Snowy Plover

Charadrius alexandrinus

Order CHARADRIIFORMES– Family CHARADRIIDAE

Issue No. 154 – Revised: November 18, 2009

Authors: Page, G. W., J. S. Warriner, J. C. Warriner, and P. W. Paton

Revisors: Page, Gary W., and Lynne E. Stenzel

Articles

Introduction

The Snowy Plover is a ground nesting bird found primarily on unvegetated to sparsely vegetated coastal beaches and shores of inland alkaline lakes. An estimated 18,000 Snowy Plovers breed in North America, where U.S. Pacific and Gulf coasts populations are imperiled by degradation of their habitat from development, human recreation and invasive species. The Pacific coast population is listed by the U.S. Fish and Wildlife Service as threatened and the Gulf coast population is state-listed as endangered in Mississippi and threatened in Florida.

Enlarge

Juvenile Snowy Plover, Summer Lake, OR, August

Since 1995, study of the Pacific coast population has generated considerable information on reproductive success (Powell and Collier 2000, Colwell et al. 2005), juvenile survival and dispersal (Stenzel et al. 2007, Colwell et al. 2007a, b), adult survival (Mullin 2006), effectiveness of management techniques (Neuman et al. 2004, Hardy et al. 2008), and effect of recreation on behavior and reproduction (Lafferty 2001, Ruhlen et al. 2003). Although Snowy Plovers frequently lose their nests to predators, people, or weather, they relay rapidly and readily (Warriner et al. 1986).

Enlarge

Figure 1. Distribution of the Snowy Plover in North America.

The Snowy Plover and Kentish Plover (*C. a. alexandrinus*) of Eurasia employ an unusual facultative polygamous breeding system in many which females in some populations, and less frequently males, desert first broods soon after

hatching to renest with new mates (Lessells 1984, Warriner et al 1986, Fraga and Amat 1996), sometimes hundreds of kilometers from their first nests (Stenzel. et al. 1994). Brood desertion and polygamous mating have been the foci of many studies of the Kentish Plover in Eurasia (e.g. Amat et al. 1999c, Székely and Cuthill 1999).

We have included the results of these studies and others on the ecology of Kentish Plover (especially by T. Székely and J. A. Amat: see Bibliography) in this account for comparison with the Snowy Plover. This comparison should improve our understanding of the behavior and the ecology of the North American Snowy Plover, even though recent phenotypic and genetic analyses suggest the two species are divergent taxonomically (Küpper et al. 2009).

Enlarge

Adult male Snowy Plover, breeding plumage, Sanibel Is, FL, February

Enlarge

Adult female Snowy Plover on nest, Lido Key, FL, April

Distinguishing Characteristics

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Distinguishing Characteristics


Enlarge
Adult male Snowy Plover, breeding plumage, Sanibel Is, FL, February


Enlarge
Color-banded Snowy Plover, Sanibel Is., FL, February

Small plover (15–17 cm long, 34–58 g) with white hind-neck collar and a breast band always restricted to lateral patches. Pale brown upperparts and dark gray to blackish legs also important in identification.

In Alternate plumage, male distinguished from female by black crown, ear covert, and foreneck patches. Many males have a distinct rusty cap at the beginning of the breeding season. Females usually have some to completely brown feathering in one or more of their foreneck patches, and lack rusty caps. A few females with completely black crown, ear covert, and foreneck patches resemble males. In Basic plumage males and females are indistinguishable. Juveniles in fresh plumage are distinguishable from adults by the absence of a forehead patch and by the presence of pale edges on mantle feathers.

Piping Plover (*Charadrius melodus*) is similarly pale above, but is larger (17-18 cm long) with a thicker, shorter bill, orange legs, and in flight reveals a complete white band across upper-tail coverts; in summer its bill has an orange base whereas Snowy Plover's bill is all black. Slightly smaller Collared Plover (*C. collaris,* 14-15 cm long) lacks white hind-neck collar, has dull yellow legs and darker upperparts, and in Alternate plumage has complete breast band. Semipalmated Plover (*C. semipalmatus*) is larger and much darker dorsally, with breast bands normally complete and legs orange or yellow. Wilson's Plover (*C. wilsonia*) has complete breast band, is larger, is darker dorsally, has gray to grayish pink legs, and has longer and heavier bill.

Snowy Plover resembles the Lesser Sandplover (*Charadrius mongolus*) and Greater Sandplover (*Charadrius leschenaultia*) of Asia in basic plumage but both these sandplovers lack the white hind-neck collar and are very rare vagrants in North America.

Introduction Distribution

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Distribution

The Americas

Breeding Range

Figure 1. *Pacific Coast.* From s. Washington to Magdalena Bay, Baja Sur, Mexico; Gulf of California at mouth of Rio Colorado (at Cienga de Santa Clara, Mellink et al. 1996) and on islands of Angel de La Guarda and (probably) Punta Arena la Ventana (Am. Ornithol. Union 1983, Palacios et al.1994); locally along west coast of Mexico from Sonora to Oaxaca (Binford 1989, Mellink and Palacios 1993, Palacios and Mellink 1995, Mellink and Riojas-Lopez 2005); and on coast of South America from sw. Ecuador to Chiloe I., Chile (Blake 1977, Am. Ornithol. Union 1983, Castro and Myers 1988).

Figure 1. Distribution of the Snowy Plover in North America.

Inland. Locally in s.-central Oregon (Harney, Lake, and Klamath counties; Gilligan et al. 1994), San Joaquin Valley, Salton Sea and e. California (Page and Stenzel 1981, Shuford et al. 2008), w. and central Nevada (Herman et al. 1988), nw. Utah (Paton and Edwards 1990), and s. Arizona (Monson and Phillips 1981). Breeding range in w. U.S. is summarized by Page et al. (1991). Also s. Saskatchewan (irregular; Gollop 1987), sw. Wyoming (irregular; Kingery 1990), sw. Montana (irregular; Eng 1981), central and e. Colorado (Andrews and Righter 1992), s. New Mexico (Page et al. 1991), central and sw. Kansas (Thompson and Ely 1989), w. Oklahoma (Baumgartner and Baumgartner 1992), lakes in south and playa lakes region of Texas (Gorman and Haig 2002), and central Mexico (states of Zacatecas, San Luis Potosí, Jalisco, and Mexico) (Howell and Webb 1994).

Gulf Coast. Discontinuously distributed along the southwest coast of Florida from Marco I. north to Anclote Key and along the coast of the Florida Panhandle, where most Florida

breeders now occur; in Alabama and Mississippi mainly on offshore islands; along the lower Texas coast from Matagorda Island to Mexican border; and south to ne. Veracruz and n. coast of Yucatán Peninsula (Howell and Webb 1995, Gorman and Haig 2002, Himes et. al. 2006; also see Fig. 1).

Atlantic. Snowy Plovers breed on islands throughout the Caribbean and Bahamas but documented sites are few. They are common year-round residents south of San Salvador I. to the Turks and Caicos Is., and an uncommon resident n. of San Salvador. In the Caribbean, breeding documented in Cuba, Hispaniola, Puerto Rico and the Virgin Islands (Raffaele 1989, Gorman and Haig 2002), and on islands off the north coast of Venezuela from Curaçao east to Margarita (Am. Ornithol. Union 1983, Voous 1983), but few specific locations noted.

Winter Range

Figure 1. *Pacific Coast.* Local from s. Washington (Widrig 1980, Pearson et al. 2008) to Nayarit, Mexico (including both coasts of Baja California) (Page et al. 1986, Howell and Webb 1995), at least rarely from Guatemala to Panama where it may be somewhat overlooked (Castro and Myers 1988, Ridgeley and Gwynne 1989, Howell and Webb 1995), and from sw. Ecuador to Chiloe I., Chile (Blake 1977, Castro and Myers 1988).

Inland. Regular at Salton Sea, Tulare Lake Basin in Kings and Tulare counties, and interior lakes in s. California; rare and irregular in s. Arizona, s. New Mexico (Shuford et al. 1995); in nw. and central Texas (Elliott-Smith et al. 2004); also reported in interior Mexico south to central volcanic belt (Howell and Webb 1994, 1995).

Gulf Coast. Along the Gulf Coast of the U.S. and Mexico to the Yucatán Peninsula with records of birds at many sites on the coast of Tamaulipas (Howell and Webb 1995, Mabee et al. 2001, Elliott-Smith et al. 2004).

Atlantic. Irregular w. Florida (Stevenson and Anderson 1994); in Bahamas they are uncommon north, but common south, of San Salvador (Gorman and Haig 2002); on Caribbean Islands they are characterized as common in the Dominican Republic and Anguilla, and uncommon in the U.S. and British Virgin Islands, St. Martin, and St. Barthélemy (Raffaele et al. 1998, Elliott-Smith et al. 2004); and on islands off the n. coast of Venezuela they have been sighted on Tobaga, Isla de Margarita, Islas los Roues, Bonaire, Curaçao, and Aruba (Elliott-Smith et al. 2004).

Outside The Americas

Cosmopolitan species with at least 3 races outside the Americas (Johnsgard 1981, Cramp 1983, Hayman et al. 1986). Nominate race, *C. a. alexandrinus*, occurs in Eurasia and n. Africa, south to Mauritania, Gulf of Aden, Socotra, and w. India, and east to se. Transbaykalia, Russia, and Inner Mongolia. *C. a. dealbatus* occurs in Japan, e. China, and Ryukyu I.; intergrades with nominate *C. a. alexandrinus* in Manchuria, Korea, and s. Ussuriland. *C. a. seebohmi* occurs in Sri Lanka (Cramp 1983).

Historical Changes

In the Americas, information limited to U.S.; more data from Mexico and Central America are needed to document full extent of current range; species was not documented breeding in nw. Sonora until 1994 (E. Palacios unpubl. data) or interior of Mexico until early 1990s (Howell and Webb 1994).

Along U.S. Pacific Coast, breeding range increasingly fragmented during 20th century. By 1990, species bred at only 2 of 5 historical sites on Washington coast and in 1994 at only 7 of 26 on Oregon coast (C. Bruce pers. comm.). During late 1970s, absent from 33 of 53 California coastal locations with breeding records prior to 1970; e.g., missing in parts of San Diego, Ventura, and Santa Barbara counties, most of Orange Co., and all of Los Angeles Co. (Page and Stenzel 1981). See Demography and Populations: population status: trends.

Extent of inland breeding range west of Rocky Mtns. only become well documented since late 1970s (Page and Stenzel 1981, Herman et al. 1988, Page et al. 1991, Paton and Edwards 1992). Snowy Plovers likely nested at some of the large terminal lakes (Tulare, Buena Vista, and Goose) in s. San Joaquin Valley, CA, until the demise of the lakes in the late 1940s and 1950s. (Shuford et al. 2008). Since the 1980s, the s. San Joaquin Valley has been inhabited again by up to 200 plovers nesting at human-made agricultural waste-water ponds (Ivey 1984, Page et al. 1991, Shuford et al. 2008). Accidental flooding of a sizable area of s. California desert in early 1900s also produced Salton Sea, a current breeding area for a few hundred Snowy Plovers (Page et al.1991, Shuford et al. 2008).

Few published data on population trends available for the eastern United States and Caribbean; from 1959-1988 trends from CBC data were negative but non-significant in Florida and Texas (Gorman et al. 2002). Range has shrunk and become more fragmented on Gulf Coast. No longer nests on upper Texas coast, north of Matagorda Co. (T. Eubanks pers. comm.), where it formerly bred at least until the 1930s (Williams 1938, Gorman et al. 2002). Breeding on Texas coast is now mainly restricted to Laguna Madre (T. Eubanks pers. comm.). In Florida has disappeared from some Gulf Coast beaches and probably from Keys (Stevenson and Anderson 1994). Also appears to have recently disappeared as a breeder on St. Croix I. in Virgin I. (Raffaele 1989). See Demography and Populations: population status: trends.

Fossil History

No information.

Distinguishing Characteristics | Systematics

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Systematics

Geographic Variation

Across North America, dorsal coloration pales from west to east, being palest in Gulf of Mexico and Caribbean populations. Birds in the Americas are grayer whereas birds in Eurasia (Kentish Plover, see Related Species, below) are browner, with the latter showing some clinal variation toward darker brown from west to east but, along the Asian coast, toward paler brown from north to south. Throughout the species' range, the presence or absence of a loral stripe varies, it generally being absent in southerly populations. In breeding males, the width or presence of a black bar on the forecrown varies among populations, as does the hue or presence of a contrasting cinnamon crown. Leg color also varies.

Subspecies

Six subspecies in three groups, with perhaps as many as four species included under the current *Charadrius alexandrinus* umbrella. By contrast, two to three closely related species may be conspecific with a more broadly defined *C. alexandrinus*; see Related Species, below.

nivosus group (Snowy Plover):

C. a. nivosus (Cassin, 1858). Includes *C. a. tenuirostris* (Lawrence, 1862). Breeds spottily along Pacific Coast from sw. Washington south to Baja California Sur, across Great Basin from sw. Montana south to e. California and central Colorado, in parts of the desert Southwest, and in the Great Plains from s. Saskatchewan south to nw. Texas; many southerly populations are resident, including those along the Pacific Coast and at the Salton Sea, California, as well as at the n. Gulf of California, Mexican Plateau, Isthmus of Tehuantepec, Yucatan Peninsula, much of the Gulf of Mexico, the Bahamas, e. Cuba, Hispanoila, Puerto Rico, the Lesser and Netherlands Antilles, and Bermuda [type locality = Presidio, San Francisco Co., California]; otherwise winters around Gulf of California, across Pacific coast of Mexico, and around Gulf of Mexico. Approximate size of nominate subspecies (see below), but tarsi short (averaging < 26 mm); dorsum pale grayish brown;

legs and feet dark gray; in the breeding male, crown concolorous with mantle, black bar on forecrown, black smudge at sides of breast, and lores dusky. Although *C. a*. "*tenuirostris*" of Puerto Rico was found to differ genetically (Funk et al. 2007), Blake (1977) remarked "so slight and nebulous is the [morphological] distinction that authorities differ not only on the respective winter ranges, but also on the allocation of breeding birds in the Southern Caribbean. Under the circumstances, no purpose is served in the recognition of two races." Hayman et al. (1986) and Binford (1989) also merged the subspecies.

C. a. occidentalis (Cabanis, 1872). Resident along Pacific slope of South America from central Ecuador to central Chile [type locality = near Santiago, Chile]. Similar to *C. a. nivosus* but averages slightly larger, lores white, and black bar on forecrown slightly wider. Not surprisingly given the extent of geographic separation, this subspecies differs genetically from *C. a. nivosus* (Funk et al. 2007).

alexandrinus group (Kentish Plover [likely a separate species; see Küpper et al. 2009 and Related Species, below]):

C. a. alexandrinus Linnaeus, 1758. Includes *C. cantianus* (Latham, 1802), *C. albifrons* Wolf and Meyer, 1805, *C. littoralis* Bechstein, 1809, *C. albigularis* (Brehm, 1831), *C. elegans* (Lichtenstein, 1854), *C. a. minor* Seebohm, 1887, and *C. minuta* (Sharpe, 1896). Breeds across Western Palearctic, including Macaronesia, north to s. Steppe region, south to Cape Verde Islands off w. Africa and to the Horn of Africa, and e. to n. India [type locality = Egypt]; resident around Mediterranean and winters south to South Africa and Indian Subcontinent. Relatively large (wing > 104 mm, bill > 19.5 mm), with the tarsi long (averaging > 29 mm); dorsum medium brown; lower auriculars dark; legs and feet dark gray; in the breeding male, bright cinnamon crown contrasts with brown mantle, black bar on forecrown, black smudge at sides of breast, and lores black.

C. a. seebohmi Hartert and Jackson, 1915. Replacement name for *C. a. minutus* Seebohm, 1887. Resident of se. India and Sri Lanka [type locality = Sri Lanka]. Like nominate subspecies but smaller (wing < 106 mm, bill < 20.5 mm), lores dusky, and, in the breeding male, crown concolorous with mantle and lacks black bar on forecrown.

C. a. nihonensis Deignan, 1941. Breeds in s. Japan, including Ryukyu Is., e. Mongolia and China, and Taiwan [type locality = Aomori, Honshu, Japan]; winters south to Philippines, w. Indonesia, and Malay Peninsula. Like nominate subspecies but dorsum darker brown, crown of breeding male a richer cinnamon-orange, patches at side of breast more extensive (Chandler and Shirihai 1995, Leader 2001), and bill averages slightly heavier. For use of the name *C. a. nihonensis* for this taxon, see Kennerley et al. (2008).

dealbatus group (White-faced Plover):

C. a. dealbatus (Swinhoe, 1870). Breeds on the southern coast of China (Fujian province south to Guangxi province), likely including Hainan I. [type locality = Amoy Xiamen, Fujian province, China, *fide* Kennerley et al. 2008]; winters from s. Vietnam southwest to the length of the Malay Peninsula and to the n.-central coast of Sumatra (Kennerley et al. 2008). Similar to *C. a. alexandrinus* but averages longer and deeper bill; dorsum pale brown; patches on sides of breast small, pale, brown (not black) lores white; lower auriculars pale; in the breeding male, black bar on forecrown wider and orange crown somewhat duller; legs and feet pinkish gray. See Kennerley et al. (2008) for details on diagnosis.

Related Species

The family Charadriidae, the plovers and lapwings, is well supported and is one of the core groups in the shorebird (Charadriiformes) radiation. Within this family, the genus Charadrius is also well defined. A mitochondrial DNA-based phylogeny of thirteen members of the genus (Joseph et al. 1999) found *C. alexandrinus* to be sister to *C. ruficapillus* (the Red-capped Plover of Australia), and these two species, along with *C. marginatus* (the White-fronted Plover of sub-Saharan Africa) and *C. javanicus* (the Javan Plover of Java), form a superspecies (Wiersma 1996). On the basis of its geographic distribution and morphology, *C. peronii* (the Malaysian Plover of Indonesia and the Philippines) may also be an allospecies in this superspecies complex.

Species limits within this superspecies are open to debate. For example, Wiersma (1996) said of *C. javanicus* that it "may well not merit full species status" and noted that it is "often" treated conspecific with *C. alexandrinus*. At the other extreme, Howard and Moore (1994) treated *C. a. occidentalis* as a species despite its strong morphological similarity to *C. a. nivosus* (see also Sibley and Monroe 1990). Species limits of *C. a. dealbatus* are being explored currently (Kennerley et al. 2008), and it is possible that this taxon will be accord species status once its breeding range and behavior are elucidated fully.

