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DIANE M. TRACY, DOUGLAS SCHAMEL,
AND JAMES DALE

Phalaropus fulicarius

Red Phalarope

FRENCH:
Phalarope roux
SPANISH:
Falaropo rojo

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The Red Phalarope is the most pelagic of the 3 phalarope species, spending up to 11 months each year in marine habitats. Its migratory routes and winter areas are entirely pelagic, in contrast to those of Red-necked (*Phalaropus lobatus*) and Wilson's (*P. wilsonii*) phalaropes, and it generally feeds on smaller invertebrate prey items than the former. Migrants in Alaska feed on crustaceans in mud plumes created by benthic-foraging gray whales (*Eschrichtius robustus*), or near bowhead whales (*Balaena mysticetus*), a habit that prompted European whalers to label Red Phalaropes "bowhead birds" (Nelson 1883) and to use flocks to locate whales.

Like other phalaropes, Red Phalaropes show reversed sexual dimorphism, with females larger and more brightly plumaged than males. The species breeds widely across the Holarctic, overlapping in the southern part of its range with the Red-necked Phalarope, but not with Wilson's. When breeding, it is most common in coastal tundra and is seldom found far inland. Where they overlap, Red and Red-necked phalaropes sometimes feed in the same macrohabitats, although Red Phalaropes often use wading-depth water, while Red-necked Phalaropes feed in swimming-depth water.

The Birds of North America
Life Histories for the 21st Century

Like its congeners, the Red Phalarope is nonterritorial, although disputes are common among females seeking access to mates, especially late in the breeding season. The male

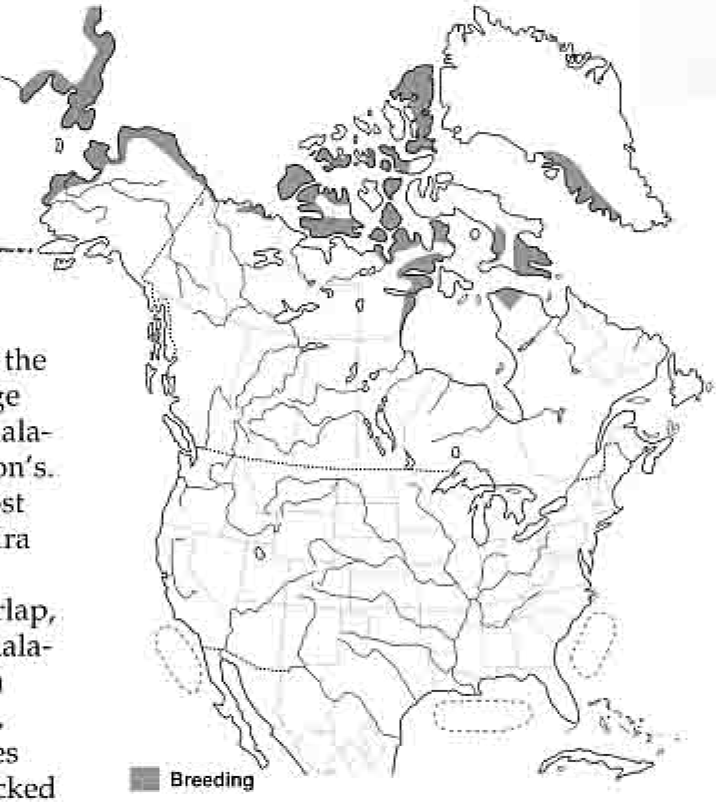

Figure 1.
Distribution of the Red Phalarope in North and Middle America and Greenland. This species also breeds in Europe and Asia and winters locally in the world's tropical and subtropical oceans, mainly in association with oceanic fronts. In North America, Red Phalaropes winter within the areas enclosed by a dashed line. See text for details.

provides all parental care, including incubation and brood-rearing of precocial young. As expected from the sex-role reversal in this species, some females are polyandrous, especially those nesting early.

In general, less is known about the Red Phalarope than other phalaropes because its breeding and wintering areas are more remote. The paucity of long-term studies on the breeding grounds and scant data from migratory and wintering areas make it impossible to disentangle shifting habitat use from long-term population changes. As in the Red-necked Phalarope, some data indicate that El Niño-Southern Oscillation events may be an important influence on population size. There is some indication of population decreases worldwide, especially in the southern part of the range.

Important information on phenology, nesting, productivity, polyandry, paternity, and site fidelity of breeding Red Phalaropes is available from studies in Canada (Mayfield 1978, 1979; Dale et al. 1999) and Alaska (Schamel and Tracy 1977, 1987, 1991). Winter range is delineated for Atlantic (Brown 1980) and Pacific Oceans (DeGraaf and Rappole 1995), and is most often associated with upwellings. Fall staging is described well for northern Alaskan coastal waters (Connors et al. 1979, Johnson and Herter 1989). Southbound migration is summarized for Alaska (Gabrielson and Lincoln 1959) and California (DeSante and Ainley 1980, Briggs et al. 1984). There are no published quantitative food data for breeding Red Phalaropes in North America; the closest study is from Siberia (Kistchinski and Chernov 1973). There are few quantitative studies of food habits at sea, at least with adequate sample size: northern Alaska littoral zone (Johnson 1978, 1979; Connors 1984), northern Alaska Beaufort Sea (Divoky 1984), Bay of Fundy (Canada; Brown and Gaskin 1988), and offshore from California (Briggs et al. 1984).

DISTINGUISHING CHARACTERISTICS

Small (20–22 cm), swimming sandpiper with lobed toes. Differs structurally from other phalaropes by broader bill. Rarely found on land except during coastal breeding and after strong winds. In Alternate (breeding) plumage, larger female more brightly colored than male. Large white cheek-patches and rich chestnut-red underparts and neck are diagnostic. Black crown extends around bill and down chin. Mantle, tertials, and scapulars blackish with bold buff edges, giving streaked appearance. Upper wings gray with bold white wing-bar, under wings and axillaries white. Bill bright yellow with black tip, legs yellowish brown. Plumage of breeding male similar but duller, and with considerably more individual variation. Cap brown with black streaks, white cheek-patch less crisply defined, underparts paler, often with extensive patches of white; bill less yellow. Some of most brightly plumaged males approach female levels of coloration; however, mottled crown diagnostic of male. In Basic (nonbreeding) plumage, sexes alike. Upperparts pale gray, neck and underparts white, crown white with variable amounts of black, and blackish eye-patch present. Bill black, often with yellowish tinge at extreme base; legs gray. In Juvenal plumage, upperparts, hindneck, and crown dark brown, broadly fringed with buff; sides of neck and breast pinkish buff to light brown; underparts white. Bill black; legs gray. Juvenal plumage observed late summer through midfall. Distinguishable from similar Red-necked Phalarope in Juvenal plumage by pinkish-buff, rather than grayish, foreneck. Hatchling differs from Red-necked Phalarope by paler ground color and wings, more white around eye, and more brown mottling to central crown.

Easily identified in Alternate (breeding) plumage. White cheek-patch, broad yellowish bill, and full red underparts distinguishes Red Phalarope from Wilson's and Red-necked phalaropes. In Basic (nonbreeding) and Juvenal plumages, difficult to distinguish Red from Red-necked phalarope (but see Gilligan and Schmidt 1980, Rubega et al. 2000). Shorter, broader bill diagnostic, but also slightly larger size; paler upperparts with no stripes, proportionately larger wings and slower wing-beats. Upperparts similar to Red-necked Phalarope, but Red-necked Phalarope has darker head, less black on nape, broader white fringes on mantle and scapulars (giving upperparts more streaked appearance) and darker gray rump (see Sibley 2000). Red Phalarope best distinguished from nonbreeding Wilson's Phalarope by dark nape, black eye-patch, white wing-bar, and dark central stripe on rump. Because of white wing-bar, may be confused in flight with Sanderling (*Calidris alba*), which has proportionally smaller wings and narrower tail and lacks black eye mark.

Of the 3 phalarope species, Red Phalarope least likely to be observed during winter because it occurs farther out to sea than Red-necked Phalarope, which is more likely to be seen on coastal ponds or estuaries. Wilson's Phalarope not pelagic; found on hypersaline lakes.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. Circumpolar. Primarily coastal tundra, usually north of 60°N. Subarctic

Alaska (Yukon-Kuskokwim Delta) and n. Alaska, then east across parts of n. Canada south to near Churchill, w. Hudson Bay. Some nesting approximately 50 km inland from coast in n. Alaska (Myers 1981), but densities decrease away from coast (Johnson and Herter 1989). Unlike Red-necked Phalarope, does not breed in alpine tundra.

In w. and n. Alaska, coastal breeder from n. Bristol Bay (Gill and Handel 1981) and s. Kuskokwim Delta (Bartonek and Sealy 1979) north to Norton Sound (Shields and Peyton 1978, Kessel 1989), St. Lawrence I. (Fay and Cade 1959, Gill and Handel 1981), Barrow (Schamel and Tracy 1977) and east to Canadian border (Johnson and Herter 1989). Gaps in distribution where coastline lacks marshes. Red Phalarope less common than Red-necked Phalarope in southern part of range and near western Canadian border.

In n. Canadian mainland, breeds along coast of n. Yukon (Birds of Yukon project unpubl.), but apparently absent from Mackenzie Delta (Gratto-Trevor 1996) and Anderson River Delta (Höhn 1959). Increasingly common farther east on Adelaide Peninsula (Macpherson and Manning 1959), Rasmussen Lowlands (McLaren et al. 1977), and nw. Hudson Bay (Brown 1986). Reported breeding on following Canadian arctic islands: Banks I. (Manning et al. 1956), Victoria I., Jenny Lind I., Bathurst I., Baffin I. (Meltofte 1985), Prince Wales I. (Manning and Macpherson 1961), Creswell Bay, Somerset I. (Alliston et al. 1976), and Prince Charles I. (Morrison 1997). Smaller numbers breeding on Ellesmere I. and Devon I., probably due to limited habitat (Pattie 1977, Meltofte 1985). Uncommon breeder on Bylot I. and adjacent sections of Baffin I. (LePage et al. 1998) and s. Hudson Bay; not found in James Bay.

Winter range. Figure 1. Range poorly delineated. At sea, predictably found along ocean fronts, associated with zooplankton concentrations, primarily in tropical and subtropical waters. Use of fronts during winter summarized by Brown and Gaskin (1988). In e. Pacific, major concentrations along offshore edge of Humboldt Current, off Peru and Chile (Meinertzhagen 1925, Alexander 1928, Murphy 1936, Brown and Gaskin 1988). Especially common offshore from Mollendo, s. Peru (Plenge et al. 1989), and greatly outnumbers Red-necked Phalarope 80–160 km offshore from Chile (DeGraaf and Rappole 1995). Some birds probably winter farther north along edge of California Current, from San Francisco south along Baja (Dawson 1923; Briggs et al. 1978, 1984; Tyler 1978). Common to frequent in small groups from s. Baja south to Costa Rica, including Cocos I. (Stiles and Skutch 1989). Uncommon, but regular in winter 8 km offshore of Colombia (DeGraaf and Rappole 1995).

Small numbers (0.3 birds/km^2) may overwinter in North-central Pacific, primarily at Subarctic Front (Gould and Piatt 1993). No evidence that Red Phalaropes overwinter in polynyas in Arctic (Gilchrist and Robertson 2000).

In w. Atlantic Ocean, some evidence that thousands of Red Phalaropes may overwinter at edge of Gulf Stream offshore from s. North Carolina to Florida (Haney and McGillivary 1985). Some historic records of regular wintering in n. Gulf of Mexico (Weston 1953), but less evidence in recent times (Haney 1985b).

Generally found farther out to sea than Red-necked Phalarope. Some evidence that Red Phalaropes most common where copepod species small, Red-necked Phalaropes most common where copepod species larger (Brown and Gaskin 1988). No latitudinal segregation of sexes on wintering range detected (Myers 1981). Alaskan and e. Siberian populations probably overwinter in Pacific off South America; w. Siberian, European, and Canadian populations probably overwinter in Atlantic, mostly off w. Africa (Brown and Gaskin 1988).

OUTSIDE THE AMERICAS

Breeding range. Circumpolar, coastal; sw. Greenland, n. Iceland, Bear I., Svalbard, Novaya Zemlya, coastal areas above 66°N in w. Siberia and 62°N in e. Siberia (Cramp and Simmons 1983). Very common breeding species in Lena (Gilg et al. 2000) and Indigirka deltas (Pearce et al. 1998), e. Siberia. Does not nest in continental Europe. Much of nesting range very remote; distribution known only generally.

Winter range. Most common in e. Atlantic Ocean, 150–300 km offshore from w. Africa. Abundant off Western Sahara to Ghana, associated with Canary Current (Bannerman and Bannerman 1968, Brown 1979) and s. Guinea Current (Taning 1933, Stanford 1953). Also off sw. Africa, associated with Benguela Current (Brown 1979, Cadée 1981). Peru, California, Guinea, and Canary Currents all have similar wind-driven upwellings (Brown 1980). Small numbers seen off n. Morocco in midwinter (Qninba et al. 1998). Most wintering phalaropes in Arabian Sea probably Red-necked Phalaropes (Alexander 1928, Bailey 1966), although some simultaneous sightings there (Meinertzhagen 1937).

Accidental in New Zealand (Brown and Latham 1978), Philippines (Wischusen et al. 1984), Japan (Kazama and Higuma 1975), and Antarctic (Risebrough et al. 1976).

HISTORICAL CHANGES

Recent surveys, 1994–1995, found 76% decrease in breeding populations in Rasmussen Lowlands, e. Canada, compared to 1975–1976 (Gratto-Trevor et al. 1998). In late 1950s, none found nesting in

Anderson River delta, n.-central Canada (Höhn 1959), where they were reported as common nesting birds in 1864–1865 (MacFarlane 1891). Decline in breeding birds at Cape Espenberg, w. Alaska, perhaps related to increased predation by arctic (*Alopex lagopus*) and red (*Vulpes vulpes*) foxes and jaegers (*Stercorarius* sp.; Schamel et al. 1999). Evidence of decreased abundance in Iceland, in southern part of breeding range (Whitfield 1995).

FOSSIL HISTORY

No fossil record known (Olsen 1985).

SYSTEMATICS

First described as *Tringa fulicaria* by Linnaeus in 1758. Later placed in genus *Phalaropus*, then considered monotypic genus. All 3 species of phalarope were at one time placed in separate genera; now classified together in genus *Phalaropus*, subfamily Phalaropodinae.

GEOGRAPHIC VARIATION; SUBSPECIES

No recognized subspecies. Birds on Spitsbergen once classified as *P. f. jourdaini* (Jourdain 1936).

RELATED SPECIES

Two related species. Wilson's Phalarope breeds on North American Great Plains; winters in saline lakes in highlands of central Andes (Colwell and Jehl 1994). Red-necked Phalarope breeds in circumpolar coastal and alpine tundra, sympatric in southern part of Red Phalarope range. Some overlap on migration and during winter (Rubega et al. 2000).

Red Phalarope more closely related to Red-necked than to Wilson's phalarope; latter may have diverged early in the lineage (Dittman et al. 1989, Dittman and Zink 1991). Based on morphometric data, phalaropes once thought near Recurvirostridae (Larson 1955), then tringine sandpipers (Jehl 1968, Strauch 1978). Early genetic analysis placed them closer to scolopacine sandpipers (Dittman et al. 1989); more recent DNA analysis suggests affinities to both tringine and scolopacine sandpipers (Dittman and Zink 1991). Additional work needed to clarify discrepancies.

MIGRATION

NATURE OF MIGRATION

Long-distance migrant between arctic breeding grounds and south temperate and subtropical/tropical oceans. Migration completely over open ocean. Southward migration more protracted than northward migration.

