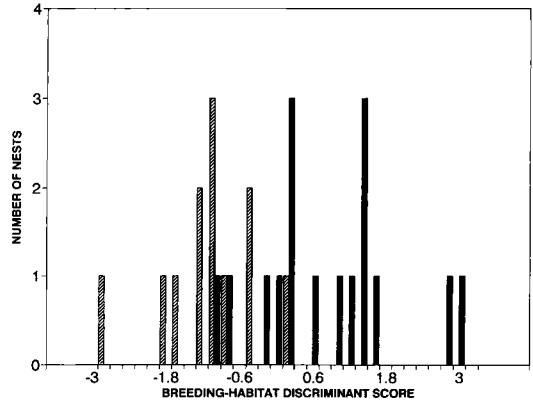


Fig. 4. Discriminant-function analysis of nest habitats of *dominica* ($n = 16$; solid bars) and *fulva* ($n = 12$; striped bars). Increasing (positive) scores indicate increasing slope and elevation, along with decreasing vegetation cover, height and richness.

Breeding distributions away from the areas of sympatry are approximate, and are taken primarily from Gabrielson and Lincoln (1959), AOU (1983), and Godfrey (1986).

Habitat differences.—Figure 2 also documents a nonrandom topographic distribution of the two forms, with *fulva* usually occurring at lower elevations than *dominica* at each of the sites. Results of the discriminant-function analysis indicate significant differences in nesting habitat between *fulva* and *dominica* (Fig. 4; $P < 0.01$). Reclassification of each nest based on its discriminant score, a measure of the extent of statistical separation between groups, correctly identified 81% of *dominica* nests (13 of 16 correctly reclassified) and 92% of *fulva* nests (11 of 12). The *dominica* nests occurred more often in areas of higher elevation and slope, with sparser and shorter vegetation, and more rocks, whereas *fulva* nests were usually at lower elevations in denser and taller vegetative cover. There is some overlap of habitat, however, with both forms using relatively dry, upland tundra. These results are consistent with our observations of the nesting habitats of both golden-plovers at YDNWR, and consistent with the observations of J. L. Dunn (*in Kessel 1989*) of an altitudinal difference in nesting habitats of the two forms on the Seward Peninsula.

Vocalization differences.—On the breeding grounds, the two forms share a behavioral repertoire that generally is similar across all *Pluvialis* species. The vocalizations accompanying these behaviors, however, differ strikingly be-

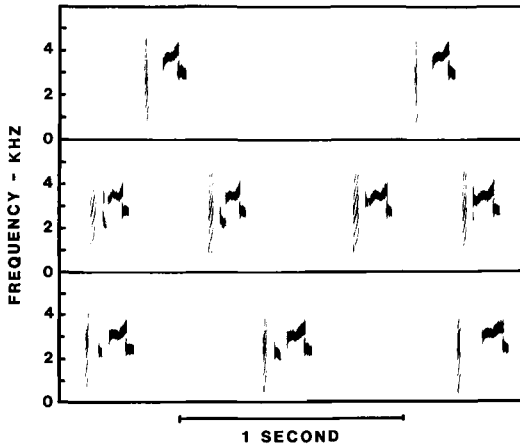


Fig. 5. Sonograms of vocalizations accompanying territorial butterfly-flight display by three male *dominica*, Feather River: top, 3 June 1988; middle, 7 June 1989; bottom, 7 June 1989.

tween *dominica* and *fulva*. The difference between forms in the vocalization accompanying the male territorial display flight is especially emphatic. During this display flight, males give repeated vocalizations while flying over their territories in a characteristic "butterfly flight" (Drury 1961), using slow, measured wing beats, with their wings almost vertical at the top of the stroke. The flight occurs from 10 to 100 m above ground, and frequently ranges widely, crossing territories of other plovers. Durations of most flights of both species range from 30 s to 3 min, with calls given at rates of 50 to 130 per minute by *dominica* and 20 to 40 per minute by *fulva*.