It is also possible that taxa in the Old World and New World will be split from each other, a Kentish Plover vs. Snowy Plover split. Ridgley and Greenfield (2001) remarked that "American birds are perhaps better treated as a distinct species (*C. nivosus*) separate from those of the Old World; their calls appear to differ," but provided no data in support. Küpper et al. (2009), however, provided data on molecular (mtDNA, a nuclear gene, and 26 microsatellites) divergence, as well as detailing differences in courtship calls and downy plumage of chicks. The genetic analyses demonstrated that *C. a. alexandrinus* is sister to *C. marginatus*, not to *C. a. nivosus*. If true, then the resultant paraphyly likely will lead taxonomists either to lump *C. marginatus* with the *C. alexandrinus* complex or split *C. alexandrinus* into Old World and New World species.

◂ Distribution Migration ▸

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Migration

Nature Of Migration In The Species

Figure 6. Annual cycle of breeding, migration and molt of the Snowy Plover.

Coastal populations of Snowy Plovers consist of migrants and year-round residents but most inland breeders are migratory. Distances of migratory movements are relatively short. The direction of movement to winter areas may be either northward or southward for Pacific coast breeders, but is northeast/southwest for birds breeding in the interior of western North America. Birds from the western Great Basin winter on the California and Baja California coasts where they comingle with breeders from the Pacific coast. Those breeding in the Great Plains winter on Gulf of Mexico coast.

Timing And Routes Of Migration

See Figure 6. ***Pacific Coast***. Populations consist of both migrants and year-round residents (Warriner et al. 1986). Birds nesting on the Oregon coast have wintered in California as far south as San Diego County (JCW). From central California coast, some birds travel north or south to wintering areas extending from Bandon, OR, to San Carlos, Baja Sur, Mexico (JSW and JCW). Spring migrants arrive in s. Washington in early March (Widrig 1980). At Monterey Bay, CA, females return earlier than males; from 1985-2005, the median dates local breeders were first detected returning after a winter absence was 25 March (n= 249) for females and 4 April (n= 540) for males. While a few individuals of both sexes returned as early as the first week of January, the central 50% (inter-quartile range) of returning females were first seen between 10 March and 9 April and males between 20 March and 16 April (LES). Individuals nesting at >1 coastal location during a single breeding season (Stenzel et al. 1994) may arrive for secondary nesting attempts any time from late Apr through 2 Jul and depart as early as late Apr (JSW and JCW). Most migrant breeders vacate Monterey Bay nesting areas from late Jun to late Oct (JSW and JCW) and winterers from other breeding areas return between 1 Jul-10 Nov ([median 29 Jul, inter-quartile range 19 Jul-20 Aug, n= 56] LES).

Inland, West of Rocky Mtns. Although present year-round in the San Joaquin Valley (SJV), CA, and deserts of s. California, some marked juveniles and adults from SJV migrate to the California coast for winter (Page et al. 1995, JSW and JCW). Birds nesting in the w. Great Basin (OR and CA) migrate to coastal California and west coast of Baja California, but most from e. Great Basin (UT) apparently do not winter along the California coast; they have been located on the west coast of Baja Sur and in Gulf of California (Page et al. 1995). Arrival at w. Great Basin breeding areas begins by late February at Owens Lake (Ruhlen et al. 2006, W. Deane in litt.) and as early as last week of Mar (Alcorn 1988) at more northerly lakes; most birds arrive in Apr and the latest probably not until Jun; males appear to arrive earlier than females (Page et al. 1979). Earliest migrants reach e. Great Basin in mid-Mar. Most arrive in Apr but some not until early Jun; males arrive about 1 wk before females (Paton 1995). Fall migration from Great Basin begins by early Jul. Most birds have departed by beginning of Sep (Paton 1995, M. Stern pers. comm.), although stragglers have been recorded as late as mid-Oct at Great Salt Lake, UT (Paton 1995), and early Nov at Mono Lake, CA, and Fallon, NV (Alcorn 1988, Shuford et al. 1995).

Great Plains. Birds nesting here are migratory with small numbers wintering in nw. Texas, Arizona, and se. New Mexico (Shuford et al. 1995, Elliott-Smith et. al. 2004). Many breeders from the Great Plains probably winter on the Gulf Coast, particularly in Texas and Mexico; R. Boyd (pers. comm.) located 2 marked breeders from Kansas in winter along the Texas coast, and the number of wintering birds on the Texas coast is larger than number of breeders (see Demography and Populations: population status: numbers). Comparison of plover numbers on a winter survey (1,191 in 1997, Mabee et al. 2001) and breeding season survey (182 in 2006, Zdravkovic et al. 2006) suggest the Laguna Madre de Tamaulipas region of Mexico is probably the winter destination of many plovers from the Great Plains.

Birds typically begin arriving in Colorado about mid-Apr (Andrews and Righter 1992), in Kansas and Oklahoma from fourth week of Mar to first week of Apr (Boyd 1972, Hill 1985, Thompson and Ely 1989), and in Texas and New Mexico by mid-Mar (Oberholser 1974, Hubbard 1985, 1987, Conway et al. 2005). Most probably reach Great Plains breeding sites in Apr; migration extends into May (Boyd 1972, Thompson and Ely 1989, Hill 1992). Fall departure begins by mid-Jul and probably extends into Oct, with stragglers occurring until early Nov (Sutton 1967, Boyd 1972, Oberholser 1974, Thompson and Ely 1989, Andrews and Righter 1992, Shuford et al. 1995).

Gulf Coast. In Florida, population appears to be partly migratory and partly resident with some breeders appearing to migrate from the state and others moving to other Florida coastal locations for winter. Surveys in 2002 indicate a breeding population of about 1.5 the number of individuals found in winter (Himes at al. 2006). In Texas the winter distribution overlaps with the breeding distribution and also includes upper part of Texas coast.

Atlantic. Birds are year-round residents in Caribbean and Bahamas (Gorman and Haig 2002).

Migratory Behavior

No information on size of migratory groups, altitude, or speed of migration.

Control And Physiology

No information.

Systematics Habitat

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Habitat

Nests on the ground, mainly in the open on sandy coastal beaches, barrier islands, barren shores of inland saline lakes, and on river bars. Also now uses man-made, agricultural wastewater ponds and reservoir margins in the interior, dredge spoils on the coast, and salt evaporation ponds on the coast and in the interior.

Enlarge

Figure 2. Nesting habitat of Snowy Plover at the Salinas River mouth, Monterey Co.

Enlarge

Volunteer monitoring threatened Snowy Plovers in key nesting habitat, coastal California; July.

Breeding Range

Figure 2. On Pacific Coast, nests on barren to sparsely vegetated sand beaches (Wilson-Jacobs and Meslow 1984), dry salt flats in lagoons, dredge spoils deposited on beach or dune habitat, levees and flats at salt-evaporation ponds, and sand and cobble river bars up to 7 miles from the beach (Page and Stenzel 1981, Tuttle et al.1998). In California, most breeding occurs on coastal dune-backed beaches, barrier beaches, and salt-evaporation ponds; infrequently on bluff-backed beaches; and also offshore on Channel Island beaches (Page and Stenzel 1981). Snowy Plovers breed regularly on gravel bars on the Eel River, Humboldt Co., CA (Colwell et al. 2005). In Baja California, barrier beaches, salt flats, and salt-evaporation ponds are primary breeding sites (Palacios et al. 1994).

Inland, breeds up to 3,048 m (Colorado; Kingery 1983) on barren to sparsely vegetated ground at alkaline or saline lakes, reservoirs, ponds, and riverine sand bars (Mabee and Estelle 2000,

Enlarge

Sign protecting Snowy Plover nesting habitat; Half Moon Bay, CA. May.

Enlarge

Snowy Plover nest on beach, Los Angeles, CA. June

Conway et al. 2005); and at sewage (occasionally), salt-evaporation, and agricultural wastewater ponds (Ivey 1984). Also nests at salt evaporation ponds at Great Salt Lake , UT. Although breeding has not been documented on salt flats devoid of water (Herman et al. 1988, GWP), nesting can occur where a distant small seep is the only apparent surface water (GWP, LES).

On Gulf Coast in Florida, most nests are located on coastal sandy beaches and barrier islands; a few on little-used paved parking lots at Eglin Air Force Base, Okaloosa Co. (Himes et al. 2006).

Spring And Fall Migration

Same as on breeding and winter ranges.

Winter Range

Primarily coastal: beaches, tidal flats, lagoon margins, and salt-evaporation ponds. Inland some birds regularly winter at agricultural waste-water ponds in San Joaquin Valley, CA, and at saline lakes (particularly Salton Sea) in s. California (Page et al. 1986, Shuford et al. 1995), in nw. and central Texas (Elliott-Smith et al. 2004), and interior of Mexico (Howell and Webb 1994).

Migration

Food Habits

Recommended Citation

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Snowy Plover

Charadrius alexandrinus

Order CHARADRIIFORMES– Family CHARADRIIDAE

Issue No. 154 – Revised: November 18, 2009

Authors: Page, G. W., J. S. Warriner, J. C. Warriner, and P. W. Paton

Revisors: Page, Gary W., and Lynne E. Stenzel

Food Habits

Feeding

Main Foods Taken

Terrestrial, freshwater, brackish, and marine invertebrates.

Microhabitat For Foraging

On coast feeds on beaches, tide flats, river mouths, lagoon margins, salt flats, and salt ponds. At beaches forages above and below mean high-water line, gathering food from above and below the sand surface, kelp (wrack), marine-mammal carcasses, or low foredune vegetation. Inland feeds on shores of lakes, reservoirs, ponds, braided river channels, and playas (mostly at seeps and along streams). Although at inland habitats most feeding is in shallow (1–2 cm deep) water or on wet mud or sand, on playas some foraging also occurs on dry flats.

Food Capture And Consumption

During daytime, feeds in typical plover fashion -- usually pauses, looks, runs, and then seizes prey from surface of beach or tide flat. Probing in sand, particularly at base of low growing plants, is used at times by Snowy Plovers foraging above high-tide line on California beaches (GWP) and, where there are concentrations of juvenile mole crabs (*Emerita*), below high tide line (D. George in litt.). Probing burrows for the beetle *Bledius* commonly observed on Oklahoma salt flats (Purdue 1976a, Grover and Knopf 1982). Shallow probing for brine fly larvae (*Ephydridae*) is employed on seeps at Mono Lake, CA, where the birds often shake the larvae before swallowing them (Swarth 1983).

Sometimes lowers head and charges with open mouth into dense aggregations of adult flies on ground, snapping bill at those flushed (Purdue 1976a). Usually snaps bill 2–3 times to crush captured flies before swallowing them (Swarth 1983). Plovers employ this charging method to capture isolated insects on California beaches. They also sometimes capture prey by hopping into clouds of kelp flies on coastal beaches (K. Neuman pers. comm.). J. Erbes (in litt.) has seen plovers jump up and capture moths and butterflies mid-air and then shake them vigorously before consuming them.

Another behavior sometimes preceding a feeding attempt is foot trembling in shallow water or on wet substrate (Feeney and Maffei 1991, R. Boyd pers. comm., JSW and JCW). At Ocean Beach, San Francisco Co., CA, wintering plovers frequently capture polychaetes during receding and low tides by employing the foot trembling behavior prior to pulling up worms (J. Erbes in litt.).

Appear to forage regularly at night; seen feeding on amphipods in near total darkness on a s. California beach (Lafferty 2001) and feeding after 22:00 during a full moon at Jalama Beach, Santa Barbara Co., CA (S. Hampton pers. comm.). On a tidal flat at Tokyo Bay, Japan, Kentish Plover feeding attempt and success rates were greater at night than during the day. As available foraging time was 1.7 times longer during night than day, Kentish Plovers could capture 3.7 times more prey (primarily nereid polychaetes and sand-bubbler crabs (*Scopimera globosa*) at night (Kuwae 2007). Comparable studies of Snowy Plover nocturnal and diurnal feeding ecology would be valuable.

Diet

During the breeding season on the s. California coast, beetles were found in 72%, adult flies in 44%, and insect larvae in 25% of 32 fecal samples of adult plovers. Rove beetles (Staphylinidae) were the most common beetle prey and long-legged flies (Dolichopodidae) and shore flies (Ephydridae) the primary dipteran prey. Fragments of other beetles (Carabidae and Cicindelidae), diptera (Anthomyiidae), hymenoptera (Braconidae), hemiptera (Saldidae), decapoda (Hippidae), and gastropoda (Nassaridae) were found in the samples. Feces from 3 fledglings contained rove beetles (3 samples), long-legged flies (2 samples), Braconidae (1 sample), and insect larvae (1 sample). The feces of one 2-week old chick contained only rove beetles. Adult plovers were also seen feeding on marine worms on several occasions (Tucker and Powell 1999).

Other information from Pacific Coast beaches and tidal flats identifies the following prey: mole crabs (*Emerita analoga*), crabs (*Pachygrapsus crassipes*), polychaetes (Neridae, *Lumbrineris zonata*, *Polydora socialis*, *Scoloplos acmaceps*), amphipods (*Corophium* spp., *Ampithoe* spp., *Allorchestes angustus*, and sand hoppers [Orchestoidea]), tanadacians (*Leptochelia dubia*), flies (Ephydridae, Dolichopodidae), beetles (Carabidae, Buprestidae, Tenebrionidae), clams (*Nutricola* sp.[formerly *Transennella*]), and ostracods (Reeder 1951, R. Wilson-Jacobs pers. comm., GWP).

Snowy Plover abundance on southern California beaches was positively correlated with the mean cover of wrack and abundance of wrack-associated invertebrates which are likely plover prey. These were identified as: taltrid amphipods (*Megalorchestia californiana*, *M. benedicti*, *M. columbiana*, *M. corniculata*); isopods (*Tylos punctatus, Alloniscus perconvexus*); beetles including a carabid (*Dyschirius marinus*), a tenebrionid (*Phalaria rotundata*), a hydrophilid (*Cercyon lunger*) three histeriids (*Neopachylophus sulcifrons, Neopachylophus* spp.), a curculionid (*Emphyastes fucicola*), seven staphylinids (*Thinopinus pictus, Bledius fenyesi, Cafius seminitens, C. canescens, Potomalota opaca, Aleochara sulcicollis,* and *Thinusa maritima*); and larvae and pupae of two dipterans (*Coelopa vanduzeei, Fucellia costalis*) (Dugan et al. 2003).

Prey consumed in San Francisco Bay salt-evaporation ponds include: flies (*Ephydra cinerea*), beetles (*Tanarthrus occidentalis*, *Bembidion* sp.), moths (*Perizoma custodiata*), and lepidopteran caterpillars (Feeney and Maffei 1991). At Great Basin saline and alkaline lakes plovers eat: flies *(Ephydra hians*, *Thinophilus spinipes*, *T. latimanus*, *Mosillus bidentatus*, *Lamproscatella salinara,* and *Lispe* sp.), beetles (*Bembidion ephippigerum*,

Tanarthrus inyo, *Bledius* sp., *Carpelimus* sp., and Cicindelidae), hemipterans (*Saldula arenicola*), and brine shrimp (*Artemia monica*) (Swarth 1983, PWCP). At salt flats on the Great Plains plover prey are: flies (*Ephydra* sp.), beetles (*Bledius* sp., *Cicindela* sp.), and terrestrial insects blown onto flats, including a wide variety of grasshoppers, lepidopterans, and beetles (Purdue 1976a, Grover and Knopf 1982). Gulf Coast prey are described as: small crustaceans, mollusks, marine worms, aquatic insects, and seeds (Howell 1924).

Food Selection And Storage

Snowy Plovers do not cache food.

Nutrition And Energetics

No information.

Metabolism And Temperature Regulation

Individuals nesting in open, hot environments alleviate heat stress by panting, pteryloerection (elevating scapular, nape, and crown feathers), belly soaking (running through relatively deep water and intermittently preening ventral feathers), standing in water between incubation bouts, increasing frequency of parental shifts during incubation, and possibly restricting activities to near water (Purdue 1976b, Grant 1982). Body temperature of incubating Kentish Plovers increases with ambient temperatures in hot (> 30o C) environments; research suggests belly-soaking is used primarily to dissipate body heat of heat-stressed incubating adults and functions secondarily to cool overheated eggs (Amat and Masero 2007).

Drinking, Pellet-Casting, And Defecation

In osmotically stressful environments, Snowy Plovers may rely on water content of insectivorous diet and water-conservation behaviors, such as standing in pools, to avoid drinking saline solutions (Purdue and Haines 1977). When fresh water is available, drinks in repeated bouts by dipping bill in water and tilting head backward. Not reported to produce pellets, although this might be expected from individuals feeding on mole crabs on sandy beaches.

◂ Habitat Sounds ▸

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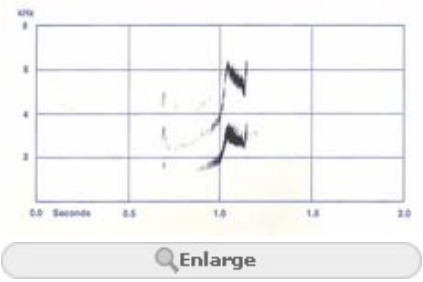
Sounds

Vocalizations

Development

Chicks make a repeated *peep* from up to 2 d before hatching until about the time they first fly. Free-ranging chicks use this call during close pursuit or capture by a predator or person and when isolated from parent (GWP). D. George (pers. comm.) reports finding 2 crouched chicks making a soft trilling call, distinct from repeated peeping call.



Enlarge

Figure 3. Turwheit calls of the Snowy Plover

Vocal Array

Adults use at least 3 primary calls during breeding season.

Purrt. Repeated several times. Given by either sex while flying singly or together from nesting territories, during courtship while scraping or tossing (see Breeding: nest) in presence of mates, during or immediately after conflicts with other plovers that have invaded their nesting territories or closely approached their broods, while a person handles their eggs or chicks, while attending their broods in the absence of any obvious intrusion by another plover or other intruder, and (in one instance) by a male fluttering over vegetated habitat toward a slough in an apparent attempt to encourage his chicks to follow (JSW and JCW).

Turwheit or Towheet. Figure 3. Usually repeated a few to many times by males, when unmated and standing or scraping in territories in absence of females (advertisement), from territories while standing or scraping in presence of a female prior to nesting (courtship), from territories in absence or presence of mates while clutches are still incomplete, and from territories during confrontations with intruding plovers while standing in Upright Posture (see Behavior: agonistic behavior), chasing invaders, or standing between bouts of fighting (threat and aggression). This call is repeated by either sex as a predator destroys their eggs (distress), while brooding or standing near their chicks in

absence of any other obvious plover or intruder, during confrontations with other plovers when attending chicks (threat and aggression), and from ground or in flight when a person closely approaches their flightless young (alarm). Call is quieter, hoarser, and more abbreviated in females than in males (JSW and JCW). Probably analogous to *peo-eet* call attributed to a Snowy Plover in Kansas after it had run from its nest at the approach of an intruder (Boyd 1972).