TIMING AND ROUTES OF MIGRATION

Northward migration. Red Phalaropes wintering off west coast of South America migrate north well offshore, where observations few. Migrate north off west coasts of South America, Central America, and North America as far as s. British Columbia. May travel straight from Pacific Northwest and British Columbia, over North Pacific (perhaps along Subarctic Front, between 37° and 41°N; Day 1992) to n.-central Gulf of Alaska or Aleutian Is.; observed off California to s. British Columbia, but not British Columbia's Georgia Strait or north coast, or se. Alaska (Gould et al. 1982, Campbell et al. 1990); many spring sightings Alaska Peninsula/Aleutian Is. (Gabrielson and Lincoln 1959, Gould et al. 1982). Then concentrate in ice leads near Bering Sea islands, w. Alaska (Fay and Cade 1959, Johnson 1976, Hunt et al. 1978, Divoky 1979, Haney and Stone 1988), northbound through Bering Strait and into Chukchi and Beaufort seas. Annually, in late Apr–early May, a flaw lead between free-floating ice and shorefast ice opens from e. Bering Sea through Chukchi Sea to Point Barrow; lead used by seabirds during migration (Woodby and Divoky 1981). Congregate in leads in sea ice while waiting for nesting habitat to become snow/ice-free (Bailey 1925, Divoky 1979). Some overland migrants at Anaktuvuk Pass (Irving 1960) and Umiat (Kessel and Cade 1958), n. Alaska. Some Red Phalaropes may complete migration overland (Divoky 1984), perhaps because of ice conditions in Beaufort Sea (see also Richardson and Johnson 1981, Woodby and Divoky 1981). Males and females migrate in mixed flocks. Females arrive slightly before males (Sutton 1932, Kistchinski 1975, Mayfield 1978) or simultaneously (Schamel and Tracy 1977, 1987; Myers 1981).

No inland migration routes. For prairie provinces and states, only occasional records, likely generated by adverse weather (Goossen and Busby 1979); spring dates 21 May–30 Jun; fall dates 13 Jul–19 Nov.

Origin of Red Phalaropes migrating along east coast of North America problematic. Most birds nesting in e. Canadian Arctic thought to winter off w. and sw. Africa (Brown 1986). In spring, migrate northwest across Atlantic to mid-Atlantic Bight (35°N), then north well offshore, along shelf-break and over Georges Bank (41°30′N; reported as common) and Scotian Shelf and into Canadian arctic waters (Brown 1986), including Labrador Sea and Davis Strait (Orr et al. 1982). Probably also winter in significant numbers off se. U.S., from N. Carolina to Florida and n. Gulf of Mexico (Haney 1985a), where individuals migrate north from mid-Atlantic Bight. From observations of birds in s. Ontario, it is suspected some may shortcut the Atlantic route, cutting through Great Lakes and Hudson Bay (Godfrey 1966).

Dates for Pacific offshore sites: Red Phalarope 1 mo later than Red-necked Phalarope for both directions in California (Tyler 1978). Probably leaves wintering areas off South America late Mar–early Apr (Murphy 1936). Costa Rica, Mar–Apr (Stiles and Skutch 1989). Bolinas Lagoon, just north of San Francisco, CA, peak 11–21 May, extremes 17 Apr and 2 Jun (Page et al. 1979). British Columbia, flocks to 1,000, early to mid-May; extremes 30 Apr and 28 May (Martin and Myres 1969, Campbell et al. 1990). Spring migration within Alaska rapid, from Gulf of Alaska in mid-May to Beaufort Sea by late May. W. Gulf of Alaska, common 21–24 May; Pribilof Is., sw. Alaska, regular late May–early Jun (Gabrielson and Lincoln 1959); Yukon-Kuskokwim Delta, sw. Alaska, mid- to late May (Gill and Handel 1981); east of St. Lawrence I., w. Alaska, 20 May–4 Jun (Fay and Cade 1959, Divoky 1978); Cape Espenberg, w. Alaska, on Arctic Circle, 25–27 May (DS and DMT); Barrow, n. Alaska, 5 Jun (Myers 1981).

Dates for Atlantic offshore sites: Red Phalaropes mean passage date for N. Carolina early Apr, up to 1 mo earlier than Red-necked Phalaropes (mid-May; Lee 1986); mid-Atlantic Bight, Apr; Georges Bank, May; e. Canadian Arctic, early Jun (Brown 1986); Guinea Current, w. Africa, flocks to 100, 7–14 Mar 1930 (Taning 1933); n. Gulf of Mexico, latest observed 21 Mar 1948, 6 Mar 1949, 16 Mar 1950, 17 Mar 1951 (Weston 1953); Georgia, latest date 8 Mar 1982–1985 (Haney 1985a, 1985b); N. Carolina, peak early Apr (Lee 1986); Massachusetts, 8 Apr–2 Jun (Hill 1965); Gulf of St. Lawrence, abundant 24–26 May 1890 (White 1891); Hudson Strait, Canada, mid-Jun, large flocks at edge land-fast ice (Macpherson and McLaren 1959); Davis Strait, near Arctic Circle, early to mid-Jun, peak mid-Jun 1978, a severe summer (Orr et al. 1982).

Southward migration. More protracted. Route probably reverse of northward migration, but because of oceanic nature of routes, details unknown. In n. Alaska, initial movements westward (Johnson and Herter 1989). Adult females, nonbreeders, and failed-nesting males begin movement to sea late Jun (Connors and Risebrough 1978, Divoky 1978, Schamel and Tracy 1987). Remaining males leave breeding grounds mid-Jul through early Aug, peak late Jul. Juveniles leave early Aug, staging in littoral and nearshore areas (Divoky 1978, 1984; Connors 1984, Craig and Schell 1984). In n. Alaska, staging birds concentrate in w. Beaufort Sea near Point Barrow, Plover Is., Simpson Lagoon, and to 150°W, where plume of warmer water from Bering Sea (Beaufort Sea Intrusion) supports higher prey densities (Divoky 1978, 1984). Whereas adult females may leave Alaskan waters by mid-Jul (Gabrielson and Lincoln 1959, Gill et al. 1977), juveniles begin moving southward in early Sep (Jacques 1930, Connors and Risebrough 1978); some found in Beaufort Sea into Oct (Johnson 1979). Late-summer conditions, especially temperature, determine bird densities in littoral zone (Connors 1984); temperatures more variable in late summer than earlier (Myers and Pitelka 1979). Some Red Phalaropes may stage in n. Bering Sea, feeding in gray whale mud plumes (Obst and Hunt 1990). Also congregate at thermal fronts in Bering Sea (Day 1992). Migrants frequently observed on waters north of Alaska Peninsula (Bartonek and Gibson 1972). Rare in w. Gulf of Alaska in fall (unlike spring); fall route may be farther west, toward central North Pacific; common in Aleutian Is. (Gould et al. 1982). Migrating birds congregate in central North Pacific at Subarctic Front (approx. 42°30′N; Day 1992, Gould and Piatt 1993). Some birds off Washington and Oregon mid-Jul to Nov (Gabrielson and Jewett 1940, Jewett et al. 1953). A few birds off California as early as mid-Jul (DeSante and Ainley 1980), peak numbers Oct–Dec (Bond 1971, Briggs et al. 1978, Briggs et al. 1984). Extreme interyear numerical variation at Farallon Is., CA: <10,000–50,000 (DeSante and Ainley 1980). Arrive in South American wintering areas beginning in Sep; more abundant in Oct; some seen there during breeding season (Murphy 1936).

On east coast of North America, first flocks return to se. Labrador and ne. Newfoundland in Jul. Regular on west side Davis Strait and shelf-break east of Labrador in Aug. Unlike spring, Red Phalaropes scarce on Georges Bank in fall, so may start southeastward movements across Atlantic farther north (Brown 1986). Large flocks stage in sw. Bay of Fundy in Aug and Sep; more abundant than Red-necked Phalarope in Gulf of Maine (Brown and Gaskin 1988). Some continue to Southern Atlantic Bight from N. Carolina to n. Florida; some probably winter there (Haney 1985a, 1985b).

Dates for Pacific offshore sites: n. Alaska, Beaufort Sea, juveniles peak 16–31 Aug (Divoky 1978); Point Barrow, AK, 18 Aug 1971, 1,300 migrated past in 2.5 h (Watson and Divoky 1974a); Beaufort Sea waters well offshore of Point Barrow, many observed 6–18 Sep 1976 (Divoky 1978); e. Bering Sea, sw. Alaska, late Jun–late Oct, adults peak at Nelson Lagoon mid- to late Jul, juveniles in mid-Aug (Gill and Jorgenson 1979, Gill and Handel 1981); Pribilof Is., sw. Alaska, earliest 22 Jul 1873, latest 4 Nov 1914 (Gabrielson and Lincoln 1959); Aleutian Is., latest 14 Oct 1975–1978 (Gould et al. 1982); central North Pacific, congregations at Subarctic Front mid-Jul to early Aug 1984–1985 (Day 1992) and Oct 1989 (Gould and Piatt 1993); British Columbia, most common Sep–Dec, extremes 23 Jun and 17 Dec (Campbell et al. 1990); British Columbia and Washington, returning females "numerous" on warm waters 100 km offshore from

s. British Columbia 26 Jul–11 Aug 1946 and 14–30 Jul 1947 (Martin and Myres 1969); California, peak 21–25 Sep 1981 (Briggs et al. 1984); Bolinas Lagoon, just north of San Francisco, irregular, peak Nov (Page et al. 1979); Mexico, first appears in north mid-Jul, common by Sep (Howell and Webb 1995), many still present early Dec (Bourne 1967); w.-central Peru, returns mid-Sep, in "phenomenal numbers" late Sep to mid-Oct 1982, 1,000+ birds/h passing on 27 Sep (Plenge et al. 1989).

Dates for Atlantic offshore sites: arrives at southern sites up to 2 mo later than Red-necked Phalarope (Haney 1985a [Georgia], Lee 1986 [N. Carolina]); Davis Strait and Labrador Sea, late Jul to mid-Aug, with peak early Aug 1978 (Orr et al. 1982); Bay of Fundy, large flocks Aug–Sep (Brown and Gaskin 1988); Flemish Cap, stragglers late Nov (Brown 1986); N. Carolina, common early Oct, then again in Dec (Lee 1986); Georgia, earliest 16 Nov 1982–1985 (Haney 1985a).

Palearctic-North American migratory route. Migrates west along Chukotsk Peninsula, far e. Siberia, in spring, indicating origin in Pacific Ocean (Portenko 1972). Radar and visual study of migration in ne. Siberia concluded postbreeding Red Phalaropes probably depart Siberia on direct routes across Arctic Ocean toward Beaufort Sea (Alerstam and Gudmundsson 1999a), where some may feed along ice edges well out in Beaufort Sea north of Alaskan coast (Johnson and Herter 1989), then join North American migration through Bering Strait and on to wintering grounds off South America. Other Siberian Red Phalaropes move east-southeast along coast toward Chukchi Sea and Bering Strait (Alerstam and Gudmundsson 1999a).

Palearctic migratory routes. Red Phalaropes from w. Siberia, from Taymyr Peninsula and westwards apparently migrate west, joining birds from Novaya Zemlya and Svalbard to move past Scandinavia and Britain toward wintering areas off w. Africa (Alerstam and Gudmundsson 1999a).

Dates: w.-central Denmark, early Oct–early Nov, 1963–1971 (Noer and Sorensen 1974); Britain, hundreds blown onto south coast and inland by gale, 15–16 Oct 1987 (Hume and Christie 1989). Most "wrecks" on European seaboard in Sep–Oct, several thousands sw. England and s. Ireland in Sep–Oct 1960. Most probably on wintering grounds by end of Nov (Cramp and Simmons 1983).

Casual records: Magellan Region, s. Chile (Venegas 1982); Antarctic, near Anvers I. 64°46'S, 12 Jan 1970, one male in breeding plumage with enlarged gonads (Risebrough et al. 1976).

MIGRATION BEHAVIOR

Little information. Forms small to moderate flocks (a few individuals to hundreds; Holmes 1939, Watson and Divoky 1974b). Some courtship during spring migration (Dawson 1923) and perhaps pairing (Hamilton 1958).

Staging in association with gray whale mud plumes: n. Bering Sea, late Jul–early Aug; mean flock size 19 Red Phalaropes (Obst and Hunt 1990); postbreeding birds in Greenland associating with bowhead whales (Kumlien 1878). Staging at oceanic fronts and prey concentrations at Point Barrow and Plover Is., w. Beaufort Sea, n. Alaska (Divoky 1984).

CONTROL AND PHYSIOLOGY

Spring-migrant females often extremely fat (S. F. MacLean pers. comm.), but not always (Portenko 1972). First-arriving males have lower body mass than those captured a week later, suggesting weight gain postarrival (DS and DMT). Juveniles accumulate fat throughout Aug (Connors and Risebrough 1979, Johnson 1979), probably from high wax content of zooplankton prey (Benson and Lee 1975). Evidence for elevated fat metabolism prior to southward migration (Musacchia 1953).

Postbreeding birds migrating over Arctic Ocean toward north coast of Alaska may use sun compass routes (Alerstam and Gudmundsson 1999b).

HABITAT

BREEDING RANGE

Circumpolar arctic and subarctic. Coastal tundra, seldom far inland (Johnson and Herter 1989, Morrison 1997). Level terrain, poorly drained, hummocky, with abundant shallow ponds in polygonized ground, with sedges (*Carex* sp.) dominating (Parmelee et al. 1967, Andersson 1973, Kistchinski 1975). Concentrates in snow-free areas of flooded tundra to feed, form pair bonds, and search for nest sites. Prefers wet marsh (64 birds/km^2), saturated marsh (45 birds/km^2), grassland 1 (29 birds/km^2), grassland 2 (14.5 birds/km^2) at Prince Charles I., e. Canada (Morrison 1997). Much habitat overlap with Red-necked Phalarope. Where the 2 species occur together; nests can be only several meters apart (DS and DMT).

Prudhoe Bay, n. Alaska, peak abundance near coast; coastal nonsaline tundra most important because more vegetation for nesting, but near saline for feeding; uses saline habitats near coast much less than Red-necked Phalarope (TERA 1994). Prefers polygonized tundra in central and n. Lena Delta, Siberia (Gilg et al. 2000). Nesting in Greenland and Ellesmere I. limited to wet, luxuriant marshes below large, persistent snowfans and boggy areas with streams and ponds (Meltofte 1985).

Red Phalarope more restricted to areas of marsh and shallow ponds, while Red-necked Phalarope also nests in areas of deeper ponds surrounded by drier habitat.

SPRING AND FALL MIGRATION

Spring migration in offshore waters, probably in association with oceanic fronts. Near breeding grounds, associated with leads in ice or edge of pack ice, where prey abundant (Divoky 1979, Brown 1980, Orr et al. 1982). May use littoral waters during storms (Haney and Stone 1988).

Fall migration preceded by onshore movement toward ocean. Females gather in loose flocks on fresh-water ponds, gradually moving seaward. Form larger flocks in brackish ponds near coast, and in littoral waters. Males, then juveniles, follow same pattern. Southbound migration using similar habitats as northbound, often well offshore, associated with main currents (Orr et al. 1982). Often found farther out to sea than Red-necked Phalarope (Kuroda 1955, Finch et al. 1978).

Postbreeding: At Barrow, n. Alaska, differs from other shorebirds in selecting gravel beaches in littoral zone where zooplankton prey concentrated (Connors 1984, Smith and Connors 1993). In contrast, littoral zone used very little by postbreeding Red Phalaropes in Greenland (Meltofte 1985). Possibly these birds fatten in Baffin Strait and/or Bay of Fundy, e. Canada.

MARINE RANGE

Entirely pelagic in winter. Frequents offshore marine waters along ocean fronts, usually far out to sea, where zooplankton prey concentrated (Murphy 1936, DeGraaf and Rappole 1995). Fronts are narrow bands of water where water density changes abruptly due to temperature or salinity; Red Phalarope frequently associated with thermal fronts. Oceanographic features of upwellings where Red Phalarope overwinters are similar (Brown 1980). Most abundant offshore from Peru and n. Chile (Murphy 1936, DeGraaf and Rappole 1995); also, Western Sahara to Ghana, in Atlantic (Bannerman and Bannerman 1968, Brown 1979). Both areas have divergence fronts associated with stable wind-driven upwellings. Usually found farther out to sea, and may feed on smaller zooplankton prey than Red-necked Phalarope (Briggs et al. 1984, Tyler et al. 1993). Red-necked Phalarope may be more associated with convergence fronts where warmer inshore waters meet colder offshore waters. Red Phalarope also associated with areas of smaller upwellings caused by: (1) turbulence over underwater reefs, (2) tidal rips, (3) current rips between islands, (4) down-current of islands, and (5) glaciers and icebergs (Brown and Gaskin 1988). Almost always associated with visible slicks on ocean surface. See also Distribution: winter range, above.

