

Subarctic, alpine nesting by Baird's Sandpipers *Calidris bairdii*

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Baird's Sandpipers *Calidris bairdii* were found nesting in alpine habitat in southwestern Alaska (60°48'N, 154°00'W), almost 250 km from the nearest known breeding site, and studied over three consecutive seasons, 1997–1999. The first birds arrived during the second week of May each spring with peak numbers recorded the third week of May. Most nests and newly hatched broods were found on sparsely vegetated dwarf shrub-lichen mat tundra on level or gently sloping areas throughout the alpine zone between 980 and 1400 m above sea level. Most eggs hatched during the third week of June and independent young were noted during the second and third weeks of July. Both parents initially tended broods, but only the male remained after chicks were about four days of age. During early brood-rearing, adults began to move chicks, often to higher elevations and over distances of several hundred metres. Throughout the area the density of nesting birds was about 0.2 pairs/km² with up to 0.9 pairs/km² found on southerly exposures of the north study slope. A summary of available information revealed the global nesting distribution of *bairdii* to be strongly associated with disturbed landscapes, especially montane areas affected by glaciation, suggesting the breeding range is likely to be much more extensive than currently known, especially in areas of Alaska, the Yukon, and possibly Chukotka.

INTRODUCTION

The Baird's Sandpiper *Calidris bairdii* is generally considered a Nearctic-nesting species with breeding centred on low, sparsely vegetated, xeric habitats in the high-Arctic portion of the Canadian Archipelago (Moskoff & Montgomerie 2002). Nesting, however, also occurs in low-Arctic regions of Alaska, Canada, and the Russian Far-East (Chukotski Peninsula), and even into subarctic portions of Beringia, where it is largely restricted to the alpine zone of several mountain groups (Brandt 1943, Gabrielson & Lincoln 1959, Portenko 1972, Cramp & Simmons 1983, Godfrey 1986, AOU 1998). Knowledge of the species' breeding biology, however, comes almost entirely from the high-Arctic portion of its range (e.g., Drury 1961, Parmelee *et al.* 1967, Reid & Montgomerie 1985, Moskoff & Montgomerie 2002), the exception being Irving's (1960) study from the central Brooks Range of Alaska.

While studying nesting Surf-birds *Aphriza virgata* and Wandering Tattlers *Heteroscelus incanus*, we found Baird's Sandpipers to be a regular breeder in subarctic, alpine habitats of the southern Alaska Range, considerably south of the species' nearest reported breeding site (AOU 1998; D. Gibson pers. comm.). Here we present information on several aspects of the breeding ecology of this southern assemblage of *C. bairdii* and compare our findings with those from other nesting areas throughout the high Nearctic.

STUDY AREA

Our study site (see Gill *et al.* 1999) was the Turquoise Lake basin (about 160 km²) on the west slope of the Neacola Mountains (60°48'N, 154°00'W) of southwestern Alaska (Fig. 1). The 8-km-long by 2.5-km-wide lake is located

763 m a.s.l. (above sea level) and is one of a series of glacially-formed, east–west oriented lakes whose moderate-to steep-sloping valley walls include remnants of the most recent series of recessional Late Wisconsin glacial moraines (Fritschen 1995). From the surface of Turquoise Lake these stair-step moraine terraces rise an additional 240–640 m onto gently rounded plateaus (Fig. 2).

Dwarf shrub-lichen mat tundra dominates the landcover of the area and is characterized by dwarf shrubs, lichens, and herbs and non-vegetated substrates including scattered boulders, stones, and patches of unvegetated gravel and clay (Kessel 1979). Dense stands of *Betula nana* and sometimes *Ledum palustre* up to 0.5 m high are common at the bottom and lower (up to 900 m a.s.l.) slopes of the basin; most drainages and wet areas at the base of terraces are lined with willows (*Salix* spp.), some 1- to 4-m tall in the most prominent drainages. The driest places, usually crests of moraines and edges of terraces, are covered with mat- and cushion-forming plants, dwarf willows, sedges and forbs (see Results). At higher elevations (900–1,200 m a.s.l.) areas of tundra and bare ground occur in patches with bare ground comprising about 40% of the surface; however, tundra becomes more sparsely vegetated and bare ground more gravelly with increasing elevation (Fig. 2). At all elevations boulders and rock fields are common.