Churr. Usually not repeated and most often made by males, sometimes during courtship activities such as scraping or debris tossing, but most often during agonistic encounters with other plovers during defense of nesting territories or broods. During these aggressive encounters, calling male stands in Upright Posture, chases, or fights with intruding plovers. Females utter this call during confrontations with other species (e.g., Black-bellied Plover [*Pluvialis squatarola*]) or conspecifics near their nests or chicks. In aggressive situations, this call is frequently combined with 2 other notes to produce a *whit whit churr* or a *purt purt churr* (JSW and JCW).

Ti. During nonbreeding season, a repeated, low, tinkling *ti* note, uttered by plovers disturbed at their roosts, often signals flight of some or all birds.

Phenology

In coastal California, calls associated with breeding are used from late Jan until Sep; *ti* of nonbreeding period is used from Aug to Apr.

Daily Pattern Of Vocalizing

Breeding-season calls given day or night, but nonbreeding-season calls only reported for daylight hours.

Places Of Vocalizing

Most calling is from ground, but all breeding-season calls also may be given in flight (JSW and JCW). In contrast to Kentish Plovers (*C. a. alexandrinus*), Snowy Plovers (*C. a. nivosus*) do not employ a flight song to advertise territories (Warriner et al. 1986).

Nonvocal Sounds

None known.

Food Habits | Behavior

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Behavior

Locomotion

Walking, Hopping, Climbing, Etc

Walking and running are employed in feeding, courtship, agonistic interactions, nest exchange, retreat from nest at approach of a predator or person, return to nest after disturbance, and most activities associated with care of the free-ranging precocial chicks. Snowy Plovers jump up onto logs or rocks with aid of their wings but do not climb vertical objects.

Flight

Typically runs when disturbed, but sometimes flies directly from nest when surprised by a potential egg predator, e.g., a flying crow or raven. Flocks of Snowy Plovers will take flight when attacked by raptors or disturbed by canines, corvids or humans. Following attacks by avian predators, flocks frequently wheel back and forth for several minutes in tight, highly coordinated formations typical of other shorebirds. After landing they are edgy and readily resume such flights with little prompting. If disturbed, but not attacked, all or portions of a roosting flock of Snowy Plovers may make low, short, direct flights to a nearby location where they land and crouch or run into footprints before crouching. Snowy Plovers with broods often fly back and forth calling when their chicks are approached too closely by people or predators. Adults also sometimes flutter over chicks that are swimming or concealed in vegetation.

Enlarge

Juvenile Snowy Plover, Summer Lake, OR, August

Enlarge

Adult male Snowy Plover stretching wings, Morro Bay, CA. April.

Snowy Plover wing-stretching, Grover Beach, California. September

Crouching Snowy Plovers (predator avoidance?) along beach Chinicuila, Mexico, March

Adult male Snowy Plover, wing-stretching; Morro Bay, CA. April.

Swimming And Diving

Even newly hatched chicks swim across ponds and slow-flowing rivers, and adults tending chicks also swim occasionally, apparently to entice chicks across water (JSW and JCW). Diving under water to escape an attacking predator has not been reported.

Self-Maintenance

Preening, Head-Scratching, Stretching, Bathing, Anting, Etc

Preening, head-scratching, stretching of 1 leg or 1 wing, bathing in still water or the swash of waves up to belly-depth, and picking at legs or toes after bathing are commonly observed behaviors. Anting not reported.

Sleeping, Roosting, Sunbathing

Sleeps with bill and front of head tucked under scapula feathers; will stand on 1 rather than 2 legs, especially during cooler weather. Incubating adults and individuals in roosting flocks periodically close their eyes and are probably sleeping. Flocks of a few to > 300 birds roost by sitting in footprints, vehicle tracks, or the lee of kelp, driftwood, or low dunes on widest areas of beaches, particularly during nonbreeding season. These roosting birds may be strung out for up to 200 m, although some individuals may be only a few centimeters apart. When disturbed by humans or dogs, roosting birds often run a few meters to new positions, often charging at, bumping, and displacing other individuals from preferred spots such as human footprints.

Daily Time Budget

Limited information for Snowy Plover: On a central California beach, during dawn to dusk surveys, wintering Snowy Plovers fed more in the morning until 10:30 (43% on average foraged) compared to later when 95% roosted unless disturbed (Lafferty 2001).

During the pre-laying and laying period female Kentish Plovers at an alkaline grassland in

Hungary averaged more time feeding than their mates: 51.0% ± 6.3 SE versus 19.4% ± 5.2 SE. Time spent in other activities included: standing, females 28.8% ± 5.6 SE, males 18.1% ± 3.1 SE; preening, females 8.4% ± 2.0 SE, males 13.7% ± 2.3 SE; and sitting, females 6.3% ± 3.2 SE, males 10.5% ± 4.4 SE. Females also spent significantly more time feeding during the pre-laying and laying period than when they were engaged in chick rearing and feeding averaged 10.0% ± 4.5 SE of the time (Székely et al. 1994a). See Breeding: incubation.

Agonistic Behavior

Physical Interactions

Although both sexes of the Snowy Plover defend nest territories against conspecifics by running at, flying at, or fighting with transgressors, males are more aggressive. Fights frequently occur between males and females when their broods come into contact. Adults sometimes peck chicks of other plovers that approach too closely.

Fights sometimes consist of prolonged battles with birds leaping breast-to-breast, their wings fluttering, as each combatant pecks and pushes at the other (JSW and JCW). In one confrontation a male repeatedly jumped up and kicked forward alternately with both feet at another male (P. Person pers. comm.). During some fights birds grab their opponent's tail with their bill and pull on feathers while turning in circles; occasionally they yank out a rectrix. Fights, with respites of 5–120 s between bouts, have lasted as long as 1.5 h on California coast (JSW and JCW).

Comparison of time male and female Snowy Plovers spend fighting conspecifics has not been well documented. After experimental separation from their mates during incubation, released male Kentish Plovers spent more time than females fighting conspecifics at Tuzla, Turkey (Székely et al.1999). After experimental removal of their mate from broods at Algarve, Portugal, there was no difference in the time the remaining male or female Kentish Plover spent fighting conspecifics to protect broods, but males spent significantly more time fighting other potential threats such as other species of shorebirds (Székely 1996)..

Communicative Interactions

Enlarge

Snowy Plover resting in beach tire tracks; Los Angeles, CA. October.

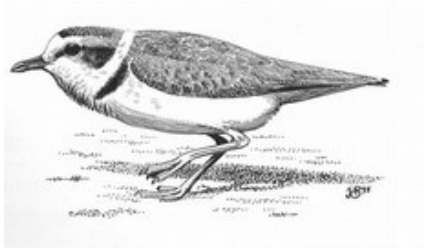

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Figure 4. Posture of male Snowy Plover during the Horizontal Display

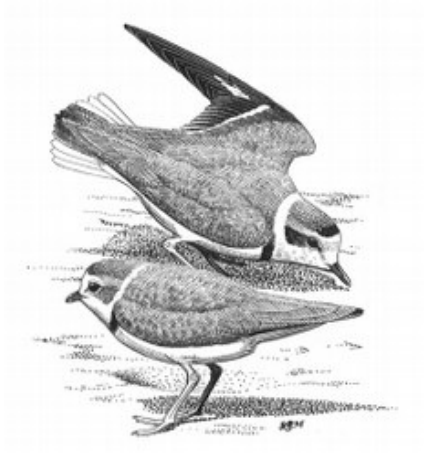

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Figure 5. Bowing courtship display of male Snowy Plover near the nest.

Male Snowy Plovers sometimes confront conspecifics by standing in an elevated posture with body upright, neck extended, and breast feathers erected (Upright Display). This display is frequently used by territory holders confronting intruders. Males also use a Horizontal Display (Fig. 4) in which bill, body, and tail are held parallel to ground, neck is extended, and throat feathers are erected as male walks in a partial crouch. Males use this display at approach of their mate by another plover or a human (mate guarding) and during courtship (JSW and JCW; also see Sexual Behavior). Both Upright and Horizontal displays have also been observed during interactions between individuals in roosting flocks up to 2 mo before onset of egg laying (JSW and JCW).

Spacing

Territoriality

Nature and Extent of Territory. Both unpaired males and pairs of Snowy Plovers defend territories against conspecifics by posturing, chasing, or fighting (see Agonistic Behavior, above). On California coast, unpaired males defend territories for up to 45 d before procuring a mate (JSW and JCW). They advertise their presence with bouts of calling from ground (see Vocalizations) and construct scrapes, presumably to attract females. Paired birds use territories for courtship, nest sites, and sometimes feeding. It is unlikely that territories function primarily for protection of food resources since off-duty parents frequently forage with conspecifics in nondefended areas, up to 6 km from their nests on California coast, up to 4 km at inland saline lakes in California (GWP), and up to 3 km at Great Salt Lake, UT (Paton 1995). On the Great Plains, territories are possibly more important for foraging; at Cheyenne Bottoms, KS, males are usually within about 30 m of nests while females are incubating (Boyd 1972), and at Great Salt Plains, OK, banded individuals are consistently in the same areas on either their nesting or feeding territories (Purdue 1976a). Broods frequently abandon nesting territories within hours of hatching; the parent(s) defend a space around the wandering broods with the area occupied by different broods sometimes overlapping.

For Snowy Plovers on central California coast, territories were always <0.5 ha at a salt pan but probably larger on the beach (Warriner et al. 1986). In southern California over 5 years, nest density varied from 0.5-3.2 nests per ha at one man-made site and 1.3-1.7 nests per ha at another; at one other man-made site there were 13.3 nests per ha in 1 year (Powell and Collier 2000). Nearest inter-nest distance was 113 m ± 86 SE in coastal southern California (Powell 2001). At Great Salt Lake, UT, some territories were as small as 0.1 ha as extrapolated from nearest neighbor distances averaging 36 m between 79 nests <100 m apart (Paton 1994a). Nearest neighbor distances averaging 80–114 m between nests suggest a mean territory size of 0.5–1.0 ha at 2 Great Plains sites (Boyd 1972, Grover and Knopf 1982). The number of breeders along sections of the Gulf coast of Florida in 2006 ranged from 0.1 > 2.0 pairs/km (Himes et al. 2006).

For Kentish Plovers, breeding density was 0.2-1.2 nests per ha in alkaline grasslands in Hungary (Székely 1992); 1.54-1.70 nests per ha on a Portuguese coastal beach (Norte and Ramos 2004); 5-16 nests per ha in Portugal; 2-6 nests per ha in Turkey (Székely et al, 1999); and 2.3 pairs per km of shoreline at the Po Delta, Italy (Valle and Scarton 1999). Reported nearest neighbor nest distances are: median 29-32 m in Spain (Fraga and Amat 1996); and a mean of 279.6 m ± 266.8 SD on the coast versus usually <25 m inland in Portugal (Norte and Ramos 2004).

Snowy Plover pairs losing clutches may or may not retain territory for renesting; in central

California those losing a clutch to predators are less likely to retain their territory than those losing it to other causes (Warriner et al. 1986). Males are more likely than females to retain same territory in consecutive years (Warriner et al. 1986).

The distance between consecutive nesting territories of polygamous Snowy Plover females is probably greater than for males as in Kentish Plovers because males may retain territories whereas females do not. Polygamous female Kentish Plovers at Piedra Lake, Spain averaged 1507.1 m ± 1136.7 SE between first and second nests compared to 405.1 m ± 738.2 SE for males (Amat et al. 1999c). After experimental removal from broods followed by release at Tuzla Lake, Turkey, new nesting territories of female Kentish Plovers were further from their previous territory (289 m ± 57 SE) than those of males (46 m ± 8 SE) (Székely et al. 1999).

Interspecific Territoriality. Territorial Snowy Plovers were observed defending territories against migrating Semipalmated Plovers and Whimbrels (*Numenius phaeopus*) at Monterey Bay, CA (D. George unpubl. data, JSW and JCW) but were often not aggressive toward Black-necked Stilts (*Himantopus mexicanus*) or American Avocets (*Recurvirostra americana*) unless they approached within 1 m of plovers' nests (JSW and JCW). Boyd (1972) reports both sexes defend against Killdeers (*Charadrius vociferus*) and American Avocets. PWCP has observed interspecific aggression toward Long-billed Curlews (*Numenius americanus*), Willets (*Catoptrophorus semipalmatus*), American Avocets, and Black-necked Stilts.

Winter Territoriality. Snowy Plovers sometimes defend winter territories on coastal beaches (Myers et al. 1979), but roosting and feeding in flocks is most frequently observed behavior.

Individual Distance

No information.

Sexual Behavior

Mating System And Sex Ratio

Snowy and Kentish Plovers are facultatively polyandrous and polygynous with instances of true polygyny also occurring rarely (Lessells 1984, Warriner et al. 1986, Fraga and Amat 1996). In this labile mating system, typically females, but also sometimes males, desert mates and broods after hatching. While males rear broods, females obtain new mates and initiate new nests. Levels of polygamy differ spatially and temporally in response to the operational sex ratio, duration of the breeding season, and success of early season nests (Warriner et al. 1986, Fraga and Amat 1996, Amat et al. 1999c).

The sex ratio, regarded as widely biased towards males (Székely et al. 1999), has been reported as 1.4:1.0 males per female in California, 1.4:1.0 in Sweden, and 1.19:1.0 in Turkey (Warriner et al. 1986, Székely 1996, Sandercock et al. 2005). Over 5 breeding seasons, the estimated number of breeding males always outnumbered females in coastal San Diego County, CA (Powell et al. 2002). Consistent with a male-biased sex ratio, are the following observations for the Kentish Plover: at the Carmargue, France after experimental removal of mates and nests, males took longer than females to remate and renest (Lessells 1983); males from Algarve, Portugal, removed from broods and then released, took longer to remate and renest than females treated similarly (Székely 1996); and significantly more females than males initiated second nests after successfully hatching earlier nests at Fuente de Piedra, Spain (Amat et al. 1999c). The response of

Kentish Plovers after experimental removal from broods and release at Tuzla Lake, Turkey also suggest remating opportunities differ between the sexes and decrease for both sexes over the course of the breeding season (Székely et al. 1999). At this location, expected remating times of released birds was shorter for females than males (median = 5.3 days versus 25.4 days) and females of the new pairs completed their clutches more quickly after release (mean =13.9 days ± 2.0 SE) than the female mates of the males (mean = 22.9 days ± 2.5 SE); remating times increased over the breeding season for both sexes but was significant only in females (Székely et al. 1999). In contrast, the interval between initiation of first and second nests of polygynous Kentish Plover males (66.2 days ± 17.7 SE) and polyandrous females (61.3 days ±16.4 SE) did not differ at Fuente de Piedra Lake Spain (Amat et al. 1999c).

The underlying cause(s) of an uneven sex ratio is unclear. At Tuzla, Turkey, the sex ratio of newly-hatched Kentish Plover chicks was not significantly different from 1:1; here it is hypothesized that there was female-biased mortality between hatching and fledging leading to a surplus of males (Székely et al 2004); however, on the central California coast, in a population characterized by polyandrous breeding, the sex ratio of yearling Snowy Plovers entering the breeding population was 1:1 (Stenzel et al. 2007).

As a product of their polygamous mating system, Snowy Plover females on the U.S. Pacific Coast frequently double brood and sometimes triple brood. Males also remate and initiate second nests, usually after chicks from first brood begin to fly, but sometimes as early as 10 d before chicks' first flights (Warriner et al. 1986, JSW and JCW). Adults of either sex may move up to several hundred kilometers for their ensuing nests (see Demography and Populations: range). This sequentially polygamous mating system has been documented on the California coast, where the breeding season is long (clutch initiations last 16 wk) and there is a surplus of breeding males (Warriner et al. 1986); along Oregon coast (M. Stern pers. comm.); at Mono Lake, CA, where male to female sex ratio was calculated at 1.4:1.0 (Warriner et al. 1986); recently in coastal Florida (R. Pruner in litt.) and at Great Salt Lake, UT (Paton 1995). On Great Plains, where nesting season is more abbreviated than in w. North America, 2 studies of marked birds did not documented any double brooding (Boyd 1972, Hill 1985). A sequentially polygamous mating system is also widespread in the Kentish Plover (Lessells 1984, Fraga and Amat 1996, Székely et al. 1999).

Courtship and Copulation. Male Snowy Plovers appear to solicit females by standing and calling from their territories (see Spacing, above). Males also solicit nearby females on and off territories with Horizontal Display (see Agonistic Behavior, above, and Fig. 4). After Horizontal Display, following sequence of events frequently occurs during successful copulations.

Male runs to a spot and begins scraping, usually in a previously constructed depression. Female runs to scrape, male steps out, and female settles in, scratching with her feet while rotating on her breast. Male bows (Fig. 5) next to female, pointing his head to ground 1 to several times, and simultaneously flashes the white on his tail by quickly fanning and retracting his rectrices. Female steps out of scrape, runs 0.5–2.0 m, and stands with her body parallel to ground or tilted slightly forward. Male follows and stands directly behind her, kicking his legs high as though goose-stepping in place. He then jumps on her back and balances on his tarsometatarsi. Settling on her back, he begins a rhythmic kneading motion by shifting his weight alternately from one leg to the other. Both birds shift their tails side-to-side with increasing frequency as coitus approaches. At moment of apparent coitus, male grasps back of female's neck with his bill and both birds topple backward with

wings partly extended. They remain in this position for only 1–2 s before resuming other activities such as standing or preening. See Boyd (1972) and Buchanan et al. (1991) for some variation on this description. In coastal California, mounting to coitus averaged 120 s ± 38 SD, range 40–300, *n*= 208); copulations occurred from 25 d before to 3 d after first egg was laid; 89% were prior to first egg with none after second egg (*n*= 172, Warriner et al. 1986, JSW and JCW).

Mate Guarding. On and off territories, males sometimes chase conspecifics from vicinity of their mates during pre-egg and egg-laying periods. See Agonistic Behavior, above.

Duration and Maintenance of Pair Bond. At onset of nesting, Snowy Plover pair bonds may be established up to 50 d before egg-laying on California coast (Warriner et al. 1986) and about 2 mo before egg-laying on Florida coast (Chase and Gore 1989). Mate retention is high in Snowy and Kentish plovers after clutch loss (Lessells 1983, Warriner et al.1986, Amat el al. 1999c); it occurred in 87% of 30 instances of clutch loss on the California coast (Warriner et al. 1986); 71% of 45 on Florida coast (Chase 1991); and 90% of 10 instances in Hungary (Székely and Lessells 1993).