FOOD HABITS

FEEDING

Main foods taken. Breeding season: adult and larval insects, and crustaceans. At sea: zooplankton.

Microhabitat for foraging. BREEDING SEASON. Early: shallow, wading-depth water (<5 cm) at edges of shallow ponds. Later, same as above, plus swimming-depth water (Wuntke and Meier 1998, DS and DMT). Female deep-feeds more commonly than male, especially when male incubating (Ridley 1980). Greenland and w. Alaska: generally edge-feeds while wading; Red-necked Phalarope generally surface-feeds while swimming (Elander and Blomqvist 1986, DS and DMT). Chironomid (midge) and *Prionocera* (cranefly) larvae abundant and active early in Jun in this habitat (Holmes 1966, Bergman et al. 1977). Often feed communally in small groups, with locations changing daily, suggesting food supply patchy in space and time. Marine foods may be used during breeding season, if nesting near ocean (Whitfield 1995, DS and DMT).

FALL STAGING. All data from n. Alaska. Swimming-depth water in ponds and near edges of lakes, and littoral beaches and barrier islands. Adult female departs first, apparently moving well out to sea; nothing known of foraging at this time. Adult male departs mid- to late Jul, making limited use of intertidal prey, feeding on emerging dipteran flies near lagoons and brackish pools (Connors and Risebrough 1979). Juveniles concentrate in very nearshore marine habitats (<100 m of barrier islands and exposed coastlines) during Aug, where they take large, slow-moving, conspicuous prey (Connors and Risebrough 1976, Schamel 1978, Divoky and Good 1979, Johnson 1979). Especially abundant near barrier island spits and bars, where land protrusions concentrate zooplankton prey. Often feeds on under-ice amphipods near grounded sea ice or in areas of <40% sea-ice cover (Divoky 1978, Orr et al. 1982, Connors 1984). Sea-ice edge creates small currents, bringing prey to surface (R. G. B. Brown unpubl.). Colville Delta, n. Alaska: 2.1 Red Phalaropes/km^2 and 15.7 Red-necked Phalaropes/km^2 associated with mudflats and saltmarsh (Andres 1994).

FALL AND WINTER PELAGIC. Pelagic distribution suggests this species highly dependent on ocean fronts (narrow bands where temperature and/or salinity change abruptly, as different water masses come into contact; Murphy 1936, Brown and Gaskin 1988). Fronts associated with strong surface thermal gradients bordered by upwelling waters (Tyler 1978; Brown 1979; Orr et al. 1982; Briggs et al. 1984; Haney 1985a, 1985b; Day 1992; Wahl et al. 1993). Often uses fronts farther offshore than Red-necked Phalarope (Brown 1986, Brown and Gaskin 1988, Tyler et al. 1993). Usually associated with visible streaks on surface (Briggs et al. 1984, Brown and Gaskin 1988). Zooplankton concentrated in fronts efficiently utilized (Brown 1980, Orr et al. 1982). Both Red and Red-necked phalaropes concentrate seaward of shelf break, over central shelf, 10–75 km offshore (Briggs et al. 1984). Not all convergence areas have correct combination of hydrographic and biological conditions for sufficient prey concentrations (Haney 1985a, 1985b; Brown and Gaskin 1988). Best feeding conditions at convergence downstream of active, stable upwelling, with high concentrations of phytoplankton (Briggs et al. 1984). High concentrations of phalaropes south of Subarctic Front in the Pacific Ocean (Day 1992, Gould and Piatt 1993) and over the shelf break mid-Atlantic Bight to Georges Bank, Scotian Shelf (spring), and east of Labrador (fall; Brown 1986). In fall, well offshore, outer edge Labrador Current over central Continental Shelf (Orr et al. 1982). Red Phalarope tends to congregate offshore of midshelf front, while Red-necked Phalarope congregates inshore of front (Haney 1985a, 1985b; Tyler et al. 1993; Wahl et al. 1993). Positive correlation of upwelling stability with bird numbers (Haney 1985a, 1985b).

Spring Migration. Ocean fronts; rip tides and polynyas (permanent open water areas) associated with islands. Later, ice edge in association with under-ice plankton (Divoky 1979). Large flocks mid-Jun at edge of land-fast ice in nw. Hudson Strait (Orr et al. 1982). May feed in littoral zone in spring, especially during cold periods when tundra invertebrates less available (Haney and Stone 1988).

Frequent association with marine macroalgae in littoral zone; patches may contain concentrations of invertebrates (Haney and Stone 1988). Found at sea mainly in plankton-rich upwellings (Hayman et al. 1986).

Food capture and consumption. Visual forager, while walking, wading, or swimming. Can pick prey from surface of ground, water, or emergent vegetation, sometimes running after flying prey and jumping to catch it; dips head below water surface while wading or swimming. Up-ends while swimming, occasionally accompanied by small jump; spins in water and pecks at center of vortex. Although it can dive to escape from potential predators, rarely recorded diving for prey (Sutton 1932). After seizing caddisfly (Trichoptera) larvae, holds larvae in bill and shakes head side to side until case released. Probing not recorded.

Mandibular papillae may serve as strainers, suggesting facultative filter-feeding (Cramp and Simmons 1983); feeds on smaller, slower prey than Red-necked Phalarope (Brown and Gaskin 1988). In Bay of Fundy, Red Phalaropes congregate where copepod biomass is less and the main species are smaller than in areas where Red-necked Phalaropes forage (Brown and Gaskin 1988). Systematic observations of feeding tactics in spring littoral zone: 84% of foraging attempts surface-picking; 9% head dunk, 3% vertical bob, and 4% spinning (n = 25; Haney and Stone 1988).

Feeding observations at sea: quick, downward, nearly vertical peck with bill aimed at individual prey, bill tip immersed; occasionally up-ends. Often swims against current in sinusoidal track, or drifts downcurrent, then flies high (presumably to locate new feeding sites) in flocks and relocates upcurrent again or at another visible streak; rarely spins while in current (Brown and Gaskin 1988).

Feeding often facilitated by associations with marine mammals (Kumlien 1878, Ryder 1957, Obst and Hunt 1990, Grebmeier and Harrison 1992) and with other bird species (van Swelm 1975, Schneider et al. 1990, Youngman 1995). See Behavior: nonpredatory interspecific interactions, below.

Filmed pelagic feeding in Bay of Fundy averaged 55 pecks/min (n = 11; Brown and Gaskin 1988). In Svalbard, 54 pecks/min (range 20–250 pecks/min) with 80% success while feeding at tundra ponds (Ridley 1980). Surface-feeding male up to 70 pecks/min; more than deep-feeding female. Incubating male off nest fed at higher rate on richest food supply, perhaps because time limited (Ridley 1980, DS and DMT). Feeding rate of 15.8 attempts/min (range 6.0–57.0) in wind-rowed algae in littoral zone (Haney and Stone 1988).

Spinning as feeding method studied more in Red-necked Phalarope (see Rubega et al. 2000). This technique concentrates and lifts prey, for increased accessibility (Obst et al. 1996). Red Phalarope spins rapidly; 57 rotations/min (n = 3; Senior 1987).

DIET

Major food items. See below for details of locations and references. On breeding grounds, chiefly insectivorous in marshes (Fig. 2). In Jun (arrival, egg-laying, incubation), largely dependent upon chironomid (midge) and tipulid (cranefly) larvae. In Jul (incubation, brood-rearing, adult departure), chironomid adults and tipulid adults and larvae important. Chironomid adults most commonly taken at this time, but larger size of tipulids makes them an important prey. Spiders (Arachnida) sometimes important early in season, if other prey not available (Danks 1971). Eight young collected during Jul contained adult Chironomidae, Tipulidae, and Trichoptera (S. F. MacLean unpubl.). In contrast to Red-necked Phalarope (Rubega et al. 2000), Red Phalarope does not feed on freshwater crustaceans until Aug, perhaps when falling water levels concentrate prey. Other prey taken on

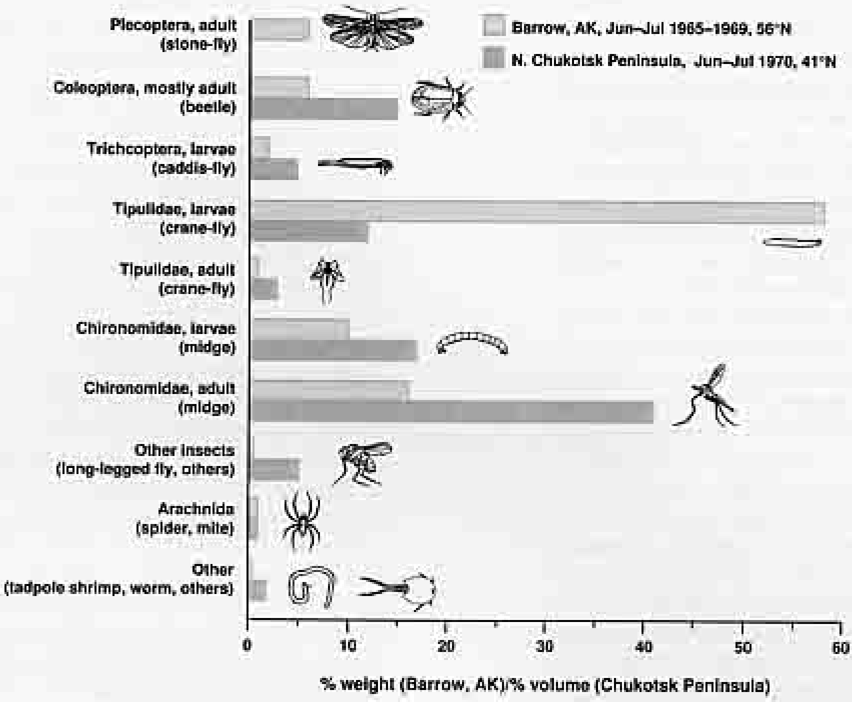

Figure 2. Food habits of Red Phalarope in coastal marshes during breeding season (from Kistchinski and Chernov 1973 and S. F. MacLean, Jr., unpubl.). Drawings by D. Hollingdale.

breeding grounds: adult and larval Insecta: Plecoptera (stoneflies), Coleoptera (beetles), Culicidae (mosquitoes), Dolichopodidae (long-legged flies), Hemiptera (water boatmen), Collembola (springtails), Ephydridae (shoreflies), *Scatophaga* (dungflies), Muscidae (houseflies), Formicidae (ants); Arachnida (spiders and mites). Crustacea: tadpole and fairy shrimp, water fleas, seed shrimp, copepods; segmented worms; snails (Wetmore 1925, Sutton 1932, Kistchinski and Chernov 1973).

At sea (staging, migration, and winter). Juvenile Red Phalaropes concentrate in very nearshore marine habitats (<100 m of barrier islands and exposed coastlines) during Aug and Sep in Alaskan Beaufort and n. Chukchi Seas. Marine copepods and amphipods main prey (Connors and Risebrough 1979, Johnson 1979). Other important prey: small cnidarians, adult intertidal dipterans, decapod larvae, mysids, chaeotognaths (arrow worms), and pteropod mollusks (sea butterflies).

Birds collected in pelagic environment, mostly on migration, fed chiefly on copepods, amphipods, fish eggs, larval fish, mysids, and euphausiids.

Quantitative analysis (includes only items ≥10% of diet by mass or volume).

BREEDING GROUNDS. Barrow, n. Alaska, 1965–1969, % mass = no. individuals x mean live mass of prey item (% number, % occurrence; S. F. MacLean unpubl., analyzed by DS and DMT), Jun (n = 30 stomachs): 45% (5, 33) Tipulidae (cranefly) larvae (mostly *Prionocera gracilis* and *Pedicia hannai*), 25% (80, 50) Chironomidae larvae, 14% (6, 10) Plecoptera (stonefly) adults, 10% (2, 33) Coleoptera (beetle) adults (mostly Carabidae). Jul (n = 26 stomachs): 64% (6, 38) Tipulidae larvae, 26% (82, 42) Chironomidae adults. Jul, chicks and juveniles (n = 8 stomachs): 51% (10, 50) Tipulidae adults, 26% (68, 75) Chironomidae adults.

Ne. Siberia, n. Chukotsk Peninsula, 1970, % volume (% occurrence; Kistchinski and Chernov 1973), 10–21 Jun (n = 19 stomachs): 37% (53) Chironomidae larvae, 29% (79) Coleoptera adults (mostly Dytiscidae and Carabidae), 11% (37) Trichoptera larvae. 29 Jun–1 Jul (n = 7 stomachs): 30% (71) Tipulidae eggs, 26% (57) Chironomidae adults, 16% (29) Tipulidae larvae and pupae (*Prionocera*), 14% (43) Tipulidae adults. 15 Jul (n = 15 stomachs): 100% (100) Chironomidae adults.

N.-central Siberia, Indigirka and Yana River deltas, 1971–1972, % volume. Summarized here; see original for details; samples collected 5 Jun–2 Aug (Kistchinski and Chernov 1973). Early Jun (dates 5–9; n = 15 stomachs), only period when insects not predominant (85–99%) prey: 47% Oligochaeta, 12%

seeds at this time. 17–19 Jun (*n* = 14 stomachs), Tipulidae (*Prionocera*) larvae (70%) and pupae (11%) predominated. 29 Jun–2 Jul (*n* = 19 stomachs), most common prey Tipulidae adults (50%), larvae (14%), and pupae (5%), followed by Gammaridae amphipods (10%). 20 Jul–2 Aug (*n* = 12 stomachs) dominant prey Hemiptera (*Chyloxanthus*; 31%), Coleoptera adults (13%) and larvae (2%), spiders (12%), Gammaridae amphipods (12%). Birds collected away from breeding habitat (13–26 Jul; *n* = 11 stomachs) fed chiefly on Chironomidae adults (76%).

Spitsbergen, 1978 (*n* = 21 fecal samples; % occurrence; Ridley 1980). Adult insects, chiefly Chironomidae and Mycetophilidae (fungus gnats), occurred in 95% of samples, abundant in 45%. Other prey items: spiders (64%), insect larvae (22%), and Crustacea (22%).

Other prey items on breeding grounds: <10%: seeds, Annelida, Gastropoda, Branchiopoda, *Daphnia*, *Brachycera*, *Collembola*, Muscidae (pupae), Culicidae (larvae), *Scatophaga*.

AT SEA. Littoral: Barrow, 1976–1978 (*n* = 44 stomachs; % mass, wet weight [% occurrence]; Connors and Risebrough 1976, 1977, 1978, 1979, Connors 1984; P. G. Connors and R. W. Risebrough unpubl.; reanalysis of original data by DS and DMT). 20 Jul–Aug. Staging, postbreeding adult males and juveniles congregated along shorelines: 24% (41) amphipods (including *Apherusa glacialis*, *Onisimus litoralis*, and *Gammaracanthus loricatus*), 23% (34) copepods (mostly Calanidae), 19% (32) unidentified crustacea, 11% (19) insects (Diptera adults, Coleoptera). Sample of 13 stomachs collected 30 Jul–31 Aug 1975; % occurrence only: 76% with copepods, 15% with Cirripedia (barnacle) larvae, and 8% with Oligochaeta.