METHODS

We were present at the study site 7 May–18 July 1997, 6 May–16 July 1998 and 4 May–16 July 1999. The main study area encompassed the upper north- and south-facing slopes and plateaus of the Turquoise Lake basin, which we visited almost daily from our camp along the northwest shore of the lake (Fig. 1). Adjacent areas, extending north 5 km to Trail



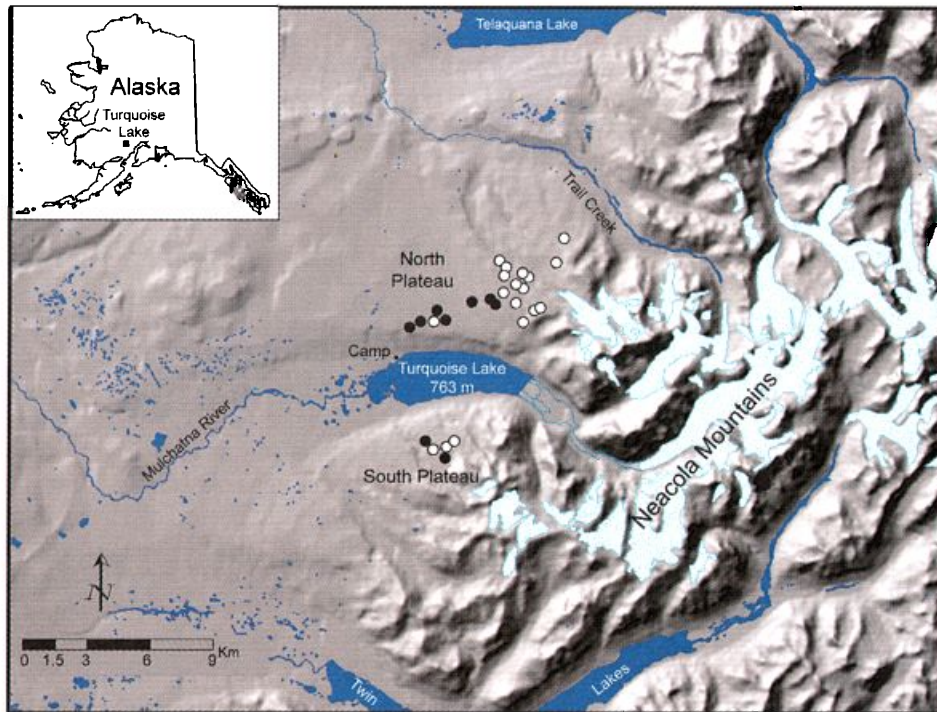


Fig. 1. Turquoise Lake study area showing locations of all nests and broods of Baird's Sandpipers found during the 1997–1999 study period. Filled circles represent nests or broods <3 days old; clear circles represent broods >5 days old.



Fig. 2. Nesting and brood-rearing habitat of Baird's Sandpipers on the upper North Plateau of Turquoise Lake. (View looking northwest, 30 June 1997 by PST.)



Creek and south 10 km to Twin Lakes, were rarely visited during the study. Because the study focused on Surfbirds and tattlers, and their nesting habitats and those of *bairdii* only partly overlapped, most of our observations of Baird's Sandpipers during the nesting period came when hiking to or working within core Surfbird nesting areas. However, since later in the season Surfbirds and Baird's Sandpipers tended to share brood-rearing areas, we collected relatively more information during this phase of the breeding cycle. Despite uneven temporal and spatial coverage of the area, we feel that during the 3 study seasons, but especially in 1997 and 1999, the time we spent over most of the landscape was sufficient to assess the species' distribution, habitat use, and minimum nesting densities for the area.

For each nest and brood that we found we recorded its location (GPS coordinates or location on 1:63,360 scale maps) and the number and behaviour of birds associated with it. All adults that exhibited distinctive, site-fixed behaviours (e.g., intense alarming, distraction display: Drury 1961, Tomkovich 1984, Reid & Montgomerie 1985) were considered nesting birds and their locations also noted. We used both types of records to assess landcover associations and to project densities, but for the latter we limited analyses only to those records that we felt represented unique observations and disregarded records that may have been replicate counts of the same brood in the same general area. We then projected densities over a 12.0-km² area (9.85 km² on the north plateau and 2.15 km² on the south plateau) for the two years (1997 and 1999) for which we had coverage of similar extent and effort.