Mate desertion, particularly by females, during the brood rearing period is widespread but timing is spatially and temporally variable in Snowy and Kentish plovers. It may be a facultative response to the needs of chicks with the female staying longer when there is greater predation pressure (Amat et al. 1999c). In w. North America, pairs typically have separated by the sixth day after the chicks hatched (Warriner et al. 1986), although pair bonds are sometimes re-established for the female's third (triple brooding) attempt (JSW and JCW). In Florida, males and females reportedly remain together for second broods much more frequently than in California (Chase and Gore 1989, Chase 1991); however, recent studies of banded birds in Florida have shown some females abandon the brood 5-7 days post-hatch and nest up to 3 times during the season (R. Pruner in litt.). In Hungary, typically the female deserted the brood on average 5.9 days ± 5.9 SE after hatching; females alone attend 6.5-15% and males alone 81.8% ≥ 17 day-old broods (Székely and Lessells 1993). Of 101 broods in Spain, 14% were deserted by the male, 84% by the female and 2 % were accompanied by both parents until fledging (Amat et al. 1999c). On the California and Oregon coasts, females begin laying second clutches as soon as 3–10 d after desertion of their first broods (M. Stern unpubl. data, JSW and JCW).

In rare cases, Snowy and Kentish plover males may form pair bonds and nest with two females (true polygyny) simultaneously (Warriner et al. 1986, Fraga and Amat 1996).

Pair bonds may also be renewed in consecutive nesting seasons; for Snowy Plovers in central California between 1977 and 1982 an individual's earliest nesting attempt was with previous year's first partner on 45% of 29 possible occasions (Warriner et al. 1986); at the same location during the 6 years of highest adult survival between 1984 and 2004, the proportion of first pairs that were maintained between years averaged 43.7% ± 4.1 SE (range 32.3-58.3% (LES); however, in southern California males were reported to not usually mate with the same female in successive years (Powell and Collier 2000). In Kentish Plovers, repairing with the previous year's first mate is reported in 6 of 11 possible instances in Spain (Amat et al.1999c) and 1 of 9 in Hungary (Székely and Lessells 1993).

Extra-Pair Copulations

Rarely observed in the Snowy Plover (JSW and JCW). DNA fingerprinting indicates most Kentish Plover pairs are genetically monogamous: only 7.9% of 89 broods and 3.9% of the

229 chicks exhibited extra pair fertilizations in Spain; these included extra pair paternity, extra pair maternity and intra-specific brood parasitism (Küpper et al. 2004).

Social And Interspecific Behavior

Degree Of Sociality

Gregarious in winter, forming loose roosting flocks of up to 300 birds; also forages in loose flocks. On w. North American playas, nesting birds often concentrate at dusk on seeps to bathe, drink and feed; periodic bouts of calling and posturing of individuals within these groups suggest that crepuscular concentrations may be important socializing centers. Plovers will aggregate in small groups around food sources such as carcasses with flies; also during daytime small groups of males with nests will feed and roost together while females are incubating (J. Erbes in litt.).

Play

Not known.

Nonpredatory Interspecific Interactions

In winter on Gulf Coast, may occur in mixed flocks of shorebirds, including Piping Plovers, with which Snowy Plovers sometimes interact (Nicholls and Baldassarre 1990). On Pacific coast, Snowy Plovers sometimes roost with Sanderling (*Calidris alba*), Semipalmated Plover (*Charadrius semipalmatus*) or other small shorebirds (J. Erbes in litt.). See Spacing, above.

During breeding season Snowy Plovers nest in close association with Least Terns (*Sterna albifrons*) in some coastal and interior areas (Powell and Collier 2000).

Predation

Kinds Of Predators

Known or suspected (s) predators, on adults: Merlin (*Falco columbarius*), Peregrine Falcon (*F. peregrinus*), Prairie Falcon (*F. mexicanus*), Northern Harrier (*Circus cyaneus*), Red-tailed Hawk (*Buteo jamaicensis*), Great Horned Owl (*Bubo virginianus*) feral cat (*Felis domesticus*), and red fox (*Vulpes vulpes*); on chicks: Loggerhead Shrike (*Lanius ludovicianus*), Common Raven (*Corvus corax*), American Crow (*C. brachyrhynchos*), Western Gull (*Larus occidentalis*), California Gull (*L. californicus*), Ring-billed Gull (*L. delawarensis*), Laughing Gull (*L. atricilla*), Gull-billed Tern (*Sterna nilotica*), American Kestrel (*Falco sparvarius*), Peregrine Falcon, Northern Harrier, Red-tailed Hawk, Red-shouldered Hawk (*Buteo lineatus*), Coopers Hawk (*Accipiter cooperii*), Great Horned Owl, Burrowing Owl (*Strix cunicularia*), Great Blue Heron (*Ardea herodius*), (s) Cattle Egret (*Bubulcus ibis*), coyote (*Canis latrans*), red fox, striped skunk (*Mephitis mephitis*), spotted skunk (*Spilogale putorius*), raccoon (*Procyon lotor*), opossum (*Didelphis marsupialis*), ghost crab (*Ocypode quadrata*), and trapdoor spider (*Aptostichus* sp.); on eggs: Common Raven, American Crow, Fish Crow (*C. ossifragus*), Western Gull, California Gull, Ring-billed Gull, Laughing Gull, Northern Harrier, Red-tailed Hawk, Great Blue Heron, Cattle Egret , Whimbrel (*Numenius phaeopus*), coyote, red fox, gray fox (*Urocyon cinereoargenteus*), island fox (*U. littoralis*), striped skunk, spotted skunk, raccoon, opossum, deer mice (*Peromyscus maniculatus*), feral cat, Beechey Ground Squirrel (*Otospermophilus beecheyi*), mink (*Mustela vison*), weasel (*Mustela* sp.), bull snake (*Pituophis melanoleucus*), ghost crab, and Argentine ants (*Iridomryres humilis*).

Response To Predators

Although adults usually run from nests when people, dogs, or avian and mammalian egg predators approach, they fly when surprised. Adults crouch on nests when Peregrine Falcons fly over (PWCP). Adults with broods react to approaching people or dogs with calls; small chicks (<10 d) usually crouch and remain motionless, whereas older chicks (>10 d) often run with their parent ≥100 m ahead of people or dogs. (Colwell et al 2007a). Chicks in Humboldt County, California almost always reacted to the approach of an avian predator by crouching regardless of size (Colwell et al. 2007a). If chicks crouch, adults respond to intruders by calling (see Sounds: vocalizations), sometimes while flying back and forth. In urgent situations, adults use distraction displays running in a crouched posture away from intruder. While running, adults may also depress their tails to ground, spread their rectrices, or flap their wings to feign injury. Sometimes they pause and lie flat on ground while continuing to flap their wings, or draw their wings in and crouch. This "broody" behavior frequently attracts other plovers which stand or run around near intruder.

◂ Sounds Breeding ▸

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Snowy Plover

Charadrius alexandrinus

Order CHARADRIIFORMES– Family CHARADRIIDAE

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Breeding

Phenology

Pair Formation

Varies geographically. In Puerto Rico, paired by Jan, when birds begin nesting (Lee 1989). Pairs observed in coastal Florida in Jan (Chase and Gore 1989). In coastal California, as early as mid-Feb; at Monterey Bay, CA, average pairing dates: 10 Mar for resident females (*n*= 6), 19 Mar for migrant females (*n*= 16), 6 Mar for resident males (*n*= 13), and 3 Apr for migrant males (*n*= 15) (JSW and JCW). Pairs observed scraping or scrapes found in coastal Orange and San Diego counties, CA as early as 20 Jan in 2008 (P. Knapp and E. Copper pers. comm.). In coastal Washington, pairs also reported by early Mar (Widrig 1980). Pairing is undoubtedly latest in northern Great Basin and Great Plains where spring arrival does not begin until late Mar or early Apr (Boyd 1972, Page et al. 1983, Hill 1985, Paton 1995).

Nest-Building

Since scraping is integral to courtship (see Behavior: sexual behavior) and nest construction (see Nest, below), timing of nest-building coincides with courtship.

First Brood Per Season

Figure 6. Nesting chronology varies geographically. Egg-laying begins in Jan in Puerto Rico (Lee 1989), about the second week of Mar in

Enlarge

Figure 6. Annual cycle of breeding, migration and molt of the Snowy Plover.

Enlarge

Adult female Snowy Plover on nest, Lido Key, FL, April

coastal Florida (Himes et al. 2006), by the last week of February in coastal Texas (Zdravkovic and Hecter 2004), and the first or second week of March on the U.S. Pacific coast. Unusually early nest initiation dates are 17 Feb 2002 in Florida (Himes et al. 2006), 23 Feb 2009 in coastal Orange Co., CA (P. Knapp pers. comm.), and 13 and 17 Feb 2008 in San Diego Co., CA (E. Copper pers. comm.); during a 5-yr study, the earliest nest in San Diego Co. was on 10 Mar and most nests were initiated from early Apr through mid Jun (Powell et al. 2002).

At Monterey Bay, CA, date of first egg in first clutches spanned a 24-day period from 5-28 Mar (median 15 Mar, *n*= 21 years) (LES). Egg laying also commences in Mar in coastal Humboldt Co., CA, where it occurs earlier on beaches than on river bars (Colwell et al. 2005), and as early as mid-Mar in coastal Oregon (Wilson-Jacobs and Meslow 1984). In deserts of s. California, clutches may be initiated by the first week of Mar (GWP), but in the Great Basin not until about third week of Apr at Mono Lake, CA (Page et al. 1983), or second week of Apr at Great Salt Lake, UT (Paton 1995). In the southern Great Basin, at Owens Lake, CA, nests are initiated as early as mid-March. After regions of the lake-bed were shallowly flooded for dust control, the onset of the nesting season did not change but the nesting season was extended with a higher proportion of nests initiated after the fourth week of May and in July (Ruhlen et al. 2006).

At Cheyenne Bottoms, KS, earliest egg on 22 Apr but most clutches not initiated until Jun (Boyd 1972), whereas commencement of laying at Great Salt Plains, OK, which is dependant on degree of habitat flooding, has varied annually from last week of Apr to mid-May (Hill 1985, pers. comm.). In the Playa Lakes Region of Texas clutches may be initiated as early as 7 April but most eggs are laid in May and June (Conway et al. 2005).

Second Brood Per Season

On the central California coast, where both sexes may double brood and females sometimes triple brood, females initiate second clutches as early as 26 Apr (median 18 May, *n*= 82) after successful hatch of first clutches, but not until 17 May (median 1 Jun, *n*= 33) if a replacement clutch was


Enlarge
Adult female Snowy Plover, with chick; Lido Key, FL, May.


Enlarge
Adult male Snowy Plover roosting, Little Estero Lagoon, Ft. Myers Beach, FL, December


Enlarge
Snowy Plover nest on unused heli pad. Los Angeles, CA. June.

necessary for first brood of chicks. Corresponding dates for males were 15 May (median 6 Jun, *n*= 56) when first clutches hatched and 14 Jun (median 1 Jul, *n*= 13) when a replacement clutch was necessary (JSW and JCW).

Third Brood Per Season

On the central California coast, third broods of females initiated as early as 4 Jun (median 25 Jun, *n*= 19) after successful hatching of 2 previous clutches. After successfully hatching 2 clutches, no males initiated a third (JSW and JCW).

Over most of species' range clutches are seldom initiated after mid-Jul (Boyd 1972, Page et al. 1983, Wilson-Jacobs and Meslow 1984, Hill 1985, Warriner et al. 1986, Lee 1989, Paton 1995), although in Florida egg-laying may extend up to the beginning of Sep in some years (Chase 1991). During 21 yr at Monterey Bay, CA, the last nest was initiated over the 12-day period from 10-21 July (median 15 July) (GWP). An unusually late initiation date for a nest was 24 Jul in San Diego County, CA (Powell 2001).

Nest Site

Selection Process

During courtship males usually make multiple scrapes, sometimes in widely separate territories; mean number per territory was 5.6 ±3.7 SD (range 1–15, *n*= 16) in coastal California (JSW and JCW). The scrape selected for most copulations, probably through female consent, typically becomes the nest site.

Microhabitat

See also Habitat. A ground-nesting species. Nests often located with respect to some conspicuous feature in fairly barren landscapes; e.g., near a piece of kelp, driftwood, clam shell, cow dropping, tumbleweed, or small growing plant (Boyd 1972, Purdue 1976a, Hill 1985, Page et al. 1985, Stern et al. 1990, Paton 1994a, J. Erbes in litt.); on small rises (Chase and Gore 1989, L. Hill pers. comm.), on small low dunes (J. Erbes in litt.); or in an area of peculiar substrate such as a patch of broken shell or glass (L. Hill pers. comm., GWP). Nests


Enlarge
Snowy Plover nest on beach, Los Angeles, CA. June


Enlarge
Adult female Snowy Plover brooding on nest, Longbeach, CA. May


Enlarge
Newly hatched Snowy Plover, with unhatched egg. Los Angeles, CA. July.

may be located under overhanging boards, branches, tufa, or live and dead plants, especially where there are high levels of avian clutch predation (Page et al. 1985, GWP).

In coastal Oregon, Snowy Plover nests were located in areas with significantly greater cover of driftwood and vegetation within 20 m of nests than at randomly selected beach sites (Wilson-Jacobs and Meslow 1984). Compared with random sites, Snowy Plovers in coastal San Diego Co. nested more by objects, in areas with more vegetation cover in beach and fill habitats, and in areas with more debris cover in beach and salt pan habitats (Powell 2001). In coastal Florida, 85 nests were all on beach slopes of less than 3° (J. Gore pers. comm.).

Enlarge

Snowy Plover nest.

Enlarge

Snowy Plover eggs.

Site Characteristics

Snowy Plover nests on San Diego Co., CA, beaches were closer to water (53.5 m ± 2.4 SE) than those on fill (87.9 m ± 9.4 SE) (Powell 2001). In se. Colorado, nesting areas characterized by significantly lesser amounts of grass, litter and vegetation within 10 cm of the ground than Killdeer nests (Mabee and Estelle 2000). At the Salt Plains, OK, Snowy Plovers nest along seasonally ephemeral streams and are often found in lines of driftwood and other debris created by flooding of the creeks (Winton et al. 2000). At Owens Lake, CA nests were scattered on open dry alkaline flats but 105 of 164 were near distinctive features such as dry washes, sparse patches of salt grass, rocks, woody debris, unimproved roadways or vehicle tracks. Nests averaged 379 m ± 38 SE (*n*= 98) from water before areas of the lakebed were shallowly flooded to reduce dust emissions. Afterwards, many nests were located within the flooded areas and averaged only 8 m ± 1 SE (*n*= 89) from water; in areas of the lakebed that were not flooded nests averaged 425 m ± 72 SE (*n*= 28) from water (Ruhlen et al. 2006).

Nest

Construction Process

Male constructs nest depression in the ground by sitting and leaning forward on his breast and scratching with his feet while rotating his body. He can construct it in minutes. Nest lining is accumulated by males and females standing near scrape, picking up bits of debris in their bills, and tossing them backward over their shoulders or along side in one fluid motion toward scrape. While incubating, males and females pick up the debris in their bills and drop it in scrape. This activity commences prior to egg laying and continues through incubation period (Boyd 1972, JSW and JCW). In windy locations, scrapes frequently must be dug out again after being filled with blowing sand. On hard substrates birds rely on existing depressions (e.g., human or coyote footprints in dried mud) for their nest cups (L. Hill pers. comm., GWP).

Structure And Composition Matter

A natural or scraped depression on dry ground usually lined with 2- to 10-mm-long pebbles, shell fragments, fish bones, mud chips, vegetation fragments, or invertebrate skeletons. Linings are typically <10 mm thick, but JSW and JCW found 5 nests with a 20-

mm-thick lining of *Salicornia* sp. elevating the eggs above wet mud in coastal salt ponds. Substrate on which nest are placed includes sandy beaches, cobble river bars, dried mud, crushed gravel road beds, shell mounds, and rarely, a depression in a log or on cracked asphalt on air fields (see Habitat for details).

Dimensions

At 174 Great Salt Lake, UT nests (PWCP), long diameter averaged 7.2 cm ± 1.5 SD (range 5.0–12.5), short diameter 6.8 cm ± 1.3 SD (range 4.5–12.0), and depth 1.4 cm ± 0.7.SD (range 0.5–3.0). Largest nests were found in old scrapes of larger shorebirds. Boyd (1972) reports 7–9 cm diameter and 1.0–2.5 cm depth for Kansas nests.

Microclimate

Although nests are often located near objects, these are usually too small to offer protection from weather (Purdue 1976b). Partial burial of eggs in nest lining in hot environments does not appear to have any thermoregulatory function for eggs (Grant 1982) but may help prevent them from blowing away in windy weather (R. Boyd pers. comm.).

Maintenance Or Reuse Of Nests, Alternate Nests

Snowy Plover nests are reused rarely and the wind typically destroys nest depressions on sandy beaches within days of hatching. Exact nest sites are sometimes used in consecutive years (PWCP, JSW and JCW). At a saline lake in Spain, Kentish Plovers occasionally deposited eggs in the scrapes of other females within 2 d after hatching or depredation of the original occupant's eggs; 6% of 316 clutches involved utilization of existing nest scrapes (Fraga and Amat 1996).

Snowy Plovers continue to line their nests during incubation. When the lining was either experimentally increased or decreased, Kentish Plovers restored the original amount of material within 24 h at nests at Tuzla, Turkey. Neither incubation behavior nor internal egg temperature differed between experimental and control nests. It is speculated that the parents may balance the benefits of nest material for anti-predator and egg insulation functions against its potential for overheating eggs (Szentirmai and Székely 2002).

Nonbreeding Nests

Multiple scrapes are typically constructed for courtship before one is chosen for egg-laying.

Eggs

Shape

Oval to pyriform.

Size

For Snowy Plovers, based on 261 eggs from three-egg clutches of 87 females on the central California coast, mean length = 31.3 mm ± 1.0 SD (range 27.6–33.8) and width 22.7 mm ± 0.6 SD (range 21.0–24.2) (JSW and JCW). Roughly similar size in Kansas (Boyd 1972) and Oklahoma (Hill 1985).