Sonograms of the butterfly-flight calls of three individuals of each form are shown in Figures 5 and 6. The *dominica* call is an abrupt "tlińk" or "tdlińk" (compare with "ktoodleë" of Drury 1961), strikingly different from the plaintive and melodic "peé-er-wée" (J. T. Nichols in Bent 1929), or "peé-chew-eé" of *fulva*. Some individual variation occurs within each form. In *dominica*, calls of different individuals, and sometimes consecutive calls of a single individual, may differ in the number of separate elements that comprise the call (Fig. 5). The first "twisted-rope" note occurs in all calls, but a note following this is sometimes absent, and the shape and duration of subsequent notes varies. To our ears, however, this variation is barely noticeable. The sonograms of *fulva* (Fig. 6) begin with a similar initial note having a twisted-rope appearance,

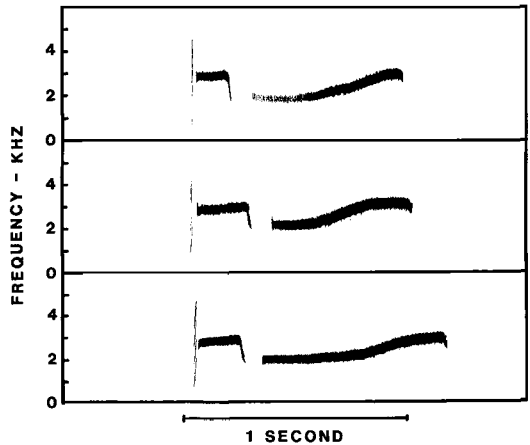


Fig. 6. Sonograms of vocalizations accompanying territorial butterfly-flight display by three male *fulva*: top, Feather River, 7 June 1989; middle, Cripple River, 31 May 1989; bottom, Crete Creek, 8 June 1989.

but subsequent notes vary, especially in duration. In spite of this minor variation within forms, however, differences between forms are clear and unambiguous. After listening to bouts of butterfly-flight-display calls of more than 50 males of each form in the area of widespread sympatry, we have not heard any mixed displays, nor intermediate vocalizations, nor have we heard any individual giving a flight display vocalization inappropriate to its plumage.

We have observed another notable difference between flight displays of the two forms. The *fulva* males frequently begin butterfly flights with a fluttering ascent, using a rapid, shallow wing beat that is distinct from both a normal wing beat and the exaggerated butterfly-flight wing beat. This flutter ascent may cover 50 to 300 m before the *fulva* male begins the butterfly flight. It is accompanied by an abruptly terminated version of the butterfly-flight call (Fig. 7A-B). The bird also may use the fluttering ascent and flutter call briefly during an interruption of a butterfly flight, sometimes in response to the flight of another golden-plover through its territory. We have not observed a fluttering flight in *dominica*.

There is also a common vocalization in *dominica* for which we have not discovered a clear equivalent in *fulva*. This vocalization (Fig. 7C-D) is given by the pursuer in aerial chases, and is a frequent aspect of *dominica* breeding behavior. The sonagram shows an obvious similarity with the butterfly-flight call of *dominica*,

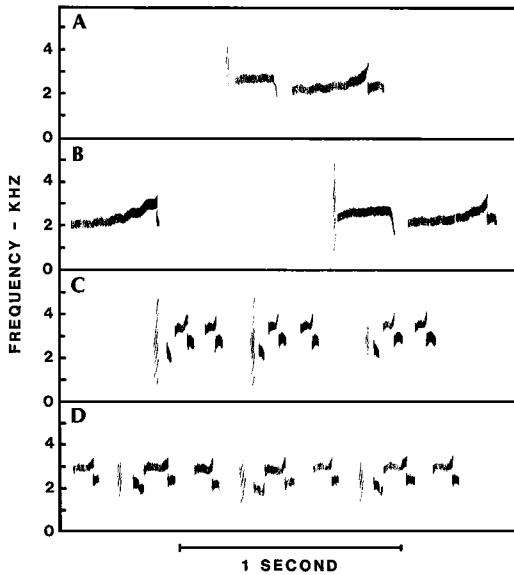


Fig. 7. (A and B) Sonograms of vocalizations accompanying flutter flight by two male *fulva*, Crete Creek (A, 7 June 1989; B, 8 June 1989); (C and D) sonograms of chase calls of two male *dominica*, Feather River (C, 3 June 1988; D, 7 June 1988).

and is usually repeated in a sequence without pauses. The call can be mimicked as "tdlińkit-tdlińkit" (this study) or "toodleéka-toodleéka" (Drury 1961).