Littoral/lagoon. Simpson Lagoon, n. Alaska, 1977–1978 (*n* = 62 stomachs; % mass, wet weight [% occurrence]; Johnson 1978, 1979, Craig and Schell 1984, S. R. Johnson unpubl.; reanalysis of original data by DS and DMT, separating Red from Red-necked phalarope data). Aug. Staging juveniles congregated along shorelines in water depths <1 m. Prey items predominantly amphipods, 50% (34), chiefly *Onisimus glacialis* and *Gammarus setosus*, and copepods, 39% (64). Ten copepod species identified, primarily *Calanus hyperboreus*, *C. glacialis*, *Metridia lucens*, and *M. longa*. Although cnidarians (jellies) not found in stomach samples, birds observed feeding on them; likely under-represented in diet studies. Significant differences between 2 collection years. In 1977 (*n* = 46 stomachs), copepods chief prey, 65% (67). In 1978 (*n* = 16 stomachs), amphipods chief prey, 93% (62), with copepods falling to just 2% of mass, although still in 67% of stomachs. In food-availability samples taken in feeding habitat, copepods dropped from 31% (by volume) in 1977 to 12% in 1978. Amphipods taken at higher rate than availability in 1978, making up 93% of diet but only 14% of available prey. Mysids taken much less than available, making up 8% of diet and 26% of availability in 1977 and 5 and 73%, respectively, in 1978. Comprehensive study of Simpson Lagoon ecosystem concluded birds not limited by prey abundance (Craig and Schell 1984).

Littoral, Arctic National Wildlife Refuge, ne. Alaska (*n* = 5 stomachs; % weight; Willms 1992). Aug, 46% isopods (*Saduria entomon*), 34% insects, 13% copepods (*Calanus hyperboreus*, *C. glacialis*), 7% amphipods.

Littoral, Cape Krusenstern, w. Alaska, 1978 (*n* = 8 stomachs; % mass, wet weight [% occurrence]; Connors and Risebrough 1979, P. G. Connors and R. W. Risebrough pers. comm.). 3–7 Jun, 36% (62) unidentified Crustacea, 29% (88) Copepoda (at least partly *Calanoida*), 24% Decapoda larvae.

Oceanic, Beaufort Sea, n. Alaska, 1976–1978 (*n* = 76 stomachs, % occurrence; Divoky 1984). Aug to mid-Sep, fall staging or migrant birds fed mostly in nearshore waters <300 m offshore to 20 m depth contour. A few stomachs from pelagic waters farther offshore combined with nearshore samples because no significant differences found. Only % occurrence reported. Unidentified crustaceans in 30% of stomachs. Gammarid amphipods in 31% of stomachs, and the ice-associated amphipod *Apherusa glacialis* in 18%. Other prey: 13% mysids, 11% copepods, 5% euphausiids (*Thysanoessa*), 1% larval fish.

Oceanic, n. Bering Sea, w. Alaska, 1985 (*n* = 7 stomachs; % occurrence; Obst and Hunt 1990, Grebmeier and Harrison 1992). 26 Jul–12 Aug, Staging or migrating birds fed in association with gray whale mud plumes. Only % occurrence available. All prey items (100%) were benthic amphipods stirred to ocean surface by feeding whales: *Ampelisca* (71), *Byblis* (71), *Protomedia* (14), and *Anonyx* (14).

Oceanic, Bay of Fundy, e. Canada, 1978 (*n* = 10 stomachs; % occurrence; Brown and Gaskin 1988). 22 Aug, fall staging or migrating birds. Only % occurrence available. Authors suggest copepods underestimated because of collecting methods. Of 10 stomachs collected during 1 d, 90% contained insects, 70% polychaetes and gastropods, 40% euphausiid adults or larvae (*Meganyctiphanes norvegica*), 40% larger copepods (*Calanus finmarchicus* >2mm), and 10% smaller copepods.

Oceanic, Atlantic Ocean, Georgia, 1982–1984, no stomach samples (Haney 1985a); concentrated prey available larval clupeiiform fish (herring) and copepod *Eucalanus pileatus*.

Oceanic, Pacific Ocean, California, 1981, % volume (% occurrence; Briggs et al. 1984). 24 Sep, off Point Reyes (*n* = 10 stomachs): 59% (80) fish eggs, 30% (70) euphausiids (mostly *Euphausia* *pacifica*). 26 Sep, off Point Montara (*n* = 6 stomachs): 54% (100) euphausiids (*E. pacifica, Thysanoessa longipes, T. spinifera*), 39% (100) fish eggs. 3 Oct, off Davenport (*n* = 37 Red Phalarope stomachs combined with 5 Red-necked Phalarope stomachs): 53% (93) of volume *Calanus* copepods, 17% (62) unidentified crustacean parts and larvae, 9% euphausiids (including *T. spinifera, E. pacifica*, and larvae).

Marine, other prey items, <10%: plastic, algae, seeds, Hydrozoa, Pteropoda, Oligochaeta, *Cladocera*, Mysidae, *Cumacea, Bachyura* (zoea), Chaetognatha.

FOOD SELECTION AND STORAGE

Laboratory studies indicated Red Phalaropes fed mostly on prey 2–5 mm in length (Dodson and Egger 1980). Pelagic prey sizes: 1.3–4 mm for *Calanus* copepods, gastropod veligers, barnacle larvae, and fish eggs; 11–16 mm for euphausiids (Briggs et al. 1984). May concentrate on smaller prey (1–4 mm) because less mobile (Dodson and Egger 1980). Amphipods taken at whale plumes approximately ≤3 mm in length (Obst and Hunt 1990). Beaufort Sea offshore prey sizes 2.5–15 mm (Divoky 1984). Apparent difficulty handling large amphipods; manipulates invertebrates up to 20–25 mm in length for several minutes before swallowing (Haney and Stone 1988). Food storage unlikely.

NUTRITION AND ENERGETICS

Very little information. Juveniles accumulate fat throughout Aug in Beaufort Sea littoral zone (Connors and Risebrough 1979, Johnson 1979, Connors 1984). These reserves may be important for survival during fall migration and winter. Arctic zooplankton accumulate waxes, a high-energy food source (Benson and Lee 1975), which Red Phalaropes presumably store. Incubating male apparently loses mass during incubation (Schamel and Tracy 1987).

METABOLISM AND TEMPERATURE REGULATION

No information.

DRINKING, PELLET-CASTING, AND DEFECATION

No information on drinking. Unlike Red-necked and Wilson's phalaropes, this species does not use hypersaline lakes and thus does not face water-balance problems associated with such habitats (Rubega et al. 2000). No reports of pellet-casting. Defecation preceded by tail-lifting; often precedes flight (DS and DMT).

SOUNDS

VOCALIZATIONS

Vocalizations are an important component of the gregarious life style of the nonterritorial Red Phalarope. Most published accounts of vocalizations in this species come from the windswept, sparsely vegetated breeding grounds, where all observers impressed with the frequency of calls. Individuals locate potential mates through monosyllabic calls that can be heard by humans up to 1 km away. Pair members keep track of each other's position while foraging in sedge marshes through frequent Twittering contact calls heard up to 15 m. Other vocalizations accompany aggressive behaviors and clearly demonstrate that a bird is already paired and not available for a new pair bond. Special calls coordinate nest-site selection between pair members; these carry only 5–10 m. No detailed or quantified study of vocalizations in this species.

***Development*.** No information available.

***Vocal array*.** Most vocalizations given only on breeding grounds; only flight call commonly given at sea. On breeding grounds, frequent vocalizations related to gregariousness and high rates of intraspecific interactions. Although most studies imply that specific calls are context dependent, more detailed study needed. Degree of differences in calls between sexes poorly understood. Most calls variants of peep or *whe-eep* and occur variably with context, often blending into each other (Cramp and Simmons 1983), making calls difficult to discriminate. Moreover, the great variety of summaries in the literature makes it difficult to disentangle and categorize call descriptions from various authors. The following description and categorization assembled from Bengtson 1968, Höhn 1971, Kistchinski 1975, Mayfield 1979, Ridley 1980, Cramp and Simmons 1983, and unpublished data (DS and DMT, JD).

FLIGHT CALLS. Consist of short, sharp, high-pitched *pit* or *wit*. Often given in rapid succession, as in *pit pit-pit-pit*. By both adult sexes and juveniles. Only call commonly given at sea, but also used on breeding grounds. Associated with birds taking flight, landing, or in flight; possibly functions as flight-intention signal.

ALARM CALLS. High-pitched, clear monosyllabic *peet* (peep of Mayfield 1979; see Fig. 3A). Also, drawn-out, disyllabic, and buzzy *whe-eep*. Equals *cruit-cruit* of Bengtson (1968). Sharper, longer, and louder than flight calls. Given by both sexes in variety of contexts by excited, disturbed, or alarmed birds, usually while standing upright and alert (e.g., in response to a predator). Other birds often become alert in response.

MALE ALARM CALL. Low-pitched, rasping, disyllabic *wee-cha* or *choo-eet* of Mayfield (1979); *tchirr-lyk* of Kistchinski (1975). Steadily repeated; by male only, usually by distressed or disturbed broody male toward chicks. Possibly used by brood as cue for individual recognition.

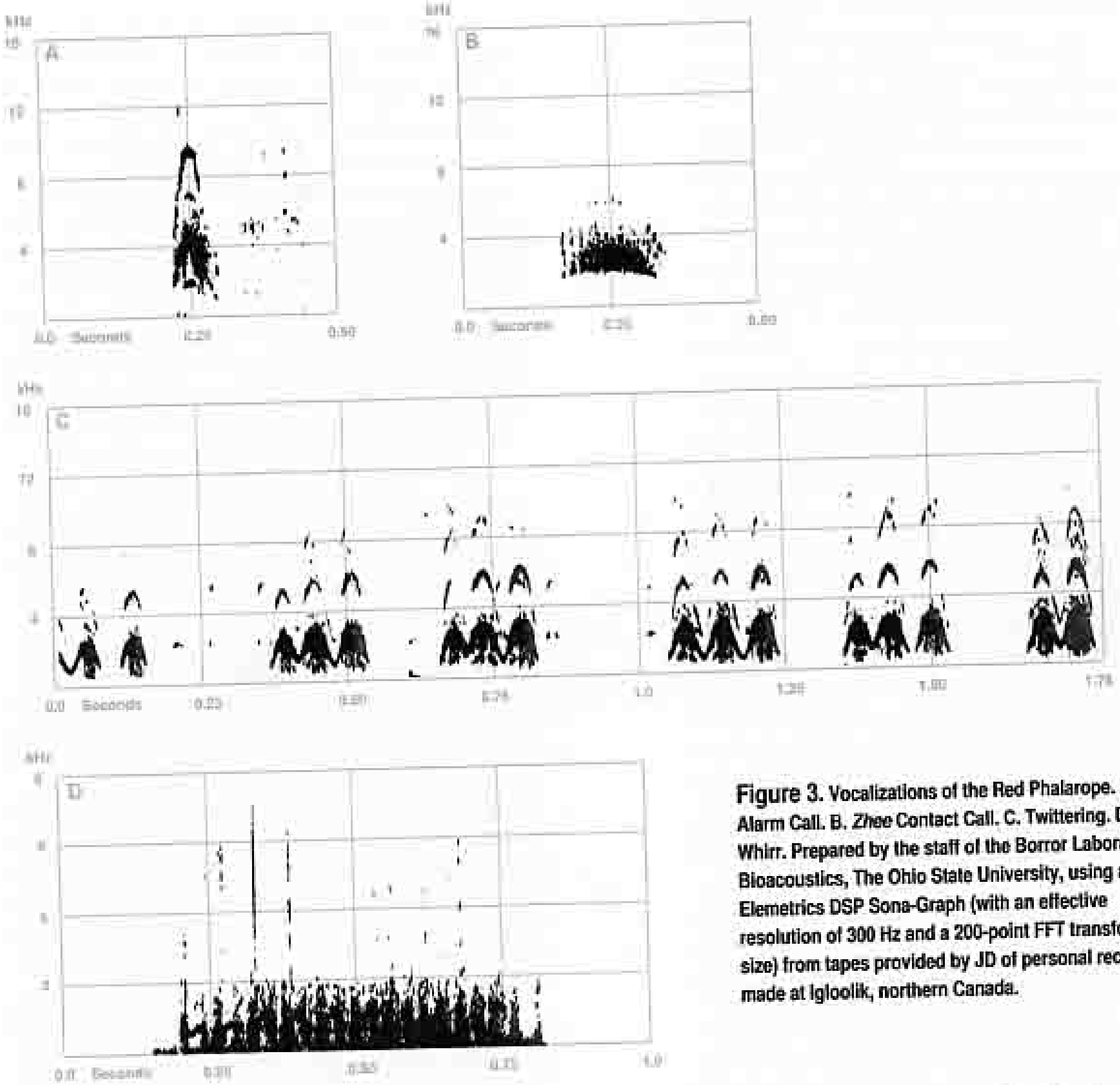

Figure 3. Vocalizations of the Red Phalarope. A. *Peet* Alarm Call. B. *Zhee* Contact Call. C. Twittering. D. Wing Whirr. Prepared by the staff of the Borror Laboratory of Bioacoustics, The Ohio State University, using a Kay Elemetrics DSP Sona-Graph (with an effective resolution of 300 Hz and a 200-point FFT transform size) from tapes provided by JD of personal recordings made at Igloolik, northern Canada.

Contact Calls. *Creep* and *preep* of Höhn (1971), *zeeet* of Mayfield (1979), *zhee* of Ridley (1980; Fig. 3B). Far-carrying and distinctive. Given by both sexes in variety of contexts; e.g., as contact call between mates, especially when not near each other or when flying and searching for mate, or as advertisement call by female. Often responded to by similar calls by others. Contact calls within individuals are stereotyped and possibly used as signature calls for individual recognition. Calls intermediate between alarm calls and contact calls occur regularly.

Twittering. Soft, warbling *witta-witta-witta* (Fig. 3C). *Tut-tut* or *to rut* of Höhn (1971), *kryu kryu kryu kryu* of Kistchinski (1975), *ti-ti-ti-ti* of Mayfield (1979). Given exclusively by mated pairs while associating during feeding, courting, or resting. Twittering made up of low, irregular, staccato peeps of varying pitch performed by both sexes simultaneously (Cramp and Simmons 1983), but occasionally performed by one sex alone (male warble). Rapid (4 peeps/s), high-pitched Twittering given by both birds at nest scrape or nest bowl. Intensity and volume variable, possibly in relation to context and/or excitement levels.

Scream. High-pitched, rodentlike squeaking or wheezing *weee weee*. Irregularly given by males if they perform a distraction display after being disturbed off nest. Similar-sounding call possibly given by mated or nesting males during Driving Flight displays.

Driving Flight Scream. Harsh squeaking given by mated males or nesting males. Accompanies Driving Flight displays, as males attack courting females (see Behavior: agonistic behavior, below).

NESTLING CALL. Soft, high-pitched *peep peep* of downy young similar to nestling calls of other shorebirds. Nondirectional.

Phenology. Most vocalizations heard only on breeding grounds; however, flight call also commonly heard at sea. More information needed on array of vocalizations given at sea.

Daily pattern. Calls given at all times; however, call rates lower around midnight when overall activity levels decrease.

Places of vocalizing. Flight call and contact calls given from ground (on land or while swimming) or the air. Other calls usually given from ground.

Repertoire and delivery of songs. Needs study.

Social context and presumed functions. See discussion of vocal array, above. Detailed study needed.

NONVOCAL SOUNDS

Wing Whirr (Fig. 3D; after Höhn [1971], Mayfield [1979], same as "Rattling" of Bengtson [1968], Kistchinski [1975], Ridley [1980]). Mechanical sound caused by rapidly beating wings during conspicuous Wing Whirr display (see Behavior, below). Performed by both sexes, but more often by female. Most often associated with courtship and copulation, although there are many exceptions. May signal willingness to mate (JD).

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Walking probably restricted to summer nesting season, except for walking on mats of vegetation at sea, rocks in nearshore waters, and mudflats. Can ascend steep tundra banks (DS, DMT).

Flight. Fast flier; few data on speed. Red Phalarope and Arctic Tern (*Sterna paradisaea*) reported to have slowest air speeds (9–14 m/s) of 17 species of waterbirds, gulls (*Larus* spp.), and skuas (Stercorariinae) migrating from Siberia (Alerstam and Gudmundsson 1999a). Takes flight directly from land or water surface; no hop or run required. Flight usually twisting and turning pattern; especially when in flocks.