For Kentish Plovers: on Hungarian grasslands, mean length = 32.0 mm ± 1.0 SD and width = 23.1 mm ± 0.4 SD (*n*= 64), and in Hungarian fish ponds mean length = 31.7 mm ± 1.3 SD (*n*= 31) and width = 23.1 mm ± 0.4 SD (Székely 1992); on Portuguese beaches mean length = 32.48 mm ± 1.19 SD, width = 23.27 ± 0.68 SD, and volume = 8.96 cm3 ±

0.64 SD, and on Portuguese salt flats, mean length = 32.47 mm ± 1.46 SD, width = 23.20 mm ± 0.56 SD, and volume = 8.91 cm3 ± 0.68 SD (Norte and Ramos 2004); and at a saline lake in Spain, mean length = 31.99 mm ± 0.11 SD (*n*= 751), width = 23.34 mm ± 0.06 SD, and volume = 8.96 cm3 ± 0.65 SD (Fraga and Amat 1996).

Egg size may vary seasonally. The average volume of Kentish Plover clutches increased with season at a saline lake in Spain (Fraga and Amat 1996) but there was no significant relationship between laying date and intra-clutch egg-size symmetry (Amat et al. 2001b). The length, width and volume of eggs in late clutches were smaller than earlier ones on a Portuguese beach (Norte and Ramos 2004). Within a Kentish Plover clutch, the second egg is reported to be typically larger than the other two in first clutches of the season (Amat et al. 2001b).

Egg size may vary with female size. The average clutch volume of Kentish Plovers increased with female size (based on culmen, tarsus, and wing length) at a saline lake in Spain (Amat et al. 2001a). Here, there was no difference in mean egg volume, or intra-clutch egg-size symmetry, between a female's first and second clutches but there was a significant positive relationship between the mean egg volume of the second clutch and the interval between successive nests (Amat et al. 2001b); egg size was also positively related with female body condition, and was highly repeatable among clutches of females within and between years (Amat et al 2001a).

Mass

For Snowy Plovers, average fresh weight of 216 eggs from 72 females at Monterey Bay, CA was 8.5 g ± 0.5 SD (range 6.7–9.8); this was about 20% of weight of female, with 80.3% of variance attributable to interclutch and 19.7% to intraclutch variation (JSW and JCW). Egg mass for Kentish Plovers is reported as 8.9 g ± 0.5 SD (*n*= 28) at a saline grassland and 8.4 g ± 0.4 SD (*n*= 5) at fish ponds in Hungary (Székely 1992). Egg weight depends on stage of incubation; in Spain incubated eggs lost an average of 0.0474 g per day (Fraga and Amat 1996).

Color

Buffy to sandy background, lightly to moderately covered with small spots and scrawls, mostly dark brown to black, but also (in small proportion) gray. Spotting density increases toward larger end.

Surface Texture

Smooth and nonglossy.

Eggshell Thickness

Averaged 0.157 mm ± 0.008 SD (*n*= 6) in eggs from Salton Sea, CA in mid-1970s (Grant 1982). Morrison and Kiff (1979) found no evidence of eggshell thinning between pre- and post-DDT-period eggs from California.

Clutch Size

Usual clutch is 3 eggs (range 2–6) in Snowy and Kentish plovers. Unusually large clutches of 5-6 eggs may be the product of two females laying in the same scrape (Warriner et al. 1986, Fraga and Amat 1996). Single-egg clutches are almost always deserted (Warriner et al.1986, Fraga and Amat 1996). In Kentish Plover in Spain, mean clutch size, which was greater in first nests (2.9 ± 0.3 SD) than in replacement nests (2.8 ± 0.5 SD) (Amat et al. 1999b), generally declined over the breeding season (Fraga and Amat 1996). Kentish Plover clutches experimentally enlarged to 4 eggs took longer to incubate and showed

lower rates of embryonic development than three-egg clutches (Székely et al. 1994). See also Demography And Populations: measures of breeding activity.

Egg-Laying

Snowy Plovers lay eggs during all hours of day and at night. In coastal California, the second egg of Snowy Plovers is more likely to be laid at night than first or third; intervals between eggs ranged from 46.5 to 118.0 h and averaged 61.6 h ± 11.9 SD (*n*= 8) between eggs 1 and 2 and 55.4 h ± 9.1 SD (*n*= 17) between eggs 2 and 3 (Warriner et al. 1986, JSW and JCW).

On California coast, Snowy Plover females spent 14–87 min (median 28 min, *n*= 32) sitting on the nest before laying an egg. Just before laying they often appeared restless and sometimes their wings quivered slightly 6–8 min before egg emerged. When some stood, contractions of lower abdomen could be seen while birds slowly raised and lowered their tails. If they were sitting on the nest, females depressed their tails on the edge of the nest as the egg emerged (JSW and JCW).

During egg-laying, adult Snowy Plovers may be absent from territories for more than a third of daylight hours (Warriner et al. 1986). Activities of adults in territory during egg-laying include sitting on partial clutches, territory and mate defense, feeding, preening, bathing, standing, sitting, and sleeping.

Interval between clutch loss and initiation of a replacement clutch by the same pair of Snowy Plovers averaged 7 d (range 6-8) in 12 of 13 instances from 1977-1982 at Monterey Bay, CA (Warriner et al. 1986). At the same location, from 1984-2001, the median and modal number of days until the first egg in the replacement clutch was 7 d (minimum 4 days) in 18 cases for which the exact date of clutch loss was known. Fourteen of the 18 nests were 8 or fewer days and the remainder were 22-44 d -- which could reflect missed clutches (LES). A new clutch may be initiated as few as 2–4 d after destruction of one that is incomplete (Warriner et al. 1986, M. Stern pers. comm.). For Kentish Plovers, 7-9 d elapse between the loss of a nest and the initiation of a new one (Székely and Lessells 1993, Amat et al. 1999b).

Intraspecific egg dumping is unusual in Snowy Plovers. Three clutches of 5–6 eggs reported from California coast probably represent cases of 2 females laying in the same scrape (Warriner et al. 1986). At Monterey Bay, CA, a pair of uniquely banded plovers had a nest with non-viable eggs that was incubated long past the projected hatch date. This same pair eventually initiated a new clutch of 2 eggs in the same nest, bringing the total to five eggs. The two eggs were clearly distinct from the first set of eggs which were “worn” and dirty in appearance (D. George in litt).

Instances of two females laying in the same scrape have also been reported for the Kentish Plover (Fraga and Amat 1996) and are indicated by DNA fingerprinting of eggs in Spain (Küpper et al. 2004). In s. Spain, 9 of 883 clutches contained eggs of more than one female: 3 six-egg nests, 1 five-egg nest, 3 four-egg nests, 1 three-egg nest, and 1 two-egg nest. In two of the six-egg nests, eggs of a second female were deposited after the three-egg nest of the original occupants had been deserted and both six-egg nests were eventually abandoned. In the other six-egg nest (which was eventually depredated), two females laid on alternate days. Two females laid eggs simultaneously in the five-egg nest which was deserted before incubation. All the remaining nests were incubated by one pair and 2 of the four-egg nests and the three-egg nest were successful (Amat 1998).

Mixed species clutches have has also been recorded in the Snowy Plover. Two Snowy Plover chicks and 1 Killdeer chick hatched from a three-egg clutch incubated by a Snowy Plover, but the fate of the chicks was undetermined (Agee 1997). At Oceano Dunes, San Luis Obispo Co., CA, in 2004, D. George (in litt.) observed a Least Tern incubating a 1-egg clutch. Subsequently, a pair of Snowy Plovers initiated a nest 18 inches from the tern nest and the plover sometimes left its nest to chase the Least Tern from its nest. The terns abandoned their nest and the plover(s) rolled the tern egg into their 3-egg nest and incubated all 4 eggs (eggs readily identifiable as 3 plover and 1 tern) for many days until all eggs were depredated by a coyote.

Incubation

Onset Of Broodiness And Incubation In Relation To Laying

Both sexes of the Snowy Plover intermittently sit on or stand over incomplete clutches; at 10 territories on central California coast, males averaged 16.6% ± 9.5 SD and females 10.3% ± 8.5 SD of daylight hours on incomplete clutches (Warriner et al. 1986). Sustained incubation typically begins when last egg is laid, although in rare instances up to 2 d elapse before it begins.

Incubation Patch

Both sexes have a single abdominal incubation patch.

Incubation Period

Varies with location and season. For Snowy Plovers on the California coast: mean = 27.4 d ± 1.5 SD, (range 26–32, *n*= 57) with average of 28.4 d compared to 26.9 d for early- versus late-season nests in the Monterey Bay area and up to 40 d when only one parent incubated (JCW, Warriner et al. 1986); an average of 28 d (range 26-33) and decreasing as the season progresses on the northern California coast where one nest incubated by a single parent took 38 d to hatch (Hoffmann 2005).

Great Basin, CA: mean = 26.9 d ± 2.5 SD, (range = 25–32, *n*= 9) with average of 28.8 d for 4 early-season nests and 25.4 d for 5 late-season nests (Page et al. 1979). Great Plains: in Kansas, mean = 25.5 d (range 24–26, *n*= 8; Boyd 1972); in Oklahoma, range 23–28 d (Hill 1985); and Florida: range 25–27 d (*n*= 30; Chase and Gore 1989). Two chicks hatched 49 d after incubation commenced at a s. California nest in 2003 (C. Sandoval in litt.).

For Kentish Plovers, the following incubation periods reported: mean = 27.2 (range 25-29, *n*= 6) in southern Spain (Fraga and Amat 1996); about 25 d at Tuzla, Turkey (Szentirmai et al. 2001).

Parental Behavior

In coastal California, the female Snowy Plover incubates during most of day and the male most of night (Warriner et al. 1986). In this cool climate, incubating adults sit on eggs, standing periodically to change position or rotate eggs. In hotter climates, birds frequently stand over eggs or sit on them after wetting their belly feathers in nearby water; both actions presumably prevent eggs from overheating (Boyd 1972, Purdue 1976a, Grant 1982). At Cheyenne Bottoms, KS, females incubate during most of day (Boyd 1972). At Great Salt Lake, UT, they tend to incubate in morning, whereas males often incubate in mid-afternoon and late evening; incubation bouts last 2-5 h during cool weather but as few as 10–15 min during hot weather (Paton 1995). At Great Salt Plains, parental shifts were in order of 8–16 h at temperatures <30°C compared to <1 h at temperatures ≥41°C

(Purdue 1976b). Nest relief is often accompanied by debris tossing or head bowing by one or both adults (Boyd 1972, JSW and JCW).

At 8 territories on central California coast, Snowy Plover males averaged 9.5% ± 9.3 SD and females 79.7% ± 9.6 SD of daylight hours incubating completed clutches (Warriner et al. 1986). In coastal Humboldt Co., CA, daytime nest attentiveness for female Snowy Plovers averaged 91% ± 17 SD; females incubated 31-100% of the time and averaged 1.4 ± 1.4 SD recesses per hour; recess duration averaged 2.1 min ± 4.1 SD; of the recesses, 20% were unrelated to any apparent cause, 48% were caused by potential egg predators, 11% by humans, and 18% were considered caused by unknown disturbances (Hoffmann 2005).

Daytime incubation by females and nighttime incubation by males also characterizes the incubation pattern of the Kentish Plover (Fraga and Amat 1996, Szentirmai et al 2001, Kosztolányi and Székely 2002). Females relieve their incubating mate at dawn when the ambient temperature is low (Szentirmai et al 2001). In southern Spain, probability of diurnal incubation by the male increased with ambient temperature in exposed nests but not at shaded ones; thermoregulatory behavior used by birds incubating in the open to dissipate heat includes gaping, panting, standing, ptiloerection, wing dropping and belly soaking; birds incubating in shade did not exhibit any of these thermoregulatory behaviors (Amat and Masero 2004); male incubation time increased as the season progressed and became hotter (Fraga and Amat 1996). In Hungary, during daylight, both sexes combined spent 91.7% ± 2.1 SE in 1991 and 96.4% ± 1.6 SE in 1992 of the time incubating; female share was 73.0% ± 12.2 SE and 71.5 ± 12.9 SE, respectively (Székely et al. 1994a). At Tuzla Turkey, females spent 11.3 h per day incubating compared to 9.4 h by males; male incubation bouts averaged 50.2 min (range 29.1-188.7) and female's 75.3 min (range 30.2-231.0) (Kosztolányi and Székely 2002). After experimental removal of one incubating parent from nests in Turkey, single-parent clutches were incubated less during daytime than control nests with two parents; after mate removal, males spent more time incubating and female incubation time did not change; although males spent more time incubating during daytime after mate removal, the increase was not sufficient to make up for the prior contribution of their mates (Kosztolányi et al. 2003).

Following the death or desertion of their mate, the remaining Snowy or Kentish plover parent usually deserts the clutch; however, some birds of both sexes incubate alone especially if they lose their mate late in the incubation period (Warriner et al. 1986). Unassisted male Kentish Plovers are reported to incubate alone up to 13 d and females up to 9 d (Kosztolányi et al. 2003).

Hypotheses for the diurnal pattern of incubation of Kentish and Snowy plovers include: the need for females to forage at night to recover an energy deficit from egg laying; the need for males to spend daylight hours defending nest territories from conspecifics; an advantage from the less brightly colored female being less visible to daytime predators; and, possibly, a greater ability of males to detect and distract nocturnal nest predators (Kostolányi and Székely 2002).

Hardiness Of Eggs

Temperature of attended Snowy Plover eggs fluctuates with ambient air temperature; eggs are probably less resistant to overheating than to cooling (Purdue 1976a, Grant 1982). In Kentish Plover the temperature of eggs is also strongly affected by ambient temperature; thus egg temperature differs between morning and afternoon (Szentirmai and Székely 2002).

Hatching

Preliminary Events And Vocalizations

Fine cracks appear at large end of Snowy Plover eggs up to 8 d before hatching; chicks are easily heard tapping against shell 3–4 d before hatching, and peeping 1–2 d before hatching (JSW and JCW). There is considerable calling back and forth between the chick and the adult a day or more before hatching (J. Erbes in litt.).

Shell-Breaking And Emergence

Distinct hole usually is not present >4 h before chick emergence (Boyd 1972). Snowy Plover eggs hatch at any time of day and at night. Interval between first and third egg was 1–33 h (*n*= 28) at closely monitored California nests; 43% hatched in <6 h (Warriner et al. 1986). Average interval for 3 eggs was 14 h at 7 Kansas nests; no relation between laying and hatching order of eggs (Boyd 1972, JSW and JCW). The clutch hatching interval in Kentish Plovers extends up to 72 hrs (Fraga and Amat 1996).

Parental Assistance And Disposal Of Eggshells

Parents run or fly up to a few hundred meters from nest with empty eggshells in their bills before dropping them (Boyd 1972, JSW and JCW). There are usually 1-4 mm eggshell fragments with partly adhering white membranes in the linings of successful nests; their presence is a good way to verify the success of a nest (Mabee 1997).

Young Birds

Condition At Hatching

Precocial; upperparts of Snowy Plovers are pale buff or creamy buff mixed with light gray. Crown, back, rump, and wings distinctly spotted with brown and black; underparts pure white. Distinct white band encircles neck, black line extends behind eye (Boyd 1972). Bill black and legs and legs gray to pinkish-gray. Egg tooth lost within 2 d after hatching. Weight at hatching averages 6.1 g (range 4.6–7.6, *n*= 504; JSW and JCW). Legs are close to adult size, but wings (mean length = 10.5 mm, range 9–12, *n*= 4; Boyd 1972), tail (just down), and bill (mean length, from feathers at base to tip of upper mandible = 7.0 mm, range 6.9–7.1, *n*= 3; JSW and JCW) are much smaller than adult size.

Weight at hatching of Kentish Plover chicks in southern Spain averaged 6.33 g ± 0.56 SD (range 5.3 -7.6, *n*= 47) and was 64.0%-73.8% of egg mass (Fraga and Amat 1996); egg mass averaged 5.7 g ± 0.4 SD (*n*= 14) in Hungary (Székely 1990).

At a saline lake in Spain there was a significant positive relationship between Kentish Plover chick mass at hatching and egg volume. Within clutches, heavier chicks hatched from larger eggs, survived better, and recruited into the breeding population in larger numbers than their lighter siblings, but there was no significant relationship between the structural size of chicks and their mass at hatching or between the size of eggs and the sex of chicks. These data suggest chicks from larger eggs may have greater fat reserves than those from smaller ones (Amat et al. 2001 a, b).

Growth And Development

Limited information. In Snowy Plovers, mass increases from average of about 6 g at hatching to 30 g by age of first flight (31 d); wing length increases from about 10 to 85 mm over the same period (Boyd 1972). In California, mass at 4 d is 5.8 g; 8 d, 8.9; 12 d, 11.5; 17 d, 17.5; 20 d, 24.5; 24 d, 25.0; 28 d, 26.4 (*n*= 1 to 4; JSW and JCW). Up to 4 d of age, only obvious development is an increase in body size and first appearance of pin feathers

in primaries. By 7 d, pin feathers are prominent in primaries, secondaries, scapulars, upper back, and along sides; and by 10 d, feathers are breaking from sheathes on crown, scapulars, neck, and sides (Boyd 1972). Juvenal primaries and secondaries are still growing and down is still apparent on head when birds begin flying at about 1 mo of age.

Kentish Plover chicks lost weight during the first 2 d after hatching in Hungary. By the 3rd d weight increased approximately linearly with age and was approximately 2.83 + 1.15 age (Székely 1990). In Spain, the growth rate of chicks was 0.105 g/d per gram of body mass (Fraga and Amat 1996).

During daytime Snowy Plover young first leave nest 1–3 h after hatching (Boyd 1972), stumbling as they walk and pecking at (and presumably eating) potential food on ground (JSW and JCW). Subsequently they make longer, increasingly frequent foraging trips, up to 100 m from nest. In or out of nest, they flatten themselves on ground when parent signals approach of people or potential predators. Chicks leave nest permanently within hours after last chick hatches. They walk, run, and swim well and forage unassisted by parents, but require periodic brooding for many days after hatching. Undisturbed chicks are either nonvocal or too quiet to be heard at any distance. Frightened chicks peep loudly while running to escape danger. As chicks age they are brooded less and for shorter durations (Colwell et al. 2007a); on the northern California coast chicks <10 d are brooded an average of 58% ± 25% SD of the time and chicks that fledge are brooded less than those that die. Brooding bouts average 4 min. Chicks >10 days old were brooded for 17% ± 24% SD of the time. By 10 days of age there was a 90% chance that chicks approached by humans would run whereas chicks approached by avian predators would crouch regardless of age (Colwell et al. 2007a).

First flight of Snowy Plovers is 28–33 d (mean = 30.9, *n*= 22) after hatching (Warriner et al. 1986). First flight of Kentish Plovers is about 28-30 d of age (Fraga and Amat 1996, Székely and Cuthill 1999).