There may be some overlap in contexts between the flutter call of *fulva* (Fig. 7A–B) and the chase call of *dominica* (Fig. 7C–D). Both forms use these respective calls in response to the flight of an intruder through their territory, although this occurs much less often in the case of *fulva*. In *dominica*, the call is given while in pursuit of the intruder, whereas *fulva* gives it while in display over the territory. There also is an interesting correspondence in composition between the two calls, in spite of their obvious difference overall. Both calls begin as the butterfly-flight call of the form, but end with a similar, sharply juxtaposed couplet. In *dominica* this is a separate repetition of the last two notes of the butterfly-flight call. In *fulva* the first part of the couplet is continuous with a shortened and wavering version of the final note of the butterfly-flight call. Yet, the result is that both calls end similarly. We have heard both calls used in interspecific, as well as intraspecific interactions.

The most similar vocalization frequently used by both forms is a complex whistle ("long call"

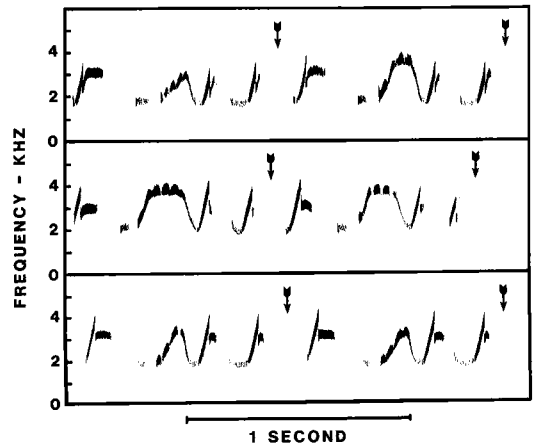


Fig. 8. Sonograms of complex whistles of three male *dominica*, Feather River: top, 7 June 1989; middle, 3 June 1988; bottom, 3 June 1988. Arrows denote repeating unit.

of Sauer 1962), which occurs in several contexts. In both *dominica* and *fulva*, most butterfly flights end with the male descending in a glide with wings held over the back in a "V." Upon landing, the bird gives a short series of consecutive complex whistles (one to three, usually two) while bobbing its head. This call may be answered by a similar complex whistle from the female. The complex-whistle call is also given in other contexts involving pair communication on the ground, in chases or other aggressive interactions both on the ground and while flying, and during butterfly-flight displays. Complex whistles of three individuals of each form are shown in Figures 8 and 9. In each sonogram the basic unit is identified between arrows; the full vocalization in each case consisted of this unit given twice consecutively. These calls are similar, but can be distinguished with practice. The *dominica* call (Fig. 8) can be mimicked by "wit-weeyoo-wit," repeated. The *fulva* call (Fig. 9) contains similar elements, but is longer and has a more bubbly, warbling quality.

Alarm calls given at the nest also differ between forms. Sonograms of three males of each form recorded near their nests are shown in Figures 10 and 11. In each figure, sonograms of low-intensity and high-intensity calls from the same individuals are shown. The shift to high-intensity alarm was elicited each time by the observer moving forward toward the calling golden-plover. The *dominica* males (Fig. 10) first reacted to the presence of the observer with a

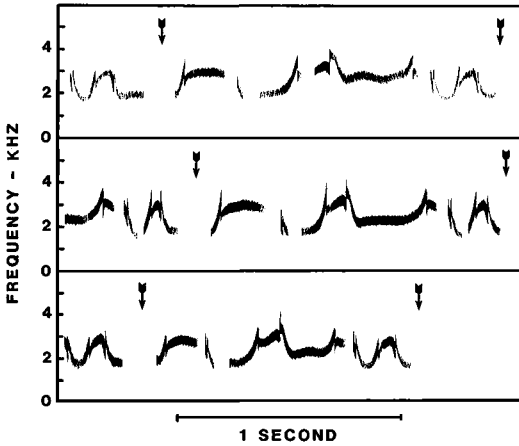


Fig. 9. Sonograms of complex whistles of three male *fulva*: top, Crete Creek, 7 June 1989; middle, Crete Creek, 7 June 1989; bottom, Cripple River, 31 May 1989. Arrows denote repeating unit.