Swimming and diving. Excellent swimmer, even in storms and large waves. Good buoyancy provided by dense plumage, more so than in most shorebirds. Turns to face approaching wave, floating over small ones, plunging through or flying over crest of large ones (King 1971). Lobed toes, as in Red-necked Phalarope, aid in swimming (see Colwell and Jehl 1994). Often spins to feed while swimming; clockwise and counterclockwise; individuals found to spin equally in both directions in Bering Sea, w. Alaska (Haney and Stone 1988); 39 rpm (Höhn 1971). Dives through waves or if frightened at close range; rarely dives for food (Sutton 1932).

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Preens several times daily on breeding grounds (see below); often on land but sometimes on water. Preening usually preceded by bathing, wing-stretching (high over back, wings almost touching) and head-scratching. As in other phalaropes, head-scratching direct under wing (Höhn 1971). Dense breast-feathers, so bathing individuals rise high in water to gain enough momentum to thrust themselves partially beneath water. Accompanied by wing-flapping, twisting from side to side and head-dunking. After bathing, bird often flutters up few centimeters above water before settling to bathe more, or to preen. Bathing often accompanied by soft peeping.

Sleeping, roosting, sunbathing. Sleeps on land or water with head tucked into scapulars. Opens eye every few seconds and scans area. No daily pattern on breeding grounds (DS and DMT).

Daily time budget. On breeding grounds, mainly feeding. Activity as percent of total, based on 24-h observation periods, prelaying and laying: Barrow, n. Alaska (n = 96 h of observation when pair members together; Ashkenazi and Safriel 1979, DS and DMT): 67% feed, 9% rest, 6% preen, 5% walk, 4% fly, 2% swim, 2% alert, 2% aggressive, 2% nest displays, <1% copulation attempts. Wales, w. Alaska (n = 36 h; Erckmann 1981): 66% feed, 14% at nest, 3% pair displays, 3% alert, 2% rest, 1% copulate, swim, walk, fly. Incubating male: 70% incubation, 21% feed, 7% miscellaneous, 2% fly (Erckmann 1981). Significantly more preening in Red Phalarope than in Semipalmated Sandpiper (*Calidris pusilla*; Ashkenazi and Safriel 1979); perhaps due to denser feathers of phalaropes. No time-budget information available for migratory or wintering birds.

AGONISTIC BEHAVIOR

Physical interactions. Very similar to other species of phalaropes. Agonistic behavior hierarchy established for Wilson's Phalarope (Howe 1975b) works well for Red Phalarope (DS and DMT). Interactions involve bills, wings, breasts, and feet; usually accompanied by vocalizations. Low-level aggression involves flying to another bird and displacing it by landing within few centimeters, or pointing bill in direction of other bird at close range (<0.5 m; see Fig. 4E). Higher-level aggression involves running or swimming toward other bird, with outstretched neck and bill pointed at other bird (Fig. 4E), or hovering within few centimeters over another. Highest-level aggression involves physical contact: biting back of head and neck (Fig. 4H) or tail; striking with wings; striking opponent's back with feet, while flying up and down; striking opponent's back with breast while flying up and down. Most interactions are brief, lasting a few seconds. Some interactions among females in groups pursuing males late in egg-laying season may continue for 30+ min when operational sex ratio skewed toward excess females (because most males are incubating; DS and DMT).

Much aggression on breeding grounds between females vying for access to males. Also aggression between males for access to females when operational sex ratio is skewed toward fewer females (Tracy and Schamel 1988). Paired birds aggressive toward unpaired birds attempting to disrupt pair bond. Protection of pair bond usually involves opposite-sex aggressive interactions; paired male aggressive toward intruding unpaired females and paired female aggressive toward unpaired male intruders (DS and DMT). Pushing and accompanying Twittering vocalizations by pair members may serve to identify pair to conspecifics and lower aggression by unpaired birds toward paired birds. Within-pair aggression primarily during first day of pair bond (DS and DMT).

Incubating male generally intolerant of females. Only tolerates his mate, if pair bond intact (Schamel and Tracy 1977). When approached by female, incubating male often displays Driving Flight (Kistchinski 1975; Fig. 4I), accompanied by Driving Flight Scream (see Sounds: vocalizations, above). Driving Flight is stereotyped behavior, with exaggerated puffing of breast, rapid hovering wing-beats, and dangling legs. Displayed usually by incubating male, rarely by paired male, and never by unpaired (and nonincubating) male. Clearly identifies male as unavailable for pairing (Ridley 1980, DS and DMT).

Similar low-level aggressive interactions noted in feeding groups during migration (Dawson 1923). No data available for at-sea interactions.

Communicative interactions. Aggressive interactions sometimes accompanied by Screams, including harsh, rasping vocalizations. Many aggressive interactions on breeding grounds may be avoided by close association of pair members, Pushing displays (Bengtson 1968; Fig. 4F), and contact calls between paired birds, all of which serve to identify an established pair. Incubating male often displays modified and abbreviated versions of Driving Flight while foraging in vicinity of females: momentarily hovers in place, with feet dangling, and brief Driving Flight Scream. This may establish identity as an incubator and dissuade female approach. Flight Calls given by single birds. When answered by conspecific, calling bird often lands near responding bird. May be used to locate actual or potential mates; may be especially important in sparse populations. Infrequent interspecific aggression noted on breeding grounds at feeding areas with Red-necked Phalaropes, Semipalmated Sandpipers, Western Sandpipers (*Calidris mauri*), Dunlins (*C. alpina*; DS and DMT).

SPACING

Territoriality. No evidence for territoriality. On breeding grounds, pair members defend small area surrounding themselves and their mates. Female occasionally chases other females from sections of small communal feeding ponds (DS and DMT). Nests sometimes within 5 m of each other (DS and DMT). No aggression between incubating males. No apparent dominance hierarchies. No information on territoriality on wintering areas, but none suspected.

Individual distance. If an individual approaches <0.5 m on breeding grounds, aggression will likely occur, unless paired. No information for individuals at sea.

SEXUAL BEHAVIOR

Mating system and sex ratio. Usually monogamous. Facultative, female-access polyandry, involving sequential males (Schamel and Tracy 1977). Polyandry made possible by male-only incubation. Male may pair with >1 female via renesting. Population sex ratio unknown. Asynchronous arrival may bias operational sex ratio locally for brief period (Kistchinski 1975, Schamel and Tracy 1977, Mayfield 1979). Polyandry not commonly recorded; 4 of 11 (36%) banded females polyandrous at Barrow, n. Alaska; 3 of 6 (50%) polyandrous in Iceland; associated with extra males in local population (Schamel and Tracy 1977, Whitfield 1995).

Pair bond. May arrive paired or form pairs soon after arrival (Schamel and Tracy 1977, Mayfield 1979). Pair formation initiated by either sex (Tracy and Schamel 1988); may require only a few hours. Characterized by (1) aerial chases; (2) initiating bird attempting to remain close to, exhibiting appeasements behaviors to, and persistently following the potential mate; (3) initiating bird attempting to drive away same-sex conspecifics; (4) some aggression between potential pair members, usually by potential mate toward initiating bird when the latter approaches <0.5 m; and (5) gradual acceptance of initiating bird by the potential mate (Tracy and Schamel 1988). Pairs can be identified by (1) mutual Pushing (Bengtson 1968; Fig. 4F), accompanied by rapid, soft Twittering, especially in presence of conspecifics; (2) association <0.5 m with no aggression; and (3) opposite-sex defense of pair bond,

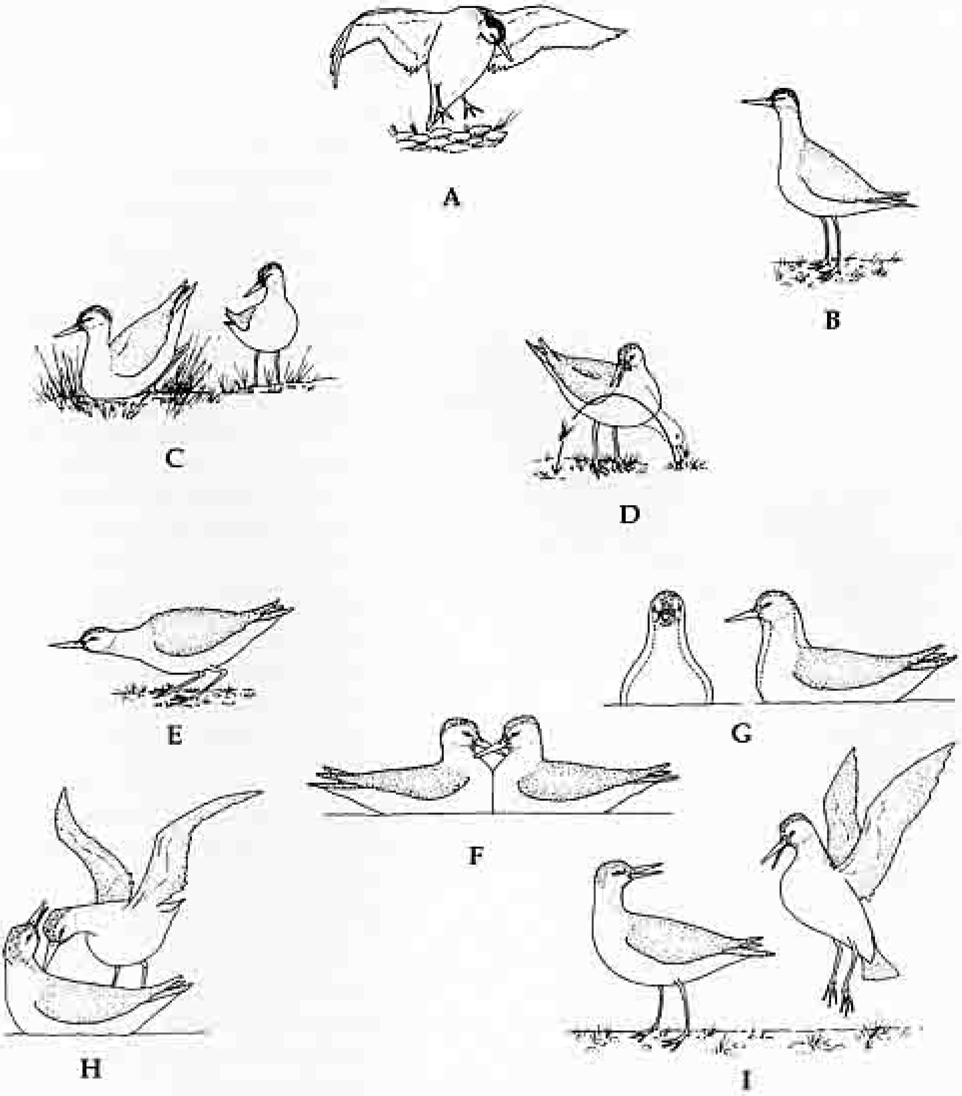

Figure 4. Behaviors of Red Phalaropes. A. Wing Whirr. B. Precopulatory Upright. C. Bowing. D. Sideways Throwing. E. Head-Forward Threat. F. Pushing. G. Imposing Posture. H. Overt Attack. I. Driving Flight. See text for details. Drawing by D. Hollingdale.

female more aggressive to intruding male, males to intruding female. Distance between pair members increases over time: first day, pair bond, <5 m apart 90% of time; second day, pair bond–first egg, <5 m apart 75% of time; first–third egg, <5 m apart 60% of time; fourth egg, <5 m apart 25% of time (as male begins incubation; DS and DMT). Both sexes initiate copulations; relative proportion initiated not known. Precopulatory displays variable; often subtle, easy to miss (Fig. 4B): Wing Whirrs (Mayfield 1979), Precopulatory Upright (Howe 1975a), Bowing (Ridley 1980), vocalizations (DS and DMT). Copulations usually on land, but occasionally on water; 6–10 s (Mayfield 1979). More commonly on land than in Red-necked Phalarope (Rubega et al. 2000). Successful copulations (determined by cloacal contact) in 55% of 91 attempts at Barrow (DS and DMT). Postcopulatory events include Wing Whirrs and Post-Copulatory Flight, where male dismounts, then flies, closely followed by female (giving appearance of female chasing male). Pair bond may end with last egg laid at nest (Mayfield 1979) or persist up to 13 d postlaying (Schamel and Tracy 1977).

Extra-pair copulations (EPCs). Little information. At Igloolik, n. Canada, 6.5% chicks ($n = 70$) resulted from extra-pair fertilizations (Dale et al. 1999), which occurred in clutches laid late in the season, suggesting they resulted from stored sperm from first males, as in Red-necked Phalarope (Schamel 2000). Extreme length of Red Phalarope sperm suggests intense sperm competition (Johnson and Briskie 1999).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Very gregarious summer, winter, and during migration. Solitary individuals uncommon. Flying individuals often call and join groups on ponds or at sea. Can form dense feeding aggregations during midge hatches or in zooplankton concentrations on freshwater ponds or at sea. Aggressive interactions minimal, except for breeding season, and usually brief (<1 s); associated with individual space for feeding. Much contact by soft vocalizations in flocks; responds to Alarm Calls by taking flight. Aggressive interactions on breeding grounds associated with competition for mates and incubating male intolerance of females. May form flocks of hundreds (Holmes 1939; Watson and Divoky 1974a, 1974b), but more commonly in flocks of tens (Obst and Hunt 1990).

Play. Not known.

Nonpredatory interspecific interactions. Feeding often facilitated by associations with marine mammals (Kumlien 1878, Ryder 1957, Harrison 1979, Obst and Hunt 1990, Grebmeier and Harrison 1992) and with other birds (van Swelm 1975, Schneider et al. 1990, Youngman 1995). Postbreeding Red Phalaropes so closely associated with Atlantic bowhead whales near Greenland that whalers tracked aerial flocks to surfacing whales (Kumlien 1878). In late Jul–early Aug in n. Bering Sea, w. Alaska, 87% of Red Phalaropes (n = 585 birds) observed on water were associated with whales, and 28% of whale sightings (n = 95 whales) included Red Phalarope sightings (Obst and Hunt 1990). Gray whales scoop benthos; small or injured benthic amphipods escaping whale baleen remain in mud plume created by whales. Flocks of Red Phalaropes remained at mud plumes an average of 17 min longer than other foraging bird species; stomachs of collected phalaropes in these plumes contained 100% benthic amphipods (Obst and Hunt 1990). Phalaropes do not follow individual whales. Instead, fly high after leaving plume, search for new mud plume, and settle in newest section of plume (Obst and Hunt 1990, Grebmeier and Harrison 1992). Also may consume invertebrate parasites associated with whales (Kumlien 1878). Postbreeding Red Phalaropes also observed feeding in close proximity to groups of walruses (*Odobenus rosmarus*) and ringed seals (*Pusa hispida*) in Bering Sea (Ryder 1957).

Observed surface-feeding on euphausiids injured by foraging murres (*Uria* sp.) near Pribilof Is., w. Alaska (Schneider et al. 1990). Also seen feeding in association with Eurasian Coots (*Fulica atra*) and Tufted Ducks (*Aythya fuligula*; van Swelm 1975), Mallards (*Anas platyrhyncos*) and Green-winged Teal (*Anas crecca*; Kramer and Palmer 1993), Avocets (*Recurvirostra avosetta*; Youngman 1995), and Long-tailed Ducks (*Clangula hyemalis*; DS).

Often nests in high densities in Arctic Tern colonies (DS and DMT).

Reindeer (*Rangifer tarandus*) trampled one nest (Schamel et al. 1979). Trampling by caribou (*R. tarandus*) can lead to significant nest losses (Troy 2000), especially in years with late snow melt, followed by high temperatures before hatching, which drives caribou coastward for relief from insects.

PREDATION

Kinds of predators; manner of predation. On breeding ground, arctic (*Alopex lagopus*) and red foxes (*Vulpes vulpes*), short-tailed (*Mustela erminea*) and least weasels (*M. rixosa*), polar bear (*Ursus maritimus*), Gyrfalcon (*Falco rusticolus*; Manniche 1910), Peregrine Falcon (*F. peregrinus*; Sutton 1932); Parasitic (*Stercorarius parasiticus*) and Long-tailed jaegers (*S. longicaudus*) are predators of eggs and/or chicks and/or adults. Sandhill Crane (*Grus canadensis*) and arctic ground squirrel (*Citellus parryi*) may occasionally be significant predators on eggs. Aluminum band from chick in Glaucous Gull (*Larus hyperboreus*) pellet (DS and DMT). Parasitic Jaegers and Glaucous Gulls observed killing and eating phalaropes in Beaufort Sea, n. Alaska (Young 1954, Divoky 1984).