Parental Care

Snowy Plover adults do not feed their chicks, although they lead them to suitable feeding areas. Adults brood chicks and act as sentinels, warning chicks of approaching predators with alarm calls. They employ distraction displays to confront predators near their broods (see Behavior: predation) and lead larger chicks away from predators. Adults also chase and fight other plovers that come too close to their broods, including pecking chicks of intruding broods (JSW, JSW). Additionally, Kentish Plovers in southern Spain employ aerial pursuits of Gull-billed Terns (*Sterna nilotica*), closely tracking tern maneuvers, making alarm calls, and effectively driving the terns away (Fraga and Amat 1996, Amat et al. 1999c). Similar behavior has not been observed in Snowy Plovers in coastal California where newly established Gull-billed Terns have recently been recorded preying on plover chicks (R. Patton in litt.)

In w. North America, Snowy Plover females generally desert broods by 6 d after hatching, leaving males in sole care of young; males stay with young until they are 29–47 d old (Warriner et al.1986, Paton 1995). In some cases involving a male's desertion or death, the female typically rears young alone (Warriner et. al. 1986). On the Pacific coast, females stay with their mates and broods longer when it is apparently too late to nest again (M. Stern pers. comm., J. Erbes in litt.). Late in the season, when lengthy hatching periods are more common, some females continue to incubate unhatched eggs, while the male attends newly-hatched chick(s) away from nest. Also, the female will sometimes stay

with the younger chick(s), while the male attends older chicks farther from the nest. Usually the brood reunites and one parent eventually abandons it (J. Erbes in litt.).

On Great Plains and Gulf Coast, both sexes often stay with chicks until they fly; if one sex deserts first, it is typically female (Boyd 1972, Chase and Gore 1989, Chase 1991).

Kentish Plover females also desert broods more than males. Of 101 broods in s. Spain, 14% were deserted by males, 84% by females, and 2% were attended by both parents until fledging. There was no difference in age of chicks when males and females deserted but there was a significant difference between years: 21 d in 1994 versus 7 d in 1996; the duration of biparental care seemed to be directly related to predation pressure by Gull-billed Terns (Amat et al. 1999c). In Hungary, females deserted broods when chicks averaged 6 d of age but timing was highly variable and unrelated to the mass or condition of females; 6% of females stayed with the brood, 27% deserted at hatching, and the rest deserted between hatching and fledging; females stayed longer with late broods (Székely and Williams 1994).

One parent has been removed from Kentish Plover broods to experimentally compare the brood-rearing ability of single birds versus pairs, and males versus females. At Algarve, Portugal, chicks tended by males survived longer than those reared by females (Székely 1996); at Tuzla Turkey, chick survival was lower in broods attended by one than by two parents at one site but not at another (Székely and Cuthill 1999); while single males spent more time brooding their young than males with mates, females displayed a similar tendency at only one of two sites. There were no sexual differences in time spent brooding, adult alert times, or time spent defending young from conspecifics in single-parent broods. It is hypothesized that biparental care may be more successful whenever mortality of young is high from predation or infanticide (Székely and Cuthill 1999).

Kentish Plover broods were experimentally increased and decreased at Tuzla, Turkey to compare the ability of plovers to raise broods of different size (Székely and Cuthill 2000); all young fledged in only 1 of 6 five-chick broods, only 1 of 8 four-chick broods, 4 of 8 two-chick broods, and 7 of 8 one-chick broods. Growth of chicks was not affected by brood size.

Cooperative Breeding

Rare observations of larger-than-normal Snowy Plover clutches with 2 females in attendance (Warriner et al. 1986) indicate that 2 females may rarely lay in same nest. Chick adoption occurs infrequently, usually when 1 parent with chicks cares for ≥1 chicks from another's brood (Warriner et al. 1986, Himes et al. 2006, M. Stern pers. comm.). Chick adoption has been observed to be initiated after two adults with broods fight for a long period of time, ultimately separating with one chick mixed into the other's brood. This can result in four-chick broods or chicks exchanged into each brood (D. George in litt.). In one atypical case, a banded male deserted his first (ever) clutch before hatching and cared for 1 chick from a neighboring male's brood for about 3 wk until the chick fledged (JSW and JCW).

Brood Parasitism

Rare instances of 4-6 egg clutches attended by one female may represent brood parasitism. See Behavior: egg laying.

Immature Stage

No information.

Behavior | Demography and Populations

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Snowy Plover

Charadrius alexandrinus
Order CHARADRIIFORMES– Family CHARADRIIDAE

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Demography and Populations

Measures Of Breeding Activity

Age At First Breeding; Intervals Between Breeding

Most Snowy and Kentish plover young breed the first nesting season following birth (Warriner et al. 1986, Sandercock et al. 2005). At Monterey Bay, CA, the median age that first-time female breeders initiated first clutches was 309 days (*n*= 50, range 252-388) and males 307 days (*n*= 53, range 257-416) from 1984-2004. The median clutch initiation dates were 12 April (range 13 March-30 May, interquartile range 7-24 April) for females and 1 May (range 27 March-11 June, interquartile range 24 April-19 May) for males (LES). Although nearly all Snowy Plovers breed annually, one exception is a 10-year old male banded as a chick at Monterey Bay in 1998: although he was not monitored sufficiently to determine if he bred in 1999 and 2000, he was not known to nest in 8 subsequent years when he was closely monitored (LES).

Clutch

Mean clutch size for 171 central California coastal nests: 2.95 ± 0.25 SD (range 2–4; Warriner et al. 1986); for southern California coastal nests: 2.84 ± 0.04 SE (Powell and Collier 2000); for 125 interior California nests: 2.92 ± 0.27 SD (range 2–3; Page et al. 1979); for 70 interior Oregon and Nevada nests: 2.93 ± 0.31 SD (range 2–4; Herman et al. 1988); for 448 Great Salt Lake, UT, nests: 2.96 ± 0.12 SD (range 2–5; Paton 1995); for 41 Kansas nests: 2.78 ± 0.42 SD (range 2–3; Boyd 1972); for 512 Oklahoma nests: 2.86 (range 2–3; Hill 1985); for Playa Lakes, Texas nests: 2.71 and 2.48 in 1998 and 1999, respectively (Conway et al. 2005); and for 20 Puerto Rico nests: 2.7 (Lee 1989).

Number of clutches annually is dependent on length of breeding season, rates of polygamy, and rates of clutch loss. In coastal California, up to 6 nests per season for plovers with high levels of clutch loss, whereas completely successful males and females had up to 2 and 3 clutches, respectively (JSW and JCW). In Florida, both sexes also initiate multiple clutches (R. Pruner in litt.). On the Great Plains, successful birds of either sex are reported to have only 1 clutch/season (Boyd 1972). At the Playa Lakes region, TX, 5 males and 1 female hatched two clutches/season (Conway et al. 2005).

Annual And Lifetime Reproductive Success

Observed clutch hatching rates from locations where conservation efforts were not being employed to increase clutch hatching success vary widely from 12.5–86.8% in 20 studies (Appendix 1). Observed rates (mean = 47.4%, range 3.3–69) average 1.63 (range 1.03–2.50) times higher than rates calculated from Mayfield's (1961) method (mean = 33.8 ± 20.0 SD, range 5.4–67) in 14 samples from 4 studies (Page et al. 1983, Hill 1985, Lee 1989, Paton 1995). Additional Mayfield estimates of annual clutch-hatching success include: 54% for 5 years combined in San Diego Co., CA (Powell et al. 2002), 53% on river gravel bars and 40% (*n*= 4 years) on neighboring beaches in Humboldt Co., CA (Colwell et al. 2005), and 57% in 2006 on the Florida coast (Himes et al. 2006). Hood and Dinsmore (2007b) recommend using the nest survival model in program MARK for calculating clutch survival because it provides for fitting complex models that can reveal seasonal variation and the effect of habitat variables at multiple scales.

A variety of factors are reported to influence clutch hatching rate. At Batiquitos Lagoon, San Diego County, CA, nest success peaked the first year after habitat restoration, then declined; this suggests high productivity may temporarily occur at newly-created sites, possibly because predators fail to cue into the presence of potential prey immediately (Powell and Collier 2000). Also in San Diego Co., the probability of nest success decreased as distance from Least Tern nests increased (Powell 2001). In se. Colorado, no significant relationship was apparent between nest fate and structural habitat variables at either the nest or at the 5 m scale (Mabee and Estelle 2000). In coastal Texas, daily nest survival declined slightly over the breeding season and was a function of both location and the daily age of the nest. Nests at inland lakes had lower daily survival than those at coastal sites. Nests with an object or debris in the immediate vicinity had higher daily survival than those that did not (Hood and Dinsmore 2007b). At Mono Lake, CA, nests next to objects were more likely to fail than nests under objects or in the open, possibly because predators there used objects as part of their search image (Page et al. 1985).

There is considerable annual and spatial variation in chick survival. Proportion of broods producing at least 1 flying young averaged 61% ± 10.9 SD (range 48–71%) in 4 studies (Page et al. 1979, Hutchinson et al. 1987, Wehtje and Baron 1993, M. Stern unpubl. data). Number of flying young/successful brood (producing at least 1 flying young) averaged 1.6 ± 0.21 SD, range 1.4–1.9) in 4 studies (Page et al. 1983, Wehtje and Baron 1993, Paton 1995, M. Stern unpubl. data). Proportion of chicks reaching flying stage averaged 0.39–0.43 at the Pajaro River mouth in Monterey Bay, CA, from 1977-1982 (Warriner et al. 1986). Chick fledging rate throughout the Monterey Bay area averaged 0.382 ± 0.014 SE (range 0.285-0.483) with a third of 2813 clutches producing ≥1 fledglings from 1984-1999 (Stenzel et al. 2007). At Point Reyes, CA, 0.46 of 83 chicks fledged in 1999-2000 (Ruhlen et al 2003). During a 4-year period in Humboldt Co., CA, 0.60 of the chicks fledged on river bars compared to only 0.29 on beaches; males were twice as productive on river bars (1.5 fledglings/male ± 1.4 SD) as on beaches (0.8 fledglings/male ± 1.0 SD); and chick survival increased seasonally (Colwell et al. 2005). Number of young reaching flying age was 0.8–0.9 per female at a central coastal California site (Warriner et al. 1986), averaged 0.35 ± 0.12 SD (*n*= 5 years) per female and 0.28 ± 0.10 SD per male in s. coastal California from 1994-1998 (Powell et al. 2002), and 0.5 per female at 1 interior California location (Page et al. 1983); rate at the interior site increased to 0.7 per female when only females making all of the season's nesting attempts at the study site were considered (Page et al. 1983).

Most chick loss occurs during the first 2 weeks after hatch (Warriner et. al 1986). At Point

Reyes, Marin County, CA, 88.9% and 80.5% of chicks disappeared before 14 days of age in 1999 and 2000, respectively (Ruhlen et al. 2003). At the same location from 2003-2008, on average 88% ± 7.9 SD (range 75-94%, *n*= 6 years) of the chicks were lost when they were 1-10 days old (Peterlein 2008); of chicks that did not fledge during the 6 years, 43.5% disappeared during daytime, 19.5% overnight, and 37.0% at an unknown time with respect to darkness (C. Peterlein in litt.).

Number Of Broods Normally Reared Per Season

Only 1/yr on Great Plains. More than 1 brood in Florida (R. Pruner in litt.) and probably coastal Texas. Rates of single, double, and triple brooding for birds present all breeding season at Monterey Bay, CA, were: females 40–44%, 54–60%, and 0–3%, respectively; and males 59–63%, 38–41%, and 0%, respectively, during 2 yr when no attempt was made to protect nests from predators. After erecting exclosures around most nests to protect them from predators for 1 yr, rates of single, double, and triple brooding were: females 17%, 67%, and 17%, respectively; males 54%, 46%, and 0%, respectively (JSW and JCW).

Life Span And Survivorship

A male, at least 15 yr old when last seen, is oldest known Snowy Plover (JSW and JCW). Most individuals do not approach this age; Paton (1994b) estimated a mean life span of 2.7 years for adults.

Apparent annual adult survival for Snowy Plovers ranged from 0.578 to 0.880 over 4 yr at Great Salt Lake, UT (Paton 1994b). Apparent survival was 64% for males and 57% for females (best-fitting model included sex dependence in survival) on the n. California coast; the difference may be attributed to greater mortality of females or greater breeding site fidelity of males (Mullin 2006).

Apparent survival of Kentish Plovers in the Netherlands was 0.65 ± 0.072 SE for males and 0.61 ± 0.060 SE for females in the first year after banding; for females it was 0.73 ± 0.170 SE in the second year after banding and 0.91 ± 0.085 SE for all years combined except the first year after banding (Foppen et al. 2006). At Tuzla, Turkey the best estimate of apparent adult survival was 0.64 with little difference between males and females (Sandercock et al. 2005).

For Snowy Plovers, mean survival rate from hatching to beginning of first breeding season was 0.179 ± 0.010 SE for chicks banded from 1984-1999 at Monterey Bay, CA (Stenzel et al. 2007) and 0.09 ± 0.01 SE for Kentish Plovers hatchlings at Tuzla Turkey (Sandercock et al. 2005).

Survival of Snowy Plover juveniles from 28 days of age to the beginning of their first breeding season averaged 0.463 ± 0.018 SE (annual range 0.283 ± 0.028 to 0.575 ± 0.061) for juveniles fledging from 1984 to 1999 on the central California coast (Stenzel et al. 2007). Apparent survival was 30% for juveniles on the northern California coast (Mullin 2006). For Kentish Plovers, apparent survival rate of juveniles in the Netherlands was 0.28 ± 0.072 SE (Foopen et al. 2006) and 0.15 ± 0.01 SE at Tuzla Lake, Turkey (Sandercock et al. 2005).

Disease And Body Parasites

Diseases

Adults susceptible to botulism in w. North America (Alcorn 1942, D. Gutherie upubl. data).

On the California coast, a Snowy Plover found lying in the wet sand with its wings partially spread and appearing to be uncoordinated was diagnosed as probably having avian tuberculosis (R. Orr in litt). In 2005, >30 adult Snowy Plovers in San Diego County, CA died from an unknown cause characterized by the plovers' inability to stand and maintain balance (B. Foster in litt).

Body Parasites

Feather lice can be found on many adults handled for banding on the Pacific coast (J. Erbes and D. George in litt.). A necropsy of an adult female Snowy Plover found dead at Oceano Dunes, San Luis Obispo County, CA, in 2006 did not identify a cause of death but did note that trematodes were established in the intestinal tract (D. George in litt.).

Causes Of Mortality

Eggs

Mainly predators (see Behavior: predation); strong winds causing dispersal or burial of eggs in sand (Stein 1993, Colwell et al. 2005); high tides (Warriner et al. 1986, Chase and Gore 1989); rain/hail (Boyd 1972, Hill 1985, Paton 1995, Koenen et al 1996a, Winton et al. 2000); parental desertion (JSW, JCW); and crushing by people, vehicles, or pets (Warriner et al. 1986, Chase and Gore 1989, Colwell et al. 2005). Eggs with well developed embryos are occasionally deserted by the parents because their hatching is delayed by more than 48 h from the rest of the brood (GWP, Fraga and Amat 1996).

Along the Pacific coast, Common Ravens, American Crows, coyote, feral red fox, and striped skunk are the most important predators of Snowy Plover eggs. Roosting flocks of gulls, terns and pelicans trample some nests (GWP). Drifting sand during high winds and tidal over wash also cause some clutch failures (Powell and Collier 2000, Neuman et al. 2004, Colwell et al. 2005, Lafferty et al. 2006).

At inland playa lakes, the main predators of eggs appear to be coyote, striped skunk, Common Raven, California Gull, and Ring-billed Gull. Rain and hail can cause considerable nest loss (Boyd 1972, Page et al. 1993, Koenen et al. 1996a, Winton et al. 2000). At Salt Plains NWR, OK, 8-9 cm of rain on 16 June 1996 destroyed 44 of 109 nests in one day (Winton et al. 2000). Also at Salt Plains NWR, numbers of Ring-billed Gulls have increased in recent years; their predation of Snowy Plover nests was first noted in 1993 and is expected to increase as gull numbers increase (Winton et al. 2000). At the Playa Lakes region of Texas, 44% of 185 failed nests were flooded by rain or destroyed by hail and 28% depredated -- most likely by mammals (Conway et al. 2005).

Chicks

Mainly predators (see Behavior: predation), separation from parent (Warriner et al. 1986), birth deformity (JSW and JCW), failure to break out of egg (JSW and JCW), drowning in high tides (JSW and JCW), trampling by horses (Lee 1989) or people (GWP, Colwell et al. 2005), people preventing adults from brooding chicks (Colwell et al. 2005), killed by unleashed dog (Lafferty et al. 2006), crushed by vehicles (P. Persons pers. comm.), blown away by strong winds (Lafferty et al. 2006), sticking to a tar ball (Lafferty et al. 2006), disease, entanglement in vegetation, death of attending parent, exposure after illness of adult (D. George in litt.), and being pecked to death by an adult defending a neighboring brood (Fraga and Amat 1996, Székely and Cuthill 1999).

Adults

Predators (see Behavior: predation), bouts of cold winter weather (Stenzel et al. 2007),

disease, hail (Boyd 1972, Grover and Knopf 1982, Hill 1985), being run over crossing highways (D. George in litt.), being run over while incubating nests on beach (JSW and JCW), being struck by off-road vehicles (R. Glick, in litt.), becoming entangled in fishing line (JSW and JCW), becoming entangled in the net top of a nest exclosure (D. George in litt.), colliding with objects (M. Parker pers. comm.), and shooting (GWP).

Range

Initial Dispersal From Natal Site

Some young from Monterey Bay, CA, do not disperse but become year-round residents; others disperse as early as 1 mo after first flight to wintering areas as far south as San Carlos, Baja Sur, and as far north as Bandon, OR. Some return to Monterey Bay to breed, whereas others nest elsewhere along Pacific Coast from Silver Strand, San Diego CA, to Damon Point, WA (LES). One young female from Monterey Bay, CA moved inland to breed at Mono Lake, CA (Warriner et al. 1986). Two other females and 1 male were seen during summer in e. Oregon without evidence of breeding; the male was not present inland long enough for a nesting attempt (LES). Another male from the Monterey Bay area was observed once on 30 June 2008 at Great Salt Lake, UT (J. Cavitt in litt.).