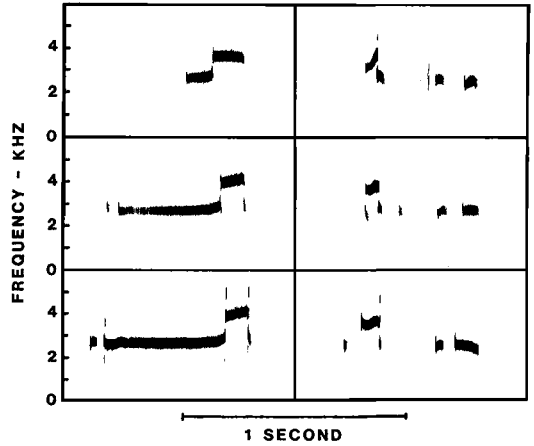


Fig. 10. Nest alarm calls of three male *dominica*, Feather River: top, 3 June 1988; middle, 18 June 1988; bottom, 18 June 1988. For each individual, low-intensity call shown on left with high-intensity call on right.

two-syllable call, "klee-yeep." As the bird became more agitated at the observer's approach, the call shifted abruptly to a variable but mainly four-syllable call, "killik-killik" (Drury 1961). The *fulva* males began calling "pee" (this study) or "pfeeb" (Sauer 1962) while the observer was far from the nest, and shifted suddenly to "deedleek" (Sauer 1962) at the observer's approach. Both forms used additional alarm calls and other calls occasionally, but the male responses to a human intruder (Figs. 10 and 11) are fairly consistent within forms and quite distinctive between forms. Female alarm calls seemed similar, but more variable than male alarm calls.

Assortative mating.—These differences in vocalizations provide a sufficient mechanism to maintain assortative mating in areas of sympatry. In 1988 and 1989, we identified both sexes in 96 pairs of golden-plovers on the southern Seward Peninsula (1988, 27 *fulva*, 29 *dominica*; 1989, 21 *fulva*, 19 *dominica*) and, in all cases, strict assortative mating prevailed; we did not discover any mixed pairs. J. L. Dunn (*in Kessel* 1989) also found no mixed pairs on the Seward Peninsula.

At sites on YDNWR, all pairs in which both members were identified exhibited assortative mating (24 *fulva*, 9 *dominica*, 1985–1990), although we detected three possible exceptions to this pattern. At the Pikhiktalik River in late June 1985, a relatively pale female golden-plover was paired with a *dominica* male. The female

may have been a *fulva*, or an unusually pale *dominica* female, or a more typical *dominica* that had started to molt out of alternate plumage. Our observations on the timing of molt at other sites are consistent with this latter interpretation.

Two males on adjacent territories at Curlew Lake also were problematic. Both exhibited the bulbous white patch on the upper breast characteristic of *dominica*. One of the two also had

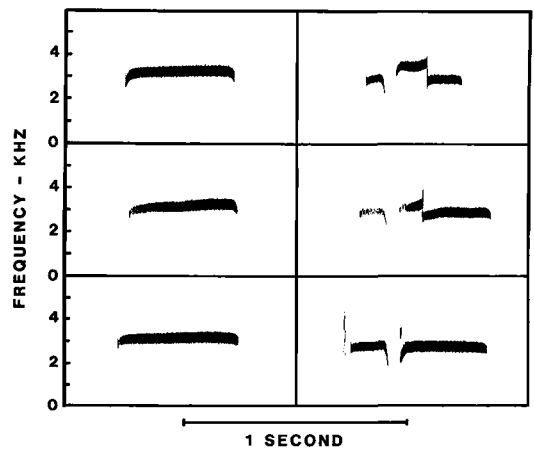


Fig. 11. Nest alarm calls of three male *fulva*. For each individual, low-intensity call shown on left with high-intensity call on right: top, Nugget Creek, 12 June 1988; middle, Horton Creek, 5 June 1988; bottom, Feather River, 18 June 1988.

black, rather than white, undertail coverts. We did not determine the number of primary feathers extending past the tertials (*sensu* Dunn et al. 1986) in either bird. However, both males gave the *fulva* flight call during butterfly flights, and both were paired with *fulva* females. During three years of work at Curlew Lake, no unequivocal *dominica* were seen. We are inclined to view these two males as examples of variation in *fulva*, rather than as unusual *dominica* males giving *fulva* vocalizations, involved in nonassortative pairings.

Pair formation.—To what extent might pairing during migration, or differences in timing of arrival on the breeding grounds, explain assortative mating and the habitat differences we observed? In view of the distinct migration routes and wintering areas, it is reasonable to consider either of these as possible mechanisms. Sauer (1962) stated that the *fulva* he observed on St. Lawrence Island arrived on his study site already paired. If all *fulva* are paired during migration south of Alaska before they can encounter any *dominica*, assortative mating would be assured. Alternatively, if the species arrive on the breeding grounds at different times during the spring melt, with the earlier arriving species immediately pairing in the earliest available habitat, both assortative mating and the differences in breeding habitat might result. Our observations on the Seward Peninsula, especially in 1989, lead us to reject both the prearrival-pairing hypothesis and the differential-timing hypothesis as having any importance in determining assortative mating and habitat use in these species.