Response to predators. Stretches neck horizontally and flattens body into water during overflight of predator (Brown 1978); moves into emergent vegetation, if nearby (DS and DMT). If startled at close range on water, will shallow-dive (DS and DMT). Incubating males mob terrestrial predators on breeding grounds, frequently joined by variety of other species; "alarm" calls given. Some incubating males perform distraction displays (feigning broken wing, Screams) when flushed from nests at short distances (<2 m; DS and DMT). Others flush at long distance (>25 m) and never perform distraction displays. Likelihood of distraction display apparently related more to individual differences and less to seasonality; some individuals usually perform distraction displays, while others never perform them (DS and DMT). Some incubating males can be lifted from their nests by hand (DS and DMT).

BREEDING

ENDOCRINOLOGY

No endocrinology work specifically on Red Phalaropes. Probably similar to Wilson's and Red-necked phalaropes (see Colwell and Jehl 1994, Rubega et al. 2000). Gonadal steroids not gender-reversed (Gratto-Trevor et al. 1990), but prolactin levels (associated with parental care) are reversed (Oring and Fivizzani 1990).

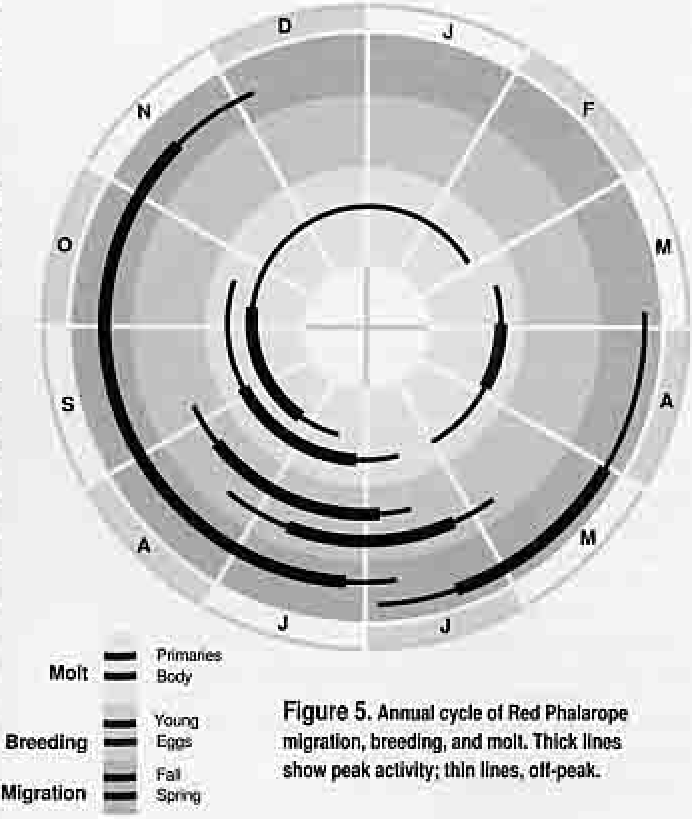

Figure 5. Annual cycle of Red Phalarope migration, breeding, and molt. Thick lines show peak activity; thin lines, off-peak.

PHENOLOGY

Pair formation. May begin en route to breeding grounds (Dawson 1923). Some arrive paired, others form pairs soon, or several days, after arrival (Bengtson 1968, Schamel and Tracy 1977, Mayfield 1979).

Nest-building. Scrape formation precedes egg-laying by 2–4 d (Mayfield 1979, DS and DMT).

First/only brood per season. Figure 5. Arrival-laying interval longest at most southern latitude, Yukon-Kuskokwim Delta, sw. Alaska (13 d; see Schamel and Tracy 1987), shortest at most northern site, Bathurst I., n. Canada (2 d; Mayfield 1979). Overall, however, length of nest-initiation period for a population shows no significant latitudinal trend; 22 d ± 6.2 SD (Barrow, n. Alaska; Schamel and Tracy 1987), 19.3 d ± 3.2 (n. Canada; Mayfield 1979). Laying begins 27 May in south (Schamel and Tracy 1987; Fig. 5), 1–6 Jun at Arctic Circle (Schamel and Tracy 1987), 10 Jun in n. Alaska and Siberia (Kistchinski 1975, Schamel and Tracy 1977), 20 Jun in n. Canada (Mayfield 1979).

Timing of nest initiation related to snow conditions. At Prudhoe Bay, n. Alaska, in multiyear study, the year with least snow cover in early Jun had earliest nest initiation (Troy 1996). In far north, limited snow-free habitats may increase predation and control timing of nest initiation (Byrkjedal 1980).

Feeding conditions during laying, timing of hatch, and the advantages of early adult departure are also important variables in determination of nesting season (Meltofte 1985). Decreased variability (increased predictability) in summer daily-temperature patterns correlated well with the nesting period at Barrow (Myers and Pitelka 1979).

Hatching in w. Alaska, late Jun–20 Jul (Schamel et al. 1979) and in n. Alaska, early Jul–late Jul (DS and DMT); begins 29 Jun in Svalbard (Ridley 1980) and 1 Jul in n. Canada (Mayfield 1979). Parental care ends late Jul in south (w. Alaska; Schamel and Tracy 1987), early Aug in north (Bathurst I.; Mayfield 1979).

Second/later brood per season. None.

NEST SITE

Selection process. From DS and DMT. Both sexes participate in nest-site selection. Site-selection displays observed during first day of pair bond and up to egg-laying. Most initiated by female >1 d before laying; male initiates most <1 d before laying. Bowing (Ridley 1980; Fig. 4C) and Rapid Twittering (5 peeps/s) initiates site-selection displays. Bowing bird's mate responds by walking to displaying bird and standing nearby, sometimes moving onto display site. Pair members do not always respond to Bowing. Some sites denuded by scraping with feet. Rarely, male tosses bits of vegetation toward scrape with Sideways Throwing (Fig. 4D). Female sometimes resumes initiation of site-selection displays when associating with incubating male (Schamel and Tracy 1977). No data on which sex ultimately chooses nest site.

Microhabitat; site characteristics. Moist areas of flat tundra; typically in sedge, with vegetation pulled over nest to form canopy; 15 cm–15 m from shallow pond or standing water (Whitfield 1995). Nests highly clumped in suitable habitat, leading to fragmented distribution (Ridley 1980); related to snowmelt patterns and/or temporal food availability. In n. Siberia and n. Canada, 5–200 m from ponds (Kistchinski 1975, Mayfield 1979). Sometimes over standing water (Brandt 1943); on rare occasions, open ridge with no concealing vegetation (DS and DMT); open nests on seaweed (Løvenskiold 1964).

NEST

Construction process. First egg typically laid in bare scrape. Male, alone, Sideways Throws bits of vegetation toward nest, from edge of nest to 50 cm (Mayfield 1979). No female assistance. Number of male visits to nest increases to onset of incubation, which often begins after laying of third egg; some sitting briefly with first egg (Mayfield 1979). Males flushed from 2 eggs probably constructing nest, not incubating, as suggested by Kistchinski (1975). Most construction completed by third egg (Mayfield 1979).

Structure and composition matter. Variable; depends on materials available. Often sedge or grass, willow (*Salix* sp.) leaves (Kistchinski 1975, Mayfield 1979), stones, lichen, feathers, saxifrage (*Saxifraga* sp.), or sometimes nothing (Løvenskiold 1964). No information on selectivity of materials.

Dimensions. Diameter 8–10 cm; depth 2–3 cm (Løvenskiold 1964). Two dried nests from n. Canada: 4.3 g, 5.1 g (Mayfield 1979).

Microclimate. Vegetative covering over nest slows cooling of eggs during periods when male absent (Kondrat'ev 1982).

Maintenance or reuse of nests, alternate nests. Not common. Of 50 nests found at Prudhoe Bay, n. Alaska, only one reused following year (Moiteret et al. 1996). On one occasion, same nest scrape used in 2 successive years, but apparently by different pairs (JD).

Nonbreeding nests. Not known to occur.

EGGS

Shape. Ovate pyriform (Harrison 1978), following typical shape found in most scolopacids. Arranged in nest with pointed ends inward. Considerable variation in degree of bluntness of pointed end.

Size. Insufficient data to assess geographical trend; none readily apparent. Dimensions (mean in mm ± SD [*n*]) of freshly laid eggs: Igloolik, n. Canada (*n* = 217), length 31.4 ± 1.3, breadth 22.3 ± 0.6 (JD); Barrow (*n* = 226), length 32.2 ± 1.3, breadth 22.6 ± 0.6; Cape Espenberg, w. Alaska (*n* = 76), length 31.8 ± 1.2, breadth 22.1 ± 0.4 (DS and DMT). Means in mm from U.S. National Museum: location unspecified (*n* = 148), length 31.5, breadth 22.0; Bent 1927); Iceland (*n* = 48), length 32.5, breadth 23.0 (Gillandt 1974); Iceland (*n* = 28), length 32.2 ± 0.6 SD, breadth 23.2 ± 0.4 SD (Whitfield 1995). Correlation between egg length and breadth is significant but weak ($p = 0.0001$, $r^2 = 0.092$); egg length more variable than egg width (JD).

Mass. Insufficient data to examine geographical trends. Mean fresh egg mass ± SD in g: Igloolik, 7.90 ± 0.55 (*n* = 139; JD); Barrow, 8.0 ± 0.53 (range 6.8–8.9, *n* = 43; DS and DMT), Cape Espenberg, 7.71 ± 0.65 (*n* = 30; DS and DMT). Mean total clutch mass of 4-egg clutches 31.75 ± 2.00 (*n* = 34 nests; representing 52% of average nonlaying female body mass; JD). This is a relatively small percentage for shorebirds, possibly an adaptation for incubation by smaller-sized males (JD), or energy-conserving for female that produces multiple clutches (Ross 1979). Incubating-male mass not significantly related to egg mass (JD). Mean mass of eggs (± SD) at early hatching pip stage: Igloolik, 6.81 g ± 0.59 (*n* = 111; JD). Eggs estimated to lose approximately 15% of mass to water loss throughout incubation (JD).

Color. Light olive, green, or deeper olive-buff. Irregular blotches, speckles of black-brown and some pale purple. Irregular large blotches, combined with profuse fine markings (Harrison 1978). Egg shapes and markings considerably more uniform within clutches than between clutches (DS and DMT, JD), possibly due in part to genetic differences among females.

Surface texture. Smooth, slightly glossy (Harrison 1978).

Eggshell thickness. From collection of 75 eggs (20 clutches) from North America between 1922 and 1963, there was a nonsignificant decline in shell thickness (Morrison and Kiff 1979).

Clutch size. Typically 4, as in other arctic-breeding shorebirds. Mean ± SD: Cape Espenberg, 3.7 (range 1–4 [*n* = 100]; DS and DMT); Barrow, 3.8 ± 0.6 (range 1–4 [*n* = 97]; Schamel and Tracy 1987); Igloolik, 3.9 ± 0.3 (range 2–4, *n* = 66), n. Canada, 3.9 (range 3–5 [*n* = 62], Mayfield 1979), n. Siberia, 3.8 (range 2–4; Kistchinski 1975). Very few reports of clutch >4: 5 eggs (*n* = 1; Mayfield 1979); 6 eggs (*n* = 1; Løvenskiold 1964); but see Brood parasitism, below.

Egg-laying. If conditions favorable, some females begin clutches within 2–3 d of arrival at breeding grounds (Schamel and Tracy 1987, JD). At Chevak, w. Alaska, yolk formation required 4–5 d (*n* = 5 eggs), shortest span of any species reported (Roudybush et al. 1979); 6–7 d (*n* = 7 eggs) for Red-necked Phalarope. Delay between arrival and laying generally longer in lower latitudes (Schamel and Tracy 1987). At Bathurst I., eggs laid at any time of day, but most (69%; *n* = 19) in latter half of day; mean interval between laying of successive eggs 23.9 h (range 21–34, *n* = 19); extreme interval of 34 h occurred during inclement weather; laying interval shorter as clutch progresses (Mayfield 1979). Most clutches completed in 4 d. Pairs disturbed during egg-laying or pairs laying late in breeding season sometimes desert nests. Male maintains close proximity (<5 m) to female while she is laying an egg, often <10 cm. Laying female sometimes calls to male with rapid Twittering (DS and DMT). Individual egg losses not replaced, but complete clutch losses sometimes replaced at new nest site; average clutch-replacement time (time between loss of clutch and first egg at subsequent nest) brief, 3–4 d; for polyandrous females, time between clutches slightly longer, 3–5 d (Schamel and Tracy 1977). May reflect increased time necessary to pair with new male. These patterns suggest repeated egg-laying is not energetically stressful for females. In Iceland, 16–18 d between successive clutches (Whitfield 1995), perhaps reflecting reduced availability of males.

INCUBATION

Onset of broodiness and incubation in relation to laying. Male incubates eggs and broods chicks alone. No incidences of female parental behavior reported in any intensive study. Short visits by both sexes to nest begin with first egg and increase through third egg, when regular incubation begins (Mayfield 1979, DS and DMT).

Incubation patches. Two oval patches, joined at midbelly. Naturally found only in males; experimentally produced in females (see Johns and Pfeiffer 1963). Patches not seen until egg-laying begins; some males with incubation patches arriving in midseason at ponds and small lakes en route to ocean may have lost clutches (DS and DMT).

Incubation period. Mean of 19 d (range 17–26) reported from laying of last egg to hatching of first egg (Brandt 1943, Mayfield 1979, Schamel and Tracy 1987). Incubation period for freshly laid eggs in artificial incubator 18.8 d (range 18–19 [*n* = 6 clutches]; JD). Incubation period 1–3 d shorter at higher latitudes (Schamel and Tracy 1987). At Barrow, clutches produced later in season had shortest incubation periods (18 vs. 21 d for early-nesting birds; Schamel and Tracy 1987, DS and DMT), as found in Red-necked Phalarope (Schamel 2000).

Parental behavior. Male incubates and broods young alone. Incidental reports of female incubation (at 3 of 17 nests; Forbes et al. 1992) and broodiness (Sutton 1932) probably erroneous through misidentification of brightly colored males as females, misinterpretation of female's laying behavior as incubation behavior, or misinterpretation of sexual interest in brooding male as parental broodiness by female (Höhn 1965, Bengtson 1968). No incidence of female parental behavior in any intensive field study. Mean nest attentiveness: n. Alaska, 83% (range 68–95%; repeated observations at 5 nests; DS and DMT), w. Alaska, 70% (39–95%; 8 nests; Erckmann 1981); Svalbard, 81% (60–90%; 1 nest; Mehlum 1991); e. Siberia, 85–88% (Kondrat'ev 1982). Attentiveness lower during daytime: w. Alaska, day 54% versus night 87% (Erckmann 1981); Svalbard, day 74% versus night 89% (Mehlum 1991); Barrow, night 96% (DS and DMT). Daytime nest recesses probably less costly to eggs and more profitable for feeding (Erckmann 1981). Attentiveness greater during cold and inclement weather (Erckmann 1981, Mehlum 1991) and at more northerly latitudes (Schamel and Tracy 1987). Median incubation bout 18 min; median recess 6.5 min, 95% <18 min (Mehlum 1991). Males lost significant mass during incubation in 3 populations: Cambridge Bay, n. Canada, 10% of body mass (Erckmann 1981); Barrow, 8% (range 0–13.5%; Schamel and Tracy 1987); Igloolik, 14% (JD). Suggests energetic cost associated with male parental care. Loss of male mass less pronounced at Cape Espenberg, in southern part of range (Schamel and Tracy 1987).