Female Snowy Plovers are slightly more likely than males to winter in their Monterey Bay, CA natal area but males are more likely to nest there. From 1984 to 1999, an estimated 38.0% of juvenile males and 39.9% of females wintered then bred in the Monterey Bay area; 36.4% of the males and 19.5 % of the females wintered away and then bred at Monterey Bay; 6.3% of the males and 13.7% of the females wintered in the Monterey Bay area but nested elsewhere; and 19.3% of the males and 26.8 % of the females wintered and nested elsewhere (Stenzel et al. 2007). The estimated natal philopatry rate to the Monterey Bay area is 59% for females and 74% for males. The mean distance between the natal site and site of first breeding is greater for females (median 6.9 km, maximum 790 km, *n*= 238) than for males (median 4.2 km, maximum 360 km, *n*= 259). Overall, 64% of natal dispersal distances are <10 km and only 16% > 50 km. Among local recruiters, 35% of females and 27% of males breed within 1 km and 73% of females and 76% of males within 10 km of natal sites (Stenzel et al. 2007).

Of 432 banded Snowy Plover chicks, 14.4% returned to their natal area on the northern California coast; males tended to be more philopatric than females; 69.4% of the philopatric plovers bred in their natal habitats; those hatching from late nests were more likely to be year-round residents than those from early nests. Philopatric Snowy Plover males nested 18.2 km ± 33.6 SD and females 16.0 ± 29.2 SD from natal nests; the two furthest dispersal distances of females were 354 and 474 km (Colwell et al. 2007b).

The resighting rate of juvenile Snowy Plovers at natal areas the year following marking was 19% in San Diego County, CA, with males twice as likely to return as females (Powell and Collier 2000) and 14.6% at Lake Abert, OR (Stern et al. 1990). Return rate of juveniles estimated from survival analysis was 21.3% at Great Salt Lake (Paton 1994b).

In Kentish Plovers, only 4% of juveniles were recaptured on study site nests one or more years after their natal year at Tuzla Lake, Turkey; there was no evidence of a sexual difference in return rates (Sandercock et al. 2005). Juvenile return rate was 13% to a breeding area in the Netherlands (Foppen et al. 2006). Of 84 Kentish Plover chicks banded in Spain, 8.3% returned and bred the following year at their natal site (Fraga and Amat 1996).

Fidelity To Breeding Site And Winter Home Range

Adult Snowy Plovers show a high degree of breeding-site fidelity but also disperse among breeding sites both within and between years (Paton 1994a, Stenzel et al. 1994). Adult resighting rates at breeding sites between consecutive years: Monterey Bay, CA: males 76.8%, females 65.8% (Warriner et al. 1986); San Diego County CA: males 72% and females 62% (Powell and Collier 2000); Mono Lake, CA: males 77.8%, females 44.9% (Page et al. 1983); Lake Abert, OR: males 64.1%, females 40.9% (Stern et al. 1990). Lower female rates are due partly to sexual differences in detection rates (Warriner et al. 1986) and dispersal rates (Stenzel et al. 1994).

Adult Kentish Plovers also exhibit a high degree of fidelity to breeding areas. Return rates were at least 54.9% for males and 40.3% for females in s. Spain (Fraga and Amat 1996) and 41% for males and 39% for females at Tuzla, Turkey (Sandercock et al. 2005). For Kentish Plover, there was no evidence that polygamous individuals had lower return rates than monogamous individuals in Spain (Amat et al. 1999b).

Snowy Plovers also exhibit strong site fidelity to wintering areas; about two-thirds of males, females, and immatures from Lake Abert, OR, that were located on their coastal California or Baja California wintering areas were present for 2 consecutive yr, and about one-third for at least 3 yr (Page et al. 1995).

Dispersal From Breeding Site Or Colony

About 50% of adult females and 25% of adult males nesting at Monterey Bay, CA, disperse to other breeding sites at least once during their lifetime; dispersal distances range from 50 to 1,140 km. Dispersal to alternate nesting areas for partial breeding seasons is far more common than for entire seasons by regular nesters at Monterey Bay. Migratory birds are more likely than residents to make these long-distance, breeding-dispersal movements; no relationship between breeding success at Monterey Bay and long-distance breeding dispersal. Individual males and females on California coast moved up to 840 km and 660 km, respectively, for successive nesting attempts within 1 nesting season (Stenzel et al. 1994). See Behavior: spacing: territoriality.

Home Range

Variable with stage of nesting cycle. Males feed up to 4 km from their nests at Mono Lake, CA, and up to 8 km at Monterey Bay, CA (JSW and JCW). Adults with broods found up to 3.2 km from their nests at Lake Abert, OR, and Cheyenne Bottoms, KS (Boyd 1972, Stern et. al. 1990); up to 5 km at Morro Bay, CA (Hutchinson et al. 1987); up to 6 km as early as 2 d after hatching at Mono Lake, CA (GWP); and up to 7 km at Monterey Bay (JSW and JCW). At Great Salt Plains, OK, home range size of radio-tagged Snowy Plovers averaged 917 ha ± 623.7 (n= 14) and did not differ between sexes; birds that lost broods had the largest ranges (L. Hill unpubl. data). Individuals move up to 50 km between sites during winter on California coast.

Population Status

Numbers

Breeding: Information (much of it dated) suggests a breeding population of about 18,000 Snowy Plovers for the Gulf of Mexico coast, the interior of the US, and the Pacific coast of the U.S. and Baja, California, Mexico combined. (Appendix 2). A USFWS survey of Snowy Plovers in the U.S. and Mexico during the summers of 2007 and 2008 should soon be available to provide a more current estimate of the size of the North American breeding population.

Counts of plovers during the breeding season tend to underestimate the number of individuals present. At Mono Lake, CA, sightings of color marked birds on censuses, indicated on average 1.90 marked males and 2.95 females were present in the area for each one seen on a survey (Warriner et al. 1986). In the lower Laguna Madre region of Texas, Hood and Dinsmore (2007a) estimated a survey detection probability of 0.58 ± 0.04 SD and extrapolated a population of 416 plovers using an occupancy abundance estimation technique. Concurrently, Zdravkovic (2004) counted 456 plovers in the same area.

Winter: On the U.S. Pacific Coast there were an estimated 4,000 wintering plovers in the early 1980's (Page et al. 1986) and 355-499 inland in s. California during the winters of 1993-94 and 1994-95; most of the interior birds were at the Salton Sea and in agricultural waste water ponds in the San Joaquin Valley (Shuford et al. 1995). Counts on the California coast each winter from 2003-04 to 2008-09 averaged 3708 ± 548 SD plovers; the number along the Pacific coast of the U.S. averaged 3849 ± 532 SD during the same period (GWP, USFWS unpubl. data). An estimated 1605 wintering Snowy Plovers are reported for the west coast of Baja, California, Mexico from shorebird surveys conducted in the early 1990's (Page et al. 1997).

Along the Gulf of Mexico coast 1191 birds were tallied in Laguna Madre region of Tamaulipas Mexico on a 1997 survey (Mabee et al. 2001). A 2000-01 survey of the U.S. Gulf coast tallied the following winter numbers: Texas 690, Louisiana 36, Mississippi 13, Alabama 0, and Florida 311; also 16 birds were found in Cuba and 17 in Puerto Rico (Elliott-Smith et al. 2004). In 2002, state-wide winter surveys produced counts of 252-305 individuals in Florida (Doonan et al. 2006).

Trends

The breeding population has likely decreased on the Gulf Coast since the late 1800s owing to habitat alteration and increased recreational use of beaches (Chase and Gore 1989, T. Eubanks pers comm.). The number of pairs along the Florida coast was estimated as 167 in 1989, 213 in 2002, and 222 in 2006, suggesting a fairly stable population during the past 2 decades (Himes et al. 2006). There are no studies of recent trends for the coast of Texas (Hood and Dinsmore 2007a). On the Great Plains, numbers along the Cimmarron River in sw. Kansas and nw. Oklahoma have decreased since the mid-1980s owing to loss of river flow (R. Boyd pers. comm.). A historic population decline is indicated along the Pacific coast by the large number of pre-1970 breeding locations that were inactive by 1980 (see Distribution: historical changes). For California, Oregon, Washington, and Nevada combined, there was an approximate 20% decline in size of the breeding population on surveys between the late 1970s and late 1980s (Page et al. 1991).

For coastal Washington, Oregon and California combined, total adult plovers on coordinated breeding-season counts rose from 1,493 in 2002 to 2,017 in 2004 and subsequently declined to 1,537 and 1,541 in 2007 and 2008, respectively (GWP, USFWS). In California, coast-wide breeding season surveys in 1977-80 totaled 1,593 adult plovers. Follow up surveys in 1989 and 1991 produced 1,371-1,376 plovers. Only 976 plovers were tallied on a 2000 count. Between 2002-2004 numbers increased from 1,387-1,904 adults, then declined to 1,680-1,719 in 2005-2006, and decreased further to 1,362-1,394 birds in 2007-2008 (GWP).

Inland, at Owens Lake, CA, there was a steep decline on breeding season counts from 499 adult plovers in 1978 to 198 in 1988. Nine counts from 1990-2001 averaged 138 ± 11

SE adults (range= 101-203). After introduction of shallow-water flooding for dust control in 2002, numbers increased annually to a peak of 658 adults in 2004 (Ruhlen et al. 2006). From 2005-08, breeding season counts averaged 502 ± 75.6 SD (range 421-602, *n*= 4) (GWP). At Mono Lake CA, 240 km north of Owens Lake, a decline is apparent from surveys locating 384 adults in 1978, 342 in 1988, 119 in 2001, 98 in 2002, and 71 in 2007 (Ruhlen et al. 2006, GWP).

Population Regulation

Page et al. (1983) suggest that density-dependent rates of clutch destruction by predators could be a factor limiting population size. Reduction in the amount of suitable breeding habitat, particularly along the U.S. Pacific and Gulf coasts, has undoubtedly been responsible for a reduction in size of the breeding population since the late 1800s.

◂ Breeding Conservation and Management ▸

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Snowy Plover

Charadrius alexandrinus
Order CHARADRIIFORMES– Family CHARADRIIDAE

Issue No. 154 – Revised: November 18, 2009
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Revisors: Page, Gary W., and Lynne E. Stenzel

Conservation and Management

Effects Of Human Activity

Shooting And Trapping

Isolated incidents of Snowy Plovers being shot on California coast (GWP) probably have not had any significant impact on this population.

Pesticides And Other Contaminants/Toxics

At agricultural waste-water ponds in the San Joaquin Valley, CA, where selenium causes embryonic deformities in Black-necked Stilts and Killdeers, deformities were not unusually high in Snowy Plovers, suggesting selenium is not as toxic to this species as to some other shorebirds (J. Skorupa pers. comm.).

At Point Reyes Beach, Marin County, CA an unusually high proportion of clutches that failed to hatch contained high levels of mercury (Schwarzbach et al. 2005). A sample of eggs from the southern California coast in San Diego County were analyzed for a wide variety of organic and inorganic contaminants in the early 1990s and none were found in sufficient concentrations to be a cause for concern (Hothem and Powell 2000).

On the Pacific coast, Snowy Plovers are often oiled during spills. Many appear to pick up the oil on their feet and transfer it to their plumage (GWP). In one well documented spill, M/V New Carrissa, at least 45 plovers on the Oregon coast


Enlarge
Volunteer monitoring threatened Snowy Plovers in key nesting habitat, coastal California; July.


Enlarge
Color-banded Snowy Plover, Sanibel Is., FL, February

were oiled (Magnam et al. 2001).

Collisions With Stationary/Moving Structure Or Objects

Although Snowy Plovers have been killed in San Francisco and Monterey bays by collisions with wire fencing erected to protect nests from predators, numbers have been too small to significantly impact populations (M. Parker pers. comm., GWP). Plovers have also been injured and killed by colliding and sometimes entangling in the net tops of exclosures erected to protect their nests (D. George in litt.). These sources of mortality should be considered in plans promoting fencing or exclosures to protect plover nests.

Enlarge
Snowy Plover resting in beach tire tracks; Los Angeles, CA. October.

Fishing Nets And Line

Snowy Plovers have been snared by discarded monofilament fishing line on the California coast (JSW and JCW). This may cause loss of toes or feet or even death of the adult. Effect of this source of mortality on populations is unknown.

Enlarge
Sign protecting Snowy Plover nesting habitat; Half Moon Bay, CA. May.

Degradation Of Habitat: Breeding And Wintering

On U.S. coasts, habitat degradation, caused primarily by expanding beach-front development and recreation, has likely been responsible for a significant decline in the size of breeding populations. Use of the exotic beach grass (*Ammophila arenaria*) to stabilize dunes along Pacific Coast has also reduced the extent of open nesting habitat (Page and Stenzel 1981, Wilson-Jacobs and Meslow 1984). Frequent mechanical raking of beaches for removal of garbage, kelp, and other debris on the s. California coast makes beaches unsuitable for nesting and probably harms food resources for wintering plovers (Page et al. 1986). Dugan et al. (2003) report that over 160 km of southern California sandy beaches are groomed regularly and that grooming decreases the species richness, abundance, and biomass of wrack-associated invertebrates that are likely important plover prey resources.

On the U.S. Pacific coast, small numbers of plovers with foot injuries have been found with fine synthetic fibers, or human hair, wrapped around a foot causing swelling and sometimes loss of toes (D. George in litt.).

In the Great Basin, at Farmington Bay, Great Salt Lake, UT, between 2003 and 2008, stands of the exotic common reed (*Phragmites australis*) expanded from 25 to 130 ha eliminating extensive open areas previously used by nesting by Snowy Plovers (J. Cavitt in litt.).

On Great Plains, breeding habitat has contracted at Great Salt Plains, OK, where half the salt flat has been flooded for water impoundments and exotic salt cedar (*Tamarix gallica*) has invaded a significant amount of remaining stream-side habitat (Hill 1993). At Salt Plains NWR, OK invasive salt cedar decreased the extent of alkaline flat by >240 ha from 1941-1989 and with water impoundments has likely resulted in a Snowy Plover population decline (Koenen et al. 1996a). The salt cedar also provides cover for predators, such as coyotes, which prey on plover eggs and chicks (Winton et al. 2000). Elsewhere in Kansas and Oklahoma, breeding habitat along rivers is degraded by damming, water withdrawals, and vegetation encroachment (L. Hill pers. comm.). In the Playa Lakes region of Texas, a decrease in the volume of springs from pumping of the Ogallala aquifer and sedimentation from agriculture has a potentially negative impact on plover nesting (Conway et al. 2005).

Disturbance At Nest, Roosts And Feeding Sites

Incubating birds often run from their nests at approach of people or pets; such disturbances may result in increased clutch losses to blowing sand on windy days (Warriner et al. 1986). Humans and dogs also disturb roosting birds on heavily used recreational beaches. At Coal Oil Point, Santa Barbara County, CA, disturbance to wintering plovers was 16 times greater at a public than a protected beach. On average, each plover was disturbed once every 27 min on weekends and every 43 min on weekdays on the public beach. Feeding rates decreased with human activity. Plovers were more likely to fly from dogs, horses or crows than from humans. They reacted to disturbance at 40 m but relatively few people and dogs beyond 30 m disturbed them. At all distances, dogs had a higher probability of disturbing plovers than humans; plovers reacted at about twice the distance to dogs as to people (Lafferty 2001).

Human/Research Impacts

On the central California coast, nests are destroyed by people stepping on them, deliberately taking eggs, trampling eggs while riding horses, crushing eggs (and occasionally incubating adults) with vehicles, and causing abandonment by camping next to nests overnight (D. George pers. comm., JSW and JCW). Also, on the northern California coast, humans have stepped on nests, driven over nests, vandalized exclosures erected to protect nests, and kept adults from brooding chicks (Colwell et al 2005). People were responsible for destruction of at least 14% of 189 nests over 6 yr at 1 coastal California site (Warriner et al. 1986) and 10% of 83 nests in nw. Florida in 1989 (Chase and Gore 1989). At Point Reyes, Marin County, CA, Snowy Plover chick loss was 72% greater than expected on weekends in 1999 and 69% greater in 2000, suggesting increased recreation on weekends negatively affected chick survival (Ruhlen et al. 2003). At Coal Oil Point, CA, one chick was killed by an unleashed dog (Lafferty et al. 2006). At Oceano Dunes State Vehicular Recreation Area, CA, 6 adult Snowy Plovers found dead between 2002 and 2008 were probably killed by being struck by vehicles (R. Glick in litt.). In se. Colorado, cattle trample nests (Mabee and Estelle 2000).

Banding of nesting birds can result in nest desertion and was believed to be responsible for the abandonment of 4 of 187 nests on the California coast (Warriner et al. 1986). Leg injury can be caused by bands that are too small (USFWS size 1B); a special band size (1P) with an internal diameter of 2.85 mm is recommended to minimize chance of leg injury to Snowy Plovers. For Kentish Plovers, injuries caused by mud accumulating between the tibio-tarsus and metal band caused swelling of the leg below the band and resulted in eventual loss of the foot; rate of injury was 1.94% of 412 banded birds. Injuries were eliminated by placing the metal band on the upper leg (Amat 1999). Similar injuries

have been observed in Snowy Plovers in California (GWP).

Introduced and expanding native predator populations, deleterious to Snowy Plover reproductive success, arise directly and indirectly from human activity. Since the late 1800s non-native Red Foxes have been introduced into California by escaping from fur farms and fox hunters, and intentional releases by pet and fur farm owners. Their populations have expanded into the San Francisco Bay, Monterey Bay, and southern coastal regions of California (Lewis et al. 1999). By the mid 1980's they were identified as a major cause of plover nest loss at Monterey Bay (Neuman et al. 2004) where efforts are currently underway to control them (GWP). Invasive red foxes are also predators of nesting Snowy Plovers on the Oregon coast (D. George in litt.).

Common Ravens have recently expanded their range into coastal regions of Monterey, San Luis Obispo and Santa Barbara, counties, CA. They were first reported depredating Snowy Plover nests at Monterey Bay, Oceano Dunes State Vehicular Recreation Area, and Vandenberg Air Force Base between 2001 and 2003 (GWP, D. George pers. comm., N. Francine in litt.). Their arrival is well documented at Monterey Bay where during extensive monitoring from 1983-2008 ravens were not recorded depredating any plover nests until 12 were taken in 2002. Although ravens were responsible for few depredated nests from 2003-2006 they took at least 36 in 2007 and 21 in 2008 (GWP).

Gull-billed Terns, a known predator of Kentish Plover chicks (Fraga and Amat 1996), only began breeding in southern San Diego County, CA in 1986. Their numbers expanded to 24-40 pairs during the 2000s (Molina 2008) and the terns are now a documented predator of Snowy Plover chicks in San Diego Bay (R. Patton in litt.).