In 1989, unusually heavy spring snows delayed the thaw on the Seward Peninsula. The tundra near Nome was almost 100% snow-covered on 22 May, when we arrived. Golden-plovers of both forms had been among the earliest arriving shorebirds, with a few individuals of *fulva* and *dominica* seen over the previous three days (R. E. Gill pers. comm.). We began observing golden-plovers in the earliest opening patches of tundra along all three roads within about 30 km of Nome on 23 and 24 May. On these two days we found both sexes and both species at scattered sites, with golden-plovers present in almost every open patch of non-brushy habitat. Our total count for two days was 36 *dominica* and 22 *fulva*. Most of these were in groups with no suggestion of pairs, no aggression, and no displays observed. For example, in

two low marshy areas along the Teller Road on 23 May, we found 18 *dominica*, 9 *fulva*, and 6 golden-plovers not seen well enough for identification, but no evidence of a single pair. These two sites were not characteristic breeding habitat for either form and, subsequently, were not occupied by breeding pairs.

We recorded the first butterfly flights by both species on 24 May 1989. These occurred over open patches of typical nesting habitat. Over the next five days we observed several pairs of both species engaged in equivalent stages of pair formation. Displays seen in both species were: nest scraping by the male; "torpedo" runs by the male near the female, with the male's head and body level and back feathers ruffled; "tipping" displays by the male in front of a nest cup, with the male facing away from the nest cup, head down and tail up, and the female in the nest cup looking up at the male's undertail coverts; and frequent brief copulations. Some of these pairing displays occurred in two early-opening patches of habitat not typical of our previous year's habitat measurements for either species. At both of these sites, no golden-plovers were present 12 days later, when extensive areas of typical golden-plover habitat were snow-free elsewhere. When we first reached our Feather River site on 5 June 1989, golden-plover densities and habitat use were similar to those measured in 1988. At this site and elsewhere we did not find any large difference in early-season availability of typical *dominica* and *fulva* breeding habitat; areas of both habitats were opening on a similar schedule.

From these observations we believe that both forms of golden-plover arrive in northwestern Alaska unpaired, and on a similar schedule. Pair formation may begin on the breeding territories, or it may begin at other sites within the breeding distribution, especially if the breeding-territory habitat remains snow-covered until late spring. This may explain Sauer's (1962) observations. When he first saw *fulva* on a study site on St. Lawrence Island (8 June), they were already paired. He observed none of the pairing displays we describe here, and even butterfly flights were infrequent. There is no evidence, however, to suggest that the birds were paired south of Alaska, and we consider it likely that they had already paired at an early-opening site elsewhere on St. Lawrence Island or adjacent Siberia or Alaska.

Interspecific interactions.—Despite the evi-

dence presented here of differences in behavior and of assortative mating in *dominica* and *fulva*, individuals do interact interspecifically quite frequently on the breeding grounds. On the Seward Peninsula, interspecific aerial chases between *fulva* and *dominica* are common, but these chase-and-flee interactions do not necessarily indicate mutual communication. The two forms are very similar behaviorally, however, sharing many displays that recall their close evolutionary relationship, and these probably facilitate more involved interspecific communication. We frequently heard complex whistles (and occasionally other vocalizations) given by both forms in reaction to the presence of the other form. We also observed interspecific, coordinated interactions that might be interpreted as boundary disputes, entailing parallel marching, aggressive postures and contact fights; these were seen as frequently as similar intraspecific interactions.

One such interaction between a male *dominica* and a male *fulva* on Seward Peninsula, 2 June 1989, lasted for 1 h and 45 min. It began with an aerial chase, but most interaction occurred on the ground, ranging over an area roughly 150 m in diameter. An initial period of parallel marching, mainly 1 to 3 m apart, but over a meandering route rather than a stable boundary, escalated into repeated charges on foot or wing by both individuals, with occasional contact. At times, *dominica* sat in a nest cup while *fulva* circled on foot within 0.5 m; later, *fulva* performed scraping displays with *dominica* observing. No females of either form were present at any time. Vocalizations were frequent and often given by one bird in consecutive or simultaneous response to a call by the other bird. We recorded 38 complex whistles by *fulva* and 21 by *dominica*.