Incubating male may flush underfoot or 30–50 m away (Höhn 1971, Mayfield 1979, DS and DMT). Numerous reports of humans touching incubating males on nests without causing them to flush (Manniche 1910, Mayfield 1979, DS and DMT). Male flushing at short distance may give distraction display: feigning broken wing and fluttering on ground (Manniche 1910, Sutton 1932, Mayfield 1979, DS and DMT), rarely "rodent run." Höhn (1971) never saw distraction display in Red Phalarope, and Kistchinski (1975) saw only one. In contrast, Mayfield (1979) noted some individuals performed these displays regularly. At Barrow, 36% of 25 closely monitored incubating males gave distraction displays. No seasonality to these displays; given in all stages of incubation, from first through last day. No documented effect on nest success; 50% of displaying males suffered egg predation, which matched population rate (DS and DMT). Distraction display often accompanied by vocalizations (Mayfield 1979, DS and DMT).

Hardiness of eggs against temperature stress; effect of egg neglect. Egg appears adapted to withstand cold temperatures, possibly resulting from high lipid content in eggs (R. Montgomerie pers. comm.). First egg in early nests can survive being unincubated for 2–3 d, with low temperatures near or below freezing; occasional long absences by males during incubation appear to have little detrimental effect on embryos (Erckmann 1981, Mehlum 1991).

HATCHING

Preliminary events and vocalizations. Faint peeping and scraping of egg tooth against shell heard from chicks 2–3 d before emergence. Male attentiveness at nest increases near hatching (DS and DMT).

Shell-breaking and emergence. Young emerge from large end. One young found dead after attempting to emerge from small end (DS and DMT). Hatching relatively synchronous (Kistchinski 1975). Mean hatch interval between first and last egg 17.7 h (range 4–43 [*n* = 34]; JD). Late-hatching young seldom abandoned. Hatching at all times of day (DS and DMT).

Parental assistance and disposal of eggshells. Hatching assistance not recorded and unlikely. Male flies with shell 10+ m from nest, often to nearby pond (DS and DMT). Minute shell fragments often left in nest; may serve as indicator of successful hatch (Mabee 1997).

YOUNG BIRDS

Condition at hatching. Very precocial. Fully covered with down at hatch. Like other shorebird chicks, downy plumage cryptic. Uppersides tawny and cinnamon buff with 3 bold black stripes running down back; yellowish-white to grayish-white underparts (details in Appearance: molts and plumages, below). Leaves nest same day as hatch (Mayfield 1979). Immediately upon leaving nest, young can walk, run, swim, and find food on own. Young chicks typically do not venture into water away from cover (Mayfield 1979). Measurements of newly hatched young at nest in Barrow: mean mass 5.1 ± 0.6 SD (n = 59); mean wing length 10.5 mm (range 10.0–11.0, n = 9); culmen 7.6 mm (range 7.0–8.2 [n = 9]; DS and DMT).

Growth and development. Data scarce. Growth in body mass follows sigmoid curve; slow mass increase from day 0–3, then rapid increase through day 18. Wing at hatch 1.0 cm; doubles in length by day 7 (2 cm), doubles again by day 12 (4 cm), and again by day 17 (8 cm). No information on timing of Prejuvenal molt, but head retains downy feathers when able to fly (DS and DMT).

No data on thermoregulatory ability of Red Phalarope chicks, specifically. Probably similar to other arctic-nesting species: small chicks less able to maintain temperature (Visser and Ricklefs 1993). This, coupled with cold environment, probably explains intensive brooding received by chicks through age 3 d.

PARENTAL CARE

Brooding. Male only. Begins with first chick at nest. At Barrow, intensive brooding day 0–4, moderate day 4–8, then occasional through day 12. Occurs more frequently at night and during cold and/or wet conditions. Brooding initiated and terminated by either chicks or male. Chick peeps and shivers when cold; male gathers chicks with brooding call. Male remains close (5–15 m) to chicks during first few days. Ranges 50–100+ m later; flies over area with loud, plaintive *Whe-eep* call, lands when chicks respond. Brooding apparently ends when chicks fail to respond to brooding call of male (DS and DMT). Male very alert to potential threats when caring for young. Uses warning calls, often while flying in large circles, apparently to alert chicks to potential danger (DS and DMT).

Feeding. Male may lead chicks to good feeding areas. Chicks precocial, feed themselves on small adult insects. One old report of males feeding downy young (see Sutton 1932). Increased feeding and walking by male near nest noted just before hatch; male thought to be sampling nearby habitat (DS and DMT). No information on feeding or intake rates of chicks.

Nest sanitation. Not reported; nest abandoned <1 d after hatching of chicks.

Carrying of young. Not reported or suspected.

COOPERATIVE BREEDING

Not reported or suspected.

BROOD PARASITISM

Intraspecific brood parasitism rare, if it occurs at all. Two reported cases with clutch >4 possibly resulting from 2 females (Løvenskiold 1964). No cases of brood parasitism detected in 18 broods examined with DNA fingerprinting (Dale et al. 1999). Interspecific brood parasitism not reported.

FLEDGLING STAGE

Departure from nest. Young depart soon after drying, <15 h after hatch of first chick (Mayfield 1979). Delayed in cold or wet weather. Not dependent upon time of day.

Growth. Able to fly at 18 d of age (n = 2; Parmelee et al. 1967, DS and DMT): mass: 46.8 g (85% adult mean), bill: 15.7 mm (68% adult mean), wing: 8.0 mm (60% adult mean). No data on growth after fledging.

Association with parents or other young. Not recorded after 12 d (DS and DMT).

Ability to get around, feed, and care for self. Few data. Young secretive until able to fly, then quite visible at ponds, where feeding aggregations form at good food sources. No evidence that brood remains together.

IMMATURE STAGE

Little information. Young from inland nesting sites drift coastward, gathering in foraging flocks on ponds and small lakes en route to ocean. Postfledging young depart tundra breeding habitats last, following adult females and males, in that order. Juveniles begin movements toward wintering areas in mid-Jul through early Aug, later farther north (Schamel 1978, Mayfield 1979, Craig and Schell 1984, Divoky 1984). In n. Alaska, congregate around barrier islands and spits (Connors 1984, Divoky 1984), often remaining until early Sep (Jacques 1930, Connors and Risebrough 1978), occasionally Oct (Johnson 1979). No recorded spatial segregation by age. In mid-Aug, sex ratio (determined by internal examination) of juveniles killed

Table 1. Reproductive success of Red Phalaropes by region. Nests that hatched at least one chick were considered successful.

	% nests (range of values)				
Region/source	Successful	Depredated	Abandoned	*n*	Years of study
W. Alaska					
Schamel et al. 1979	73 (60–93)	17 (7–30)	7 (0–12)	49	1976–1981
DS and DMT	18 (0–40)	80 (50–100)	2 (0–10)	32	1994–1999
Erckmann 1981	67	12	12	33	1977–1978
N. Alaska					
Bergman et al. 1977	40 (17–80)	59 (20–83)	0	41	1971–1973
Erckmann 1981	19	81	0	16	1976
Moiteret 1996	77 (53–100)	23 (0–47)	0	56	1989–1992
DS and DMT	60 (47–73)	33 (27–39)	7 (0–14)	44	1973–1974
N. Canada					
Mayfield 1979	47 (17–100)	51 (0–77)	2 (0–6)	36	1970–1973

by collisions with power lines at Barrow, not significantly different from parity (*n* = 70).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Likely begin breeding as yearlings, but essentially no information. Only 1 known yearling ever recorded (*n* = 185 banded chicks), a breeding male (Schamel and Tracy 1977, 1991). Annual breeding likely, based upon limited return of banded adults, but return rates of banded adults low (10–20% [*n* = 154 banded adults]; Colwell et al. 1988, Schamel and Tracy 1991). Some indication of higher return rate in more southern part of range in Alaska (Schamel and Tracy 1991) and in isolated nesting habitats in Iceland (Whitfield 1995).

Clutch. Typically 4 eggs in 1 or 2 clutches (Gillandt 1974, Whitfield 1995). One female known to produce 3 clutches in 1 breeding season (Schamel and Tracy 1977). Most shorebird ovaries examined in w. Alaska contained 12–15 ova, but Red Phalaropes contained 40–55 ova, suggesting higher potential reproductive output (Brandt 1943).

Annual and lifetime reproductive success. Annual success variable (Table 1). Depends on predator abundance, especially foxes; if fox population is high and lemming (*Lemmus* sp.) population is low, predation on eggs and adult birds can be severe (Larson 1960; Mayfield 1976, 1979; Erckmann 1981; DS and DMT). The distribution and habitat use of birds in the Arctic may be determined by access by arctic foxes (Speller 1969). In northern part of breeding distribution, late snow melt can prevent nesting about every third year (Bird and Bird 1941, Mayfield 1978), apparently through unavailability of both food and nesting habitat. Inadequate data to determine if delayed phenology, by itself, affects productivity. Mean brood size at hatch at Barrow 3.4 (*n* = 34 nests [range 3.3–3.6; 2 yr]; Schamel et al. 1979), Bathurst Inlet, n. Canada, 3.5 (*n* = 12 nests [range 2.7–4.0; 3 yr]; Mayfield 1979). Little information on success rate from egg to fledging: estimated 10% from n. Canada (Mayfield 1979), 10–20% from n. Siberia (Kistchinski 1975). Lifetime reproductive success not known, in part due to lack of long-term studies with banded birds and in part to low site fidelity.

Number of broods normally reared per season. One brood/male maximum. Polyandrous females may produce several clutches, but rarely >2 (Schamel and Tracy 1977, Whitfield 1995). In n. Alaska, 36% (*n* = 11) of females obtained 2 males one season (Schamel and Tracy 1977); in a small, isolated population in Iceland, 33% (*n* = 3) to 67% (*n* = 3) obtained 2 mates (Whitfield 1995). In s. Canada, 33% of broods (*n* = 18) contained extra-pair young, which could have resulted from residual sperm from first males in a polyandrous mating (Dale et al. 1999). These figures remarkably similar, suggesting no regional variation. Annual variation probably depends on male availability (Schamel and Tracy 1977).

Proportion of total females that rear at least one brood to nest-leaving or independence. No quantitative data, in part because pair bond can be quite brief, as well as paucity of studies with banded individuals. In n. Canada, "some" females fail to obtain mates (Mayfield 1979). Based on Red-necked

Phalarope (Rubega et al. 2000), probably 5–15% of females do not obtain mates.

LIFE SPAN AND SURVIVORSHIP

Almost no data. Small sample size of banded birds and low site fidelity (see Range, below) complicate data interpretation. Male banded as incubating adult in w. Alaska recaptured 5 yr later; at least 6 yr old (DS and DMT). At Barrow, n. Alaska, missing toes, broken leg bones, and/or tarsal joint injuries found in 10% ($n = 74$) of adult males, but in no females ($n = 27$); at Cape Espenberg, none of 55 males and 28 females had similar injuries (DS and DMT).

DISEASE AND BODY PARASITES

Diseases. No information.

Body parasites. Acanthocephala (*Polymorphus petrochenkoi*) from Alaska (Schmidt 1969).

CAUSES OF MORTALITY

Exposure and starvation. Emaciated migrants in Oct "cast up in numbers" along beaches in s. California in 1934 (Miller 1936: 14). If wind conditions unsuitable to maintain stable upwellings or water too turbid, birds may starve (Bond 1971). Weakened and dead Red Phalaropes recorded in 1969 in Humboldt Bay, n. California (Gerstenberg 1972).

El Niño-Southern Oscillation (ENSO) events may have adverse effect on species, but few data available. Breeding densities of both Red and Red-necked phalaropes decreased at Prudhoe Bay, n. Alaska, by >50% from 1982 to 1984, perhaps related to 1983 ENSO (Troy 1996). In s. Washington State waters, Red Phalarope very common in 1980, but extremely low during 1983 ENSO; numbers on rise through 1988 (Wahl et al. 1993).

Predation. No quantitative information at population level. Only incidental, anecdotal accounts of predation at sea (Sutton 1932, Young 1954, Divoky 1984). Increase in fox and crane abundance in recent years lowered hatching rates in w. Alaska (DS and DMT); unclear if this phenomenon widespread. Nest trampling by caribou headed coastward to avoid mosquitoes led to significant nest losses in n. Alaska (Troy 2000). See Behavior: predation, above.

Competition with other species. No information, but unlikely.

RANGE

Natal philopatry. Only 1 yearling out of 185 chicks banded at Barrow, n. Alaska, and Cape Espenberg, w. Alaska, known to have returned (Schamel and Tracy 1977, 1987).

Fidelity to breeding site and winter home range. Little information. Lowest fidelity of the phalarope species (Colwell et al. 1988). In n. and w. Alaska, only 4–15% of adult males ($n = 104$) returned the year following banding; almost none thereafter; only 3 of 50 adult females (6%) returned (Schamel and Tracy 1977, 1991; Moiteret et al. 1996).

Dispersal from breeding site. No information.

Home range. Typical core home range for breeding pair 3–5 ha, but can fly 300–2,000 m from nesting area to ephemeral food sources (DS and DMT). Following clutch completion, female ranges over larger area in search of new mate.

POPULATION STATUS

Numbers. Numbers fluctuate from year to year and throughout season. Population estimates quite crude. Estimate of worldwide population, based on distribution of breeding habitat and breeding densities, using at-sea estimate as a correction factor and using a conservative estimate of annual productivity: 5 million individuals (DS and DMT). This included 3.4 million adults and 1.6 million fledged juveniles. Estimates by geographic area: Alaska, 750,000 individuals; Canada, 500,000; Greenland, Iceland, Svalbard, tens of thousands; Russia, 1.9 million (DS and DMT). North American population estimated between 1 million and 2.5 million (Morrison et al. 2000).

Population estimates by region: Mackenzie Delta, 0 (Gratto-Trevor 1994); Anderson Delta, 0 (Höhn 1959); Adelaide Peninsula, 20,000 (Macpherson and Manning 1959); Rasmussen Lowlands, 212,000 (McLaren et al. 1977) and 40,000 (Gratto-Trevor et al. 1998); Banks I., 35,000 (Manning et al. 1956), Prince Wales I., 70,000 (Manning and Macpherson 1961); Creswell Bay, on Somerset I., 3,500 (Alliston et al. 1976); n. Canada: Prince Charles I., 283,200 (Morrison 1997).

At-sea estimates: e. Bering Sea, 700,000 during peak migration (Gould et al. 1982); n. Gulf of Alaska, 145,000 during peak migration (Gould et al. 1982); Davis Strait, ne. Canada, 300,000 late Jun (Orr et al. 1982).

Density estimates from breeding grounds show large differences, due to interyear variation, habitat differences, and perhaps effect of El Niño. Reported nesting densities in best habitats range from 8 to 70 nests/km^2 (Schamel et al. 1979). On south to north gradient, interyear variation factor of two at Cape Espenberg, w. Alaska (36–72 nests/km^2; Schamel et al. 1979), factor of five at Barrow, n. Alaska (Myers and Pitelka 1975a, 1975b; Myers et al. 1978a, 1978b), and factor of 14 variation at Bathurst I., n. Canada (Mayfield 1978). Data from Barrow indicate strong correlation between nest densities and regional snow melt phenology over 9 yr ($r = 0.97$, $p < 0.001$; DS and DMT). Nesting density highest when snow melt delayed because birds concentrated in earliest available habitat.

Selected sites in Alaska (values given are nests/km^2): Safety Sound, w. Alaska, 0 (B. K. Sandercock unpubl.); Wales, w. Alaska, 25–34 (J. Erckmann unpubl.); Cape Espenberg, w. Alaska, 36–72 (Schamel et al. 1979); Barrow, n. Alaska, 8–43 (Myers et al. 1975a, 1975b, 1978a, 1978b); Prudhoe Bay, n. Alaska, 4–8 (W. Hansen unpubl.), 2–12 (Troy 2000), 0–3 (Moiteret et al. 1996); Canning Delta, ne. Alaska, 26–48 (Martin 1983); Okpilak Delta, ne. Alaska, 14 (Spindler 1978).

Selected sites in Canada: Cambridge Bay, ne. Canada, 20 (Mayfield 1979); Jenny Lind I., ne. Canada, 12 (Mayfield 1979); Bathurst I., n.-central Canada, 0–14 (Mayfield 1978); Igloolik, n. Canada, 2–3 (Forbes et al. 1992); Prince Charles I., ne. Canada, 16–64 (Morrison 1997).

Outside North America: n.-central Greenland, 5 (Elander and Blomqvist 1986).