At Great Salt Lake UT, success rates of nesting by plovers in some locations are approaching zero because of exploding numbers of raccoons and Red Foxes (J. Cavitt in litt.).

Management

Conservation Status

The population breeding along Pacific Coast of U.S. and Baja California is listed by U.S. Fish and Wildlife Service as Threatened. The species also receives some protection through the following state designations: Washington: Endangered; Oregon: Threatened; California: Species of Special Concern; Mississippi: Endangered; Florida: Threatened; Puerto Rico: Threatened; Kansas: Threatened.

Measures Proposed And Taken

The Pacific Coast population was designated Threatened by the U.S. Fish and Wildlife Service in March 1993; subsequently, critical habitat has been identified and a recovery plan published (USFWS 2007). The plan suggests a recovery target of 3,000 breeding adults for the U.S. Pacific coast and regional targets for six contiguous coastal sub-units between the Canadian and Mexican borders. A population viability analysis indicates 1 fledgling per male per year is necessary for population stability based on adult and juvenile survival rates that might be optimistic (GWP). The recovery plan suggests closing upper beach areas to the public during the nesting season, predator management, and habitat restoration as primary conservation actions. It also calls for and contains protocols for annual range-wide surveys of breeding adults between late May and early June and for wintering plovers in January.

By 2008, many upper beach areas were signed closed and roped off from the public during the nesting season in coastal Washington, Oregon, and in California; habitat restoration, chiefly removal of exotic *Ammophila arenaria* to open up nesting habitat, was being pursued; and fencing of selected individual nests as a protection against predators, and/or removal of nest predators was employed at some locations (Colwell et al. 2008, Lauten et al. 2008, Page et al 2008, Pearson et al. 2008). The range-wide survey of breeding adults had been conducted annually since 2002 and the winter survey since January 2004.

In response to protection of individual nests with fencing, and later removal of feral red foxes and skunks by the U.S. Fish and Wildlife Service to improve adult and chick survival rates in s. Monterey Bay, CA, clutch hatching success increased from 43% ± 12 SD (n= 7) during pre-management years to 68% ±12 SD (n= 9) during the management period; however, chick fledging rates declined simultaneously from 42% ± 6 SD to 30% ± 12 SD, respectively. The result was a similar number of chicks fledged per male between the two periods (0.86 ± 28 SD and 0.81 ± 0.29 SD, respectively). During the management phase the number of desertions accompanied by the apparent death of an adult increased, suggesting exclosures may increase adult mortality rates (Neuman et al. 2004). At Monterey Bay, CA, small skunks are able to squeeze between the 5 cm by 10 cm wire mesh used for nest exclosures (GWP) but their depredation of nests has not been great enough to negate the overall value of exclosures for increasing nesting success. Also, at this location there have been a few instances of Great Horned Owls entering and becoming trapped inside nest exclosures with netting tops (D. George and C. Eyster pers. comm.).

Hatching success of exclosed nests was significantly greater than unexclosed nests on Humboldt County, CA beaches; however, exclosed nests also experienced a significantly higher desertion rate with adult mortality being the suspected cause of some abandonment (Hardy and Colwell 2008). In se. Colorado there was no significant difference in nest survivorship between nests inside and outside nests exclosures because the fencing did not prevent small rodents and snakes from preying on eggs (Mabee and Estelle 2000).

As a result of these studies, it is recommend that nest exclosures be used only sparingly and temporarily (Neuman et al. 2004). Nest exclosures can be a valuable management tool but because they increase the frequency of nest abandonment and the potential for adult depredation, they should be monitored closely (Hardy and Colwell 2008).

In extreme circumstances captive breeding is also a potential tool for increasing populations; young, reared from eggs in captivity and released 41–72 (median 57) days after hatching, have successfully nested in coastal California (Page et al. 1989). At Coal Oil Point, Santa Barbara County, CA, researchers responded to high rates of nest loss from skunks by replacing plover eggs with wooden facsimiles, placing real eggs in incubators until they were ready to hatch, and then returning them to their original nest where they were hatched by the parent birds (C. Sandoval in litt.). Small numbers of chicks or eggs that were separated from their parents are regularly reared at Monterey Bay Aquarium, CA; they are released after they are able to fly and many subsequently nest on the California coast.

It has been suggested that clearing invasive vegetation in different places in different years to create temporary nesting areas may mimic the cyclical nature of plover habitat and release populations from high predation pressure along the Pacific coast (Powell and Collier 2000).

At Coal Oil Point Santa Barbara County, CA fencing a wintering area resulted in a 50% decline in disturbance of birds, a return to nesting after an absence of decades, and increased protection against trampling of eggs by humans; however, docents are necessary during most daylight hours to enforce compliance of the closed area (Lafferty et al. 2006). Modeling suggests that a 400 m stretch of beach with a 30 m buffer and a prohibition against dogs provides the most protection for wintering Snowy Plovers and the least impact to beach recreation (Lafferty 2001).

In Florida, some larger Snowy Plovers nesting areas are currently protected through signing and roping prior to egg laying around the beginning of March (J. Himes in litt.). At other sites nests are signed and roped-off as they are found. Still, there are many miles of beach where nesting occurs, nests are not posted, and human disturbance is an issue (R. Pruner in litt.).

Inland, at Salt Plains NWR in Oklahoma, ridges constructed on playa to prevent nests from flooding and electrical fences erected around nesting areas to reduce mammal predation did not reduce losses to flooding or significantly reduce annual egg depredation (Koenen et al 1996b).

Effectiveness Of Measures: The Species' Response

Along the U.S. Pacific coast an increase in adult numbers on range-wide surveys from 2002-2004 (see Population: trends) may have been the response to protective actions at many coastal sites. However, since then numbers on the range-wide surveys have declined, possibly due to low overwinter survival (GWP). Since initial coast-wide surveys in California from 1977-80, plovers have disappeared as breeders from Del Norte Co. (M. Colwell, pers comm.), and are absent to nearly absent on San Miguel I. where 84 adults were found in July 1979 (Page and Stenzel 1981). In contrast, intensive protective actions have resulted in the recolonization of Coal Oil Point, Santa Barbara County, CA by nesting Snowy Plovers (Lafferty et al. 2006). The size of the breeding population has increased in Oregon (D. Lauten pers. comm.) but the populations in Washington State and in Humboldt County, CA, have recently found to be sinks that rely on immigrants from California and Oregon for sustaining their viability (Colwell et al. 2008, Pearson et al. 2008).

◂ Demography and Populations Appearance ▸

Recommended Citation

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Snowy Plover

Charadrius alexandrinus

Order CHARADRIIFORMES– Family CHARADRIIDAE

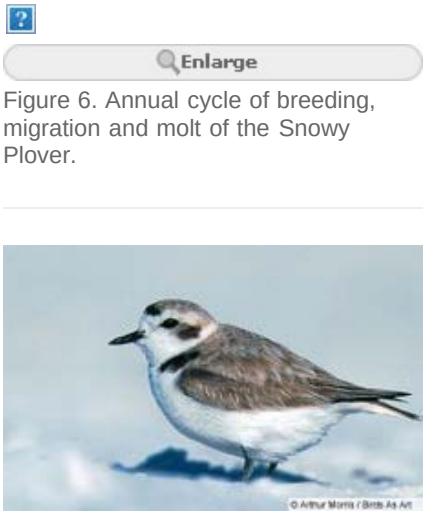
Issue No. 154 – Revised: November 18, 2009

Authors: Page, G. W., J. S. Warriner, J. C. Warriner, and P. W. Paton

Revisors: Pyle, Peter

Appearance

Snowy Plovers have 10 functional primaries, 14-15 secondaries (including 3-4 tertials), and 12 rectrices. Plovers are diastataxic (see Bostwick and Brady 2002) indicating that a secondary has been lost evolutionarily between what we now term s4 and s5. Wings are moderately pointed and tail is short and squared. Geographic variation in appearance moderate worldwide. The following plumage-aspect descriptions pertain to the North American subspecies *C. a. nivosius*; see Systematics: Geographic Variation for variation in up to five other recognized subspecies in South America and Eurasia. No geographic variation in molt strategies reported, except as related to timing of molt in Southern Hemisphere populations, coinciding with opposite day-length regimes.



Enlarge

Figure 6. Annual cycle of breeding, migration and molt of the Snowy Plover.

Enlarge

Adult male Snowy Plover, breeding plumage, Sanibel Is, FL, February

Molts

Molt and plumage terminology follows Humphrey and Parkes (1959) as modified by Howell et al. (2003, 2004). Snowy Plover exhibits a Complex Alternate Strategy (*cf.* Howell et al. 2003), including complete prebasic molts, a partial preformative molt, and limited prealternate molts in both first and definitive cycles (Bent 1929, Palmer 1967a, Oberholser 1974, Prater et al. 1977, Cramp and Simmons 1983, Pyle 2008; Fig. 6). Molts follow a "Northern Hemisphere Strategy" as defined by Pyle (2008). Definitive plumage aspect is often attained following the first prealternate

molt but following the second prebasic molt in less-advanced individuals.

Prejuvenal (First Prebasic) Molt

Complete, May-Jul, at or near natal site. First appearance of pin feathers in primaries by d 4. By d 7, pin feathers are prominent in primaries, secondaries, scapulars, upper back, and along sides; and by d 10, feathers are breaking from sheathes on crown, scapulars, neck, and sides (Boyd 1972). Juvenal primaries and secondaries are still growing and down is still apparent on head when birds begin flying at about 1 mo of age.

Preformative Molt ("First Prebasic Molt" Of Previous Authors)

Partial, Jun-Dec, sometimes extending as late as Mar, primarily on non-breeding grounds. Includes most to all body plumage, usually some proximal secondary coverts, and sometimes 1-3 tertials, but no other wing or tail feathers. Onset is dependent on hatching date. In earliest hatchlings begins by late Jun, in latest hatchlings not until mid-Sep.

First And Definitive Prealternate Molts

Limited, Feb-Apr, primarily on non-breeding grounds. First (Definitive) and subsequent prealternate molts similar in timing and extent although first molt averages less extensive and may also average later in timing. Cramp and Simmons (1983) report that this molt can include most to all body feathers, some secondary coverts, most tertials, and some to all rectrices in European populations, but in North American populations prealternate molts appear limited to head and breast feathers (Pyle 2008). Reports of prealternate molt beginning as early as Oct in California may have been based on males with well-marked basic plumage (see Definitive Basic

Enlarge
Adult female Snowy Plover on nest, Lido Key, FL, April


Enlarge
Juvenile Snowy Plover, Summer Lake, OR, August


Enlarge

Plumage, below).

Definitive Prebasic Molt
Complete, Jul-Nov, primarily on or near breeding grounds but can complete on non-breeding grounds. Primaries replaced distally (p1 to p10), secondaries replaced proximally from s1 and s5 and distally from the tertials, and rectrices probably replaced distally (r1 to r6) on each side of tail, with some variation possible (GWP).

Adult female Snowy Plover, with chick; Lido Key, FL, May.

Newly hatched Snowy Plover, with unhatched egg. Los Angeles, CA. July.

Plumages

Following based primarily on detailed plumage descriptions in Ridgway (1919), Bent (1929), Palmer (1967b), Oberholser (1974), Johnsgard (1981), Cramp and Simmons (1983), Hayman et al. (1986), Rosair and Cottridge (1995), Paulson (1993, 2005), and O'Brien et al. (2006); see Prater et al. (1977) and Pyle (2008) for specific age-related criteria. Sexes show similar aspects in juvenal and formative plumages, slight dimorphism in definitive basic plumage, and moderate dimorphism in alternate plumages.

Natal Down (May-Jul).
Completely covered by down. Upperparts pale buff or creamy buff mixed with light gray. Crown, back, rump, and wings distinctly spotted with brown and black; underparts pure white. Distinct white band encircles neck, black line extends behind eye (Boyd 1972).

Juvenal (First Basic) Plumage (Jun-Aug).
Crown, nape, mantle, rump, ear coverts, and foreneck (patch) drab or light drab with pink-buff edgings on tips of feathers. Forehead, hindneck, and all of underparts white. Inner secondaries mostly white, primaries dusky with white shafts and an increasing amount of white on inner feathers. Up to outermost 3 pairs of rectrices white; remainder progressively darker inwardly, with central pair grayish brown to sepia, sometimes with paler tips.

Formative Plumage (Sep-Mar).
Aspect similar to that of Juvenal Plumage but formative feathers with less-extensive or no pink-buff edging. Contrasts between worn juvenal and fresher formative feathers visible in wing, can be useful in separating first-cycle and definitive-cycle individuals. Primaries and rectrices also average narrower and more worn than in Definitive Basic Plumage.

First Alternate Plumages (Mar-Aug)
Aspect generally similar to Formative Plumage. In males, front part of crown, ear coverts, lores (sometimes), and foreneck black or mixed black and white; remainder of crown and nape orange-buff, often mottled white. In females, front part of crown, ear coverts, foreneck vary from drab to mostly black, except for a few brown feathers; remainder of crown and nape usually drab (occasionally light buff); lores white (GWP). See Definitive Alternate Plumage for further information on sex determination. Duller head plumage along with wing and tail characters described above (Formative Plumage) can be used to separate First from Definitive Alternate plumage aspects.

Definitive Basic Plumage (Sep-Feb)

Aspect similar to that of Formative Plumage but wing feathers uniformly fresh and primaries and rectrices broader. Males often show some dusky or blackish to forehead, auriculars, and/or sides of breast typical of breeding-plumage aspect (see Alternate Plumages). Other males and most females lack any indication of breeding aspect.

Definitive Alternate Plumages (Mar-Sep)

Similar to First Alternate Plumage but males with more extensive and blacker patches in forehead, auriculars, and sides of breast. Females with these areas averaging duskier and often mottled with some blackish feathers. Females show narrower forehead band (typically < 4 mm) than males (typically > 4 mm), with some definitive-alternate females and first-alternate males showing intermediate widths (Pyle 2008). Uniform wing feathers and broader and fresher primaries and rectrices can be used to separate definitive from first alternate individuals.

Individual variation in plumage of Kentish Plovers has been studied in Eurasia. Males with larger breast bands (badges) had earlier nests than those with smaller ones, and males with larger badges also had larger clutch volumes suggesting that badge size might signal male quality and affect either the female's investment in eggs or male success in territorial defense (Lendvai et al. 2004b). However, there was no evidence that birds with artificially enhanced breast bands had improved chances of obtaining a mate for second clutches after experimental removal from initial clutches. Males with enhanced badges spent less times fighting conspecifics than control males (Lendvai et al. 2004a).

Male Kentish Plover have longer flank feathers than females but there was no evidence that inter-male variation in these feathers influenced mating times; enlarged flank feathers may be an adaptation to parental care rather than a sexual ornament (Lendvai et al. 2004a). It has been hypothesized that males have longer flank feathers because they incubate at night when temperatures are cooler than during daytime when females incubate (Kis and Székely 2003).

Bare Parts

Bill

Black.

Iris

Dark brown.

Bare Skin

Eyelids black.

Legs And Feet

Slate gray to black, occasionally dull yellowish or pinkish.

◂ Conservation and Management Measurements ▸

Recommended Citation

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Snowy Plover

Charadrius alexandrinus

Order CHARADRIIFORMES– Family CHARADRIIDAE

Issue No. 154 – Revised: November 18, 2009

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Measurements

Linear

Limited data for Snowy Plovers suggest males might have slightly longer tarsi, tails and wings than females (Appendix 3). Data too limited for comparisons across the species' range. Not included in Appendix 3 are Boyd's (1972) culmen measurements of Snowy Plovers at Cheyenne Bottoms, KS: males, mean = 15.6 mm (range 15–16, *n*= 16); females, mean = 15.1 mm (range 14–16.5, *n*= 30). Kentish Plover have significantly longer tarsi than females (Fraga and Amat 1996, Lendvai et al. 2004a)

Mass

Limited data for Snowy Plovers indicate that average weights of 40-43 g are similar for the sexes (Appendix 3). There are too few data for comparisons across the species' range. No data on seasonal shifts in body mass.

Male Kentish Plovers are reported to weigh more than females in Spain – 43.1 g ± 2.8 SD (*n*= 154) versus 42.2 g ± 3.0 SD (*n*= 158), respectively (Fraga and Amat 1996); there were seasonal differences in weights of males but not females, with male mass decreasing significantly from 46.0 g ± 1.83 SD to 42.0 g ± 3.65 SD (*n*= 4) between first and second nesting polygamous attempts and female's increasing insignificantly from 41.0 g ± 6.56 SD to 47.0 g ± 4.04 SD (*n*= 3). In the Netherlands and France, the body mass of both sexes decreased during the breeding season (Fraga and Amat 1986).

At Tuzla, Turkey, body mass of incubating Kentish Plover females decreased during the day either from fat and or water depletion. Decrease was from 41.8 g (range 41.0-43.5) in morning, to 40.3 g (range 39.8-40.4) at mid day, to 39.8 (range 37.9-40.4) in the afternoon (Szentirmai et al. 2001).

◂ Appearance Priorities for Future Research ▸

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Priorities for Future Research

Owing to continued degradation of this species' habitat, especially in the coastal portion of its breeding range, annual surveys of population size, such as those currently conducted for the U.S Pacific coast, would be desirable for coastal Florida, Texas, West Indies, and Mexico. Obtaining detection rates for plovers would increase the value of all broad-scale breeding and wintering coastal surveys (Elliott-Smith et al. 2004). Study of the migration and winter destinations of Snowy Plovers in the southeast U.S and Mexico are needed to clarify where interior and coastal populations spend the non-breeding season (Himes et al. 2006). For this region, studies are also needed on adult and juvenile survival rates, adult and juvenile dispersal, levels of reproductive success required for population stability, and population sources and sinks. Determination of levels of sequential polygamy in interior and Gulf coast populations would also be valuable for comparison with the Pacific coast population.

Particularly in coastal regions, where recreational use of plover habitat is growing, comprehensive management plans are needed to check the potential for further declines in populations of this vulnerable shorebird. Applied research on methods to restore, enhance, and create suitable habitat across the species' range would also be valuable and should be accompanied by careful study to document the response of plovers to these conservation actions. The limitations, if any, of food availability on breeding success also deserves further study.

For the Pacific coast population, recently published information on adult and juvenile survival and dispersal should be used to revise the USFWS population viability analysis; in particular, a revised estimate of the level of productivity required for population stability is needed. Identification of sources and sinks and causes of winter mortality are two other important research areas to pursue.

◂ Measurements Acknowledgments ▸

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◂ Priorities for Future Research About the Author(s) ▸

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