This example indicates a remarkable amount of communication, and suggests interspecific territoriality, but should not be viewed as invalidating our contention that these are separate species. We have seen comparable interactions between *dominica* and the Black-bellied Plover (*P. squatarola*) and between *fulva* and *squatarola*. On both Nelson Island and at Franklin Bluffs on the North Slope of Alaska, we have observed *squatarola* and *dominica* males engaged in ritualized border displays including parallel marches and squabbles with physical contact (B. J. McCaffery unpubl. data). At both sites, *dominica* males did not yield ground in the fights

with their larger relatives. On the Seward Peninsula, we noted simultaneous butterfly flights and chases between *fulva* and *squatarola*, and complex whistles given by *fulva* in apparent reaction to *squatarola* flights over a *fulva* territory. Ingvar Byrkjedal (pers. comm.) has observed aggressive interactions involving chases and complex whistles between *fulva* and the Greater (or Eurasian) Golden-Plover (*Pluvialis apricaria*) on the Yamal Peninsula. Apparently, interspecific aggression is not rare in the Charadrii. *Pluvialis apricaria* also engages in fierce territorial battles with the Lapwing (*Vanellus vanellus*) in northeastern Scotland (Parr 1979). In Siberia, *P. squatarola* regularly challenges and expels *P. apricaria* from its territories (Flint and Kondratiev 1977). Interspecific territoriality has even been documented between *fulva* and the Ruddy Turnstone (*Arenaria interpres*) on St. Lawrence Island (Sauer 1962).

Despite the relative ease with which most breeding golden-plovers can be classified, birds that cannot be classified by plumage alone are encountered at a low frequency, especially on YDNWR. Arguing that such "aberrant" birds are not unexpected, McKittrick and Zink (1988) offered hybridization as only one of several hypotheses that can account for intermediate plumage phenotypes. We cannot rule out the possibility that these intermediate forms are hybrids, but we have discovered no conclusive evidence to support this hypothesis during six field seasons. In fact, we know of only one definite case in which the male of one form approached a female of the other form in what may have been a pairing context. On 28 May 1986, an unpaired *dominica* male within an established territory in the Andrafsky Hills approached an intruding *fulva* pair five consecutive times. The male *dominica* repeatedly approached in the aggressive hunched posture described by Drury (1961). On one occasion, the *dominica* male got between the *fulva* male and female, abandoned the aggressive posture, and slowly approached the female. When he closed to within 1 m of her, the *fulva* male attacked. The *dominica* male may have been attempting to court the *fulva* female. Whether this courtship would have proceeded further in the absence of the *fulva* male is unknown. However, we have never documented a confirmed mixed pair; if these exist at all, they are rare occurrences within a consistent and widespread pattern of assortative mating.

DISCUSSION

Assortative mating.—Previous analysis suggested sympatric breeding in the two forms (Connors 1983), but the evidence from museum specimens was not definitive. Field observations reported here eliminate any potential ambiguity. We found *dominica* and *fulva* to breed in close and frequent sympatry over large areas of the Seward Peninsula, and in at least occasional sympatry in other areas as far south as Nelson Island. Frequency of sympatry north of Seward Peninsula is unknown, but sympatry probably occurs, at least occasionally. At the heart of their sympatric range on the Seward Peninsula, the two forms mate assortatively in areas where contact between forms is common.

Vocalizations.—Our field data indicate striking differences in breeding vocalizations between *fulva* and *dominica*, and also some potential mechanisms to maintain assortative mating. We have not recorded and compared the full vocalization repertoire of the forms, but common breeding vocalizations used in territorial advertisement and defense, in intrapair communication, and in nest defense differ markedly. The aerial-display-flight vocalizations are so distinctive that they show little relationship past the first brief note, and geographic variation of these vocalizations across the breeding ranges of the two forms appears to be slight (E. H. Miller and P. G. Connors in prep.). At least one common vocalization of each form appears to have no clear, contextual counterpart in the other's repertoire, and *fulva* has a distinctive flutter flight that we have never observed in *dominica*. In the area of widespread sympatry, we have never heard intermediate calls, mixed calls, or "wrong" calls in relation to any bird's plumage. These vocalization results indicate both independent evolution of the forms and well-developed mechanisms that maintain assortative mating.