Trends. Apparently less common in n. Gulf of Mexico, compared with 40 yr ago; flocks of thousands (Weston 1953) versus infrequent sightings of singles (Duncan and Havard 1980). Surveys in e.-central Canadian Arctic showed breeding populations in 1994–1995 decreased 76% (from 165,000 to 40,000) from numbers in 1975–1976; not known, however, whether decrease represents persistent and continuing decline (Gratto-Trevor et al. 1998). Less common at Cape Espenberg in 1990s than in 1970s, probably owing to increased predation (Schamel et al. 1999). No indication of population decline in n. Alaskan population (Troy 1996). Has become less common in Iceland (Whitfield 1995). Apparent decrease from 1930s to 1979 in ne. Greenland (Elander and Blomqvist 1986).

POPULATION REGULATION

Little known; needs study. Delayed snow melt in northern areas of breeding range may adversely impact productivity in some years (Mayfield 1978). Increased predators also decrease productivity, and may increase adult mortality on breeding grounds (Larson 1960, Mayfield 1976, Schamel et al. 1999). Unknown whether food can be limiting factor on breeding grounds. ENSO may be a major threat, due to changes in oceanographic patterns and decreases in zooplankton, which could lead to starvation.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. No information.

Pesticides and other contaminants/toxins. Little information. Captive Red Phalaropes quickly learn to avoid experimentally oiled feeding pans, but even one learning episode may be lethal in nature (Connors and Gelman 1979); probably highly susceptible to oil pollution because of dependence on littoral and oceanic habitats.

Ingestion of plastics, lead, etc. All dead phalaropes (n = 20) found in Nov in s. California had 1.7–4.4 mm plastic balls (up to 36 balls) in stomachs (Bond 1971); individuals emaciated, approximately 50% lighter than normal, though unclear whether plastic ingestion was the cause. A 14-yr study of Red Phalaropes reported 69% of individuals collected off n. California (n = 55) had ingested plastics; no obvious signs of ill effects. Plastics may be mistaken as prey (Moser and Lee 1992).

Collisions with stationary/moving structures or objects. During 5-d foggy period in mid-Aug at Barrow, n. Alaska, at least 70 juveniles died from collisions with power lines. At this time, small flocks of Red Phalaropes were foraging in ponds near the coast, and in the littoral zone; power lines were perpendicular to their travel route (DS and DMT).

Fishing nets. No information. Due to mesh size, not likely a problem.

Degradation of habitat. Reindeer introduced to Spitsbergen in 1978 grazed accessible plants down to 2 cm, leaving Red Phalarope nests more exposed (Meier and Wuntke 1998). Suggestion that petroleum exploration and development in n. Alaska correlated with decrease in nesting Red Phalaropes, but not Red-necked Phalaropes (Meehan 1986; based upon 2-yr study); other factors could have affected the difference.

Disturbance at nest and roost sites. Regular disturbance at nests may induce abandonment, although only anecdotal accounts available. Abandonment not common, even in intensive studies (Table 1, DS and DMT).

Direct human/research impacts. During human disturbance in tern colony, terns pecked and killed unattended Red Phalarope chicks (Meier and Wuntke 1998). Trapping males at nests and blood-sampling may have induced occasional nest desertion, especially in late-season nests and in males caught early in incubation at Igloolik, n. Canada (JD).

MANAGEMENT

Not currently threatened or endangered. Some data indicate world populations are declining; see Trends, above. No current management for this species. Likely vulnerable to oil spills (Connors and Gelman 1979). Increased development in breeding range could cause increased mortality via power lines. Appears to avoid areas of oil development on breeding grounds (Meehan 1986, TERA 1994).

APPEARANCE

MOLTS AND PLUMAGES

Descriptions based upon Höhn 1965, Prater et al. 1977, Gilligan and Schmidt 1980, Cramp and Simmons 1983, Hayman et al. 1986, Paulson 1993. See Figure 5 for summary of timing of molt.

Hatchlings. Precocial and downy. Crown black and variably mottled in center with buff-brown/ ocher. White around eye and on chin. Forehead warm buff, often with distinct black spot just above upper bill. Thin black stripes running along lores to just behind eye, and less distinct black band down nape. Upperparts tawny and cinnamon buff with 3 bold black stripes running down back. Black on rump and on sides just above thigh. Yellowish buff on throat, paling to white on central breast and grayish white on lower breast and belly. Wings cinnamon-brown with white pads and slightly spotted with black at edge.

Juvenal plumage. Prejuvenal molt complete; precise timing unknown (Jul–early Aug). Crown and hindneck blackish brown, with crown-feathers thinly edged with buff. Chin, lores, and forehead pale buff to white. Ear-coverts buffy gray. Blackish feathers at spot in front and below eye to ear-coverts, whitish postocular stripe. Mantle, scapulars, tertials, wing-coverts, and upper tail-coverts dark brown, boldly edged with buff, giving scalloped appearance (especially on mantle). Back and rump dark gray with slight buff tinge. Underparts white. Breast, flanks, and sides of neck suffused with pinkish buff in fresh-plumaged birds. Central rectrices dark gray with black tips, edged with cinnamon-buff. Outer rectrices similar but less boldly patterned. Wing as in Definitive Alternate plumage.

Basic I plumage. First Prebasic molt partial. Timing variable, Aug–Dec. Head- and body-feathers completely replaced, wing- and tail-feathers retained. Basic I plumage same as Definitive Basic plumage except for more black on crown, black streaks at front of mantle and pinkish-buff tinge retained on foreneck, all fading away as winter progresses (Paulson 1993).

Little information on molt in immatures during remainder of second calendar year, during which they presumably remain at sea. Limited data from specimens suggest a partial Prealternate I molt occurs during spring that produces an Alternate I plumage worn May–Aug, but Alternate I plumage has not been described (Cramp and Simmons 1983).

Definitive Basic plumage. Definitive Prebasic molt complete. Primaries replaced from innermost outward. Occurs at sea before autumn migration, after departure from breeding grounds. Timing variable; molt starts earlier in most females and some failed breeding males (early to mid-Jul) and later in breeding males and a few females (early Aug). Body-feathers and primaries start first, followed by secondaries and tail. Individuals that complete molt before migration have completely replaced body-feathers by mid-Sep and primaries by late Sep. Primary molt suspended during migration if incomplete (or delayed if still not started), until restarted on wintering grounds (Nov–Dec). Many migrants in flocks show plumages intermediate between Alternate and Basic. Latest individuals complete primary molt by Mar, with noticeable difference between worn inner and fresh outer primaries (Cramp and Simmons 1983). More study needed on patterns of molt, particularly at sea.

Sexes similar. Forehead, crown, lores, chin, and neck white. Nape black, extending variably into back of crown. Bold black patch from spot in front of eye to lower ear-coverts, separated from black nape by white stripe extending from above eye, along upper ear-coverts, and down sides of nape. Mantle and scapulars pale blue-gray. In fresh plumage, feathers on upperparts thinly edged with white. Tertials blue-gray, thinly margined with white. Underparts white. Sides of breast and flanks variably streaked with gray. Wing and tail as in Definitive Alternate.

Definitive Alternate plumage. Definitive Prealternate molt partial to incomplete; occurs mid-Mar through early Jun; head, body, tertials, and sometimes a few rectrices replaced. Sexually dimorphic, with females brighter and more boldly patterned than males.

FEMALE. Less variable than male. Forehead, crown, nape, lores, and chin uniform dark gray or black. Center of nape gray. Bold, white oval patch on sides of face surrounding eye, extending to sides of nape. Upperparts black, scapulars and tertials margined boldly with cinnamon-buff (less so on mantle), giving distinct streaked appearance. Wing-coverts medium gray, fringed with white. Lower back and rump gray with some rufous at sides. Upper tail-coverts black, outermost coverts rufous. Neck, chest, and underparts rich uniform chestnut-red, sometimes with few scattered white feathers on belly. Central rectrices black, outer ones more gray. Upper wing dark gray with broad white stripe running lengthwise, formed by white distal halves on greater secondary wing-coverts and prominent white tips on inner greater primary wing-coverts. Flight feathers shading to dull black on outer primaries; shafts white. Secondaries narrowly bordered white. Under wing and axillaries entirely white.

MALE. Like female but duller and more variable; bright males approaching female level of coloration. Forehead, crown, and nape cinnamon-brown, variably streaked with black and buff. Mottled crown of male most reliable sexing feature. Chin and in front of eye dark gray. Patch above and behind eye white to pale buff, cheeks and ear-coverts cinnamon-buff. Upper back, scapulars, and tertials black to dark gray, bordered broadly with buff to cinnamon-buff (mantle more broadly edged than in female, scapulars and tertials less so). Lower back blackish, rump and tail-coverts cinnamon-rufous with central feathers streaked with black. Underparts and foreneck cinnamon-rufous to chestnut-red, often flecked with white feathers and with variable white patch on belly spreading upward onto breast (range 0–70% of underparts white [*n* = 35]; JD). Inner rectrices blackish with buff to white borders; outer rectrices grayer and less boldly edged with white. Wing as in female.

Male much more variable than female, particularly color and amount of white on underparts, and boldness of markings on head. Variable enough for use in individual identification in field (Ridley 1980). Variation on continuous gradient (Cramp and Simmons 1983, JD); evidence regarding distinguishable morphs (Kistchinski 1975) and different geographical races not apparent. See Systematics: geographic variation, above. Variations maintained in 8 distinctly plumaged males over successive breeding seasons (JD, DS and DMT), suggesting plumage color and pattern is fixed and genetically determined.

BARE PARTS

From Cramp and Simmons 1983.

Bill and gape. Alternate plumage: Bill yellow with orangish base. Tip of bill black. Amount of black tip quite variable; more black in male than in female. Basic plumage: Bill black with gray overcast; may have slight yellow at extreme base. Horn or gray in downy young.

Iris. Dark brown.

Legs and feet. Alternate plumage: pale blue with yellow lobes. Basic plumage: gray with yellow gray lobes. As in all phalaropes, toes with scalloped lobes, which assist in swimming. Lobes present at hatch; downy young swim well.

MEASUREMENTS

Appendix. Females significantly larger than males, but much overlap in all measurements. No geographic differences detected (Appendix, and Cramp and Simmons 1983). Sexual size dimorphism present and significant in juveniles 25–40 d old. No data on this species at sea.

PRIORITIES FOR FUTURE RESEARCH

As with the Red-necked Phalarope, the largest gaps in our knowledge about the Red Phalarope are those related to winter ecology. There are apparent massive decreases in numbers of Red-necked Phalaropes seen on migration off the coasts of Canada and Japan (Rubega et al. 2000). In the case of Red Phalarope, the migratory pathway is farther out to sea; similar declines could have occurred without notice. The best information available suggests these birds are strongly tied to a few important oceanic fronts (Brown and Gaskin 1988). Oceanographic perturbations that change these fronts could severely impact this species, or at least relocate its distribution. Likewise, pollution events (including oil spills or dumping of plastic) in these areas of concentration would threaten numbers (Bond 1971, Connors and Gelman 1979). New remote sensing techniques, especially by satellite, combined with shipboard observations or land-truthing, will allow more precise habitat mapping for this and related species (Briggs et al. 1984, Haney 1985b, Morrison 1997).

In this account, we have speculated that individuals from different breeding areas use different wintering areas. With the advent of smaller satellite transmitters, it may become possible to track individuals throughout the year. Besides resolving the issue of mixing of populations on the wintering grounds, this would also help determine the extent of individual dispersal in this species on its breeding grounds. Currently, we simply know that a small percentage of individuals return to the same small section of tundra in subsequent years postbanding (Schamel and Tracy 1991); we do not know whether others are a few or hundreds of kilometers away, or whether they are dead.

We suspect El Niño-Southern Oscillation events have a negative effect on Red Phalaropes (Wahl et al. 1993), since they disrupt upwellings where zooplankton are abundant. Such potential effects need more careful documentation. This could be achieved by a combination of shipboard surveys of migratory and/or wintering populations, combined with long-term breeding-density estimates from a suite of monitoring locations.

The bills of Red Phalaropes are significantly flatter, and more complicated, than those of the other 2 phalarope species (Cramp and Simmons 1983). Red Phalarope may select smaller prey than Red-necked Phalarope (Brown and Gaskin 1988), at least at sea. Red Phalarope feeding mechanisms and prey size preferences are currently under examination (M. A. Rubega pers. comm.).

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Appendix. Linear measurements (mm) and body mass (g) of Red Phalaropes from breeding areas. Data given as mean ± SD (*n*). * = flattened chord.

	Alaska		Canada		
	Barrow[1]	Cape Espenberg[1]	Cambridge Bay[2]	Baffin I.[3]	Igloolik[4]
Bill length					
Adult male	22.4 ± 0.9 (94)	22.2 ± 0.7 (55)	21.9 (20.5–23.5, 8)	22.3 ± 0.3 (14)	22.2 ± 1.5 (48)
Adult female	23.5 ± 0.8 (36)	23.5 ± 0.6 (28)	23.2 (22.0–24.5, 8)	22.8 ± 0.2 (13)	22.7 ± 1.2 (14)
Juvenile male	21.3 ± 0.9 (49)				
Juvenile female	22.6 ± 0.9 (37)				
Wing length					
Adult male	130.9 ± 3.4 (96)*	132.0 ± 3.0 (55)*	123.8 (119–127, 9)	127.1 ± 0.8 (16)	128.4 ± 2.3 (48)[4]
Adult female	139.0 ± 3.4 (36)*	140.0 ± 2.7 (28)*	131.2 (127–134, 8)	132.1 ± 0.8 (15)	134.9 ± 2.9 (14)[4]
Juvenile male	128.0 ± 3.0 (49)*				
Juvenile female	135.0 ± 3.0 (37)*				
Body mass					
Adult male	49.7 ± 3.8 (93)	49.1 ± 3.0 (55)	53.5 (43.0–60.0, 12)		52.9 ± 3.8 (45)[4]
Adult female	62.2 ± 6.1 (29)	60.1 ± 6.4 (28)	62.2 (49.4–77.0, 8)		57.2 ± 4.7 (13)[4]
Juvenile male	46.1 ± 3.1 (12)				
Juvenile female	52.1 ± 4.9 (7)				

[1] DS and DMT.
[2] Parmelee et al. 1967.
[3] Manning et al. 1956.
[4] JD.

ABOUT THE AUTHORS

Diane M. Tracy has been a Research Associate with the Institute of Arctic Biology at the University of Alaska Fairbanks, where she received a M.S. in wildlife management. Tracy and coauthor Douglas Schamel were the first to document polyandry in the Red Phalarope during their first collaboration at Barrow, Alaska. They are coauthors of the Birds of North America Red-necked Phalarope species account with M. A. Rubega. Current address: 3865 Potter Road, Fairbanks, AK 99709. E-mail: ffdls@uaf.edu.

Douglas Schamel is an Associate Professor of Biology in the Department of Biology and Wildlife at the University of Alaska Fairbanks. While completing work on a M.S. on breeding eiders in 1973, he took a field assistant position at Barrow, Alaska, to study breeding Red Phalaropes. He has been hooked on phalaropes ever since. Schamel and coauthor Diane Tracy studied Red Phalaropes at Barrow for several summers before relocating their field operations to western Alaska. There, they found both Red and Red-necked phalaropes. With help from Tracy and children, Jay and Juliann, Schamel recently completed a Ph.D. dissertation at Simon Fraser University, investigating male and female reproductive tactics in Red-necked Phalaropes. Current address: Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775. E-mail: ffdls@uaf.edu.

James Dale grew up in Montreal. He received his B.Sc. from Queen's University (1992). His experiences with Red Phalaropes came from working as a research associate with Dr. Bob Montgomerie, studying sexual selection and extra-pair matings in populations occurring at Igloolik Island, Nunavut. He recently finished his Ph.D. at Cornell University on the behavioral ecology of Red-billed Queleas (*Quelea quelea*) breeding in Zimbabwe (2000). He is currently collaborating with Dr. David B. Lank (Simon Fraser University) on a postdoctoral research project on behavioral ecology of Ruffs. Address: Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6. E-mail: jamesdale68@yahoo.com.

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