Breeding habitat.—The forms also differ in breeding habitat. The limited measurements presented here define a statistically significant difference between nest habitats. The measured habitat overlap (Fig. 4) may actually understate the degree of habitat distinction between territories of the two forms, because these data refer only to habitat within 15 m of each nest, a small area compared with the entire territory. Many factors may determine species-character-

istic habitat selection at the level of the entire territory. One factor that may influence selection of the particular nest site within the territory is cryptic concealment for the incubating bird. Byrkjedal (1989) has shown that cryptic concealment of *dominica* nests enhances nest success. Because *dominica* and *fulva* are extremely similar in appearance while incubating, they both may select similar nest microhabitats within the range of habitats available on their territories.

Our data also may understate the degree of difference between average habitat types of the forms, because our sites were selected to provide comparisons of the forms on closely neighboring territories. Many nests were in or near the transition zone between habitat types; nests in areas of more extreme habitat differences may have been underrepresented. The habitat distinctions are sufficiently clear that we quickly learned to accurately predict species occurrence based on a cursory, intuitive assessment of the habitat. In addition to these major differences in behavior and ecology reported here, several other lines of evidence indicating evolutionary differences between the forms have been noted from previous studies.

Distribution.—The forms differ not only in breeding distributions, which overlap in northwestern Alaska (Fig. 3), but in wintering distributions, which do not overlap. The *dominica* form winters in South America, while *fulva* winters in southern Asia and on many Pacific islands south to Australia and New Zealand (AOU 1983). South of Alaska, migration ranges are essentially nonoverlapping, except for very small numbers of birds of both forms that migrate (and in the case of *fulva*, winter) along the Pacific coast of North America.

Morphology.—The two forms differ significantly in morphology (Connors 1983), but with some overlap (less than 10%) even after multivariate statistical analysis based on measurements of wing, tarsus and culmen. The form *dominica* has a longer wing, but shorter tarsus and culmen than *fulva*.

Plumage.—The same specimen study also identified plumage characteristics useful in separating males in breeding plumage. Our field work, relying also on differences identified by Dunn et al. (1986), indicated that field identification of breeding plumage birds of both sexes is possible, and is easier than identification of

museum skins. Juvenile and adult basic plumages also are clearly separable (Hayman et al. 1986).

Molt and maturation.—Molt and maturation schedules also differ. In *dominica*, first-year birds typically migrate northward to breeding grounds when less than one year old (Stresemann and Stresemann 1966). They apparently undergo wing molt prior to this migration, arriving with fresh primaries (Johnson 1985). In *fulva*, some, but not all, first-year birds migrate to breeding grounds when less than one year old (Johnson and Johnson 1983, Connors 1983). These birds do not, however, acquire fresh primaries until after the breeding season. Most first-year *fulva* remain on insular Pacific wintering areas during their first potential breeding season (Kinsky and Yaldwyn 1981, Johnson and Johnson 1983).

Molecular genetics.—The one remaining line of evidence that could bear on the taxonomic status of the two forms is molecular-genetic information. Specimens we collected from Seward Peninsula in 1989 have recently been analyzed for differences in mitochondrial DNA (Frank B. Gill, P. G. Connors, J. L. Maron in prep.). Detailed results will be reported separately, but the preliminary results are consistent with all other lines of evidence: *fulva* and *dominica* specimens are genetically distinct, with no indication of interbreeding.

Conclusion.—The diversity and consistency of evidence make the conclusion of full speciation inescapable. This decision is reached whether one applies the biological-species concept (Mayr 1969, 1970) or the phylogenetic-species concept (Cracraft 1983, McKittrick and Zink 1988). These are independently evolving forms that breed assortatively in areas of sympatry. They have been considered subspecies only because their plumages are sufficiently similar that ornithologists had found them difficult to separate. It is now apparent that even this aspect of the two forms is more distinctive than previously appreciated. The golden-plover situation is comparable to the past subspecies treatment of the Long-billed and Short-billed dowitchers (*Limnodromus scolopaceus* and *L. griseus*), whose taxonomic status was resolved only after sufficient attention was given to the differences between the forms (Pitelka 1950). The golden-plovers differ as dramatically, and should be treated as separate species under the names *Pluvialis dom-*

inica (American Golden-Plover) and *Pluvialis fulva* (Pacific Golden-Plover) as previously proposed (Connors 1983).

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