Vocalizations were recorded with a stereo cassette-recorder (Sony WM-D6C) and a directional microphone (Sennheiser K6). Sonograms were prepared on Avisoft-SASLab Light software (version 3.74) with effective bandwidth of 55 Hz at 256-point FFT transform size.

Lastly, we ringed a total of seven adults and 27 pulli; individual adults were subsequently identified by their unique colour band and flag combinations. For chicks initially captured away from nests, we determined ages (and thus hatch dates) according to growth curves developed by Tomkovich (1985). Sex of birds ($n = 4$) was determined from blood samples taken at time of capture and later analyzed according to Griffiths *et al.* (1998).

RESULTS

Breeding biology

Arrival

The mean daily minimum and maximum temperatures during the first week following our arrival each year were -2.8 and 15.6°C in 1997, -4.0 and 7.4°C in 1998, and -3.9 and 7.0°C in 1999. In 1997, spring was early and temperatures were high. In 1998 and 1999 snow persisted late into the season and conditions were cool and wet. In all years snow fell regularly into early June. Despite 1997 being the earliest of the three years, Baird's Sandpipers were first recorded that year on 15 May, almost a week later than first seen in 1998 (7 May) and 1999 (9 May), comparatively late years. During the 3 seasons, birds were seen almost daily (45 of 53 total days) from their arrival until late May; numbers of birds encountered peaked between 13 and 20 May each year with high, single-day counts ranging from 4–9 individuals. Many

birds appeared be paired upon arrival based on 11 initial observations of birds as 'couplets', including five 'pairs' initially seen on the ground and six in passage to the west. What appeared to be passage migrants were recorded until 23 May, 28 May, and 30 May during the three respective years.

Behaviour and vocalizations

Flight displays were first recorded on 17, 9, and 13 May in 1997–1999, respectively, or 2–4 days after we first observed birds each year. In both 1997 and 1998, birds displayed on lowlands adjacent to the lake far from any known nesting site and chased conspecifics (presumably migrating birds) for great distances before returning to the lake and resuming flight displays over the frozen lake surface and/or adjacent stony tundra. Most breeding displays and vocalizations, including flight displays and rhythmically repeated calls, song, and "laughs" were typical of those documented from other portions of the species' breeding range (Drury 1961, Miller *et al.* 1988, Moskoff & Montgomerie 2002). One particular observation of an unusual vocalization from this period is, however, noteworthy. On 14 May 1999 on the west-central portion of the north plateau, we observed two birds in active flight display within 30–50 m of each other and presumed this to be a nesting area. These same displaying birds appeared to shift the centre of their display flights several times over a 30-min period, with adjacent *bairdii* occasionally occupying and displaying over an area just vacated by the other displaying bird. One or both of the displaying birds occasionally joined in rapid, three-bird chases or ceased aerial display but remained flying when another bird would land nearby, assume an upright posture, and give a soft mournful call best described as "teeu-it."

In structure (Fig. 3), this vocalization resembled the species' "laugh" (after Miller *et al.* 1988: 261) but with distinct differences: 1) the "teeu-it" was always a single element, usually repeated with an interval between elements of 1.5–2.0 sec. (e.g., one 40-sec.-long series composed of 17 elements), whereas "laugh" consists of mostly two elements repeated at intervals of about 150 ms; 2) individual elements in the "teeu-it" were about 750 ms long whereas the first element of the "laugh" is about 500 ms and second element is 425 ms; and 3) although the frequency and amplitude of harmonics of the "teeu-it" were similar to those of the "laugh," the second half of "teeu-it" decreased slightly whereas the "laugh" rises gently in frequency and amplitude before an abrupt terminal rise common to both calls. The second harmonic of the "teeu-it" contained much more energy than the fundamental (barely visible in second and third elements, Fig. 3).

No birds were subsequently found nesting in areas where the above calls and displays were noted; conversely, all nests and young broods that we did find were in areas where flight displays were never recorded. Admittedly, however, we infrequently visited nesting areas during early phases of the breeding cycle.

Nesting

Females about to lay eggs (with enlarged vent, clumsy movements) were seen on the north plateau on 22 May in both 1998 and 1999. The earliest initial laying date during the study period was 20 May 1997 (Fig. 4). Among the three nests found, two contained four eggs and one had three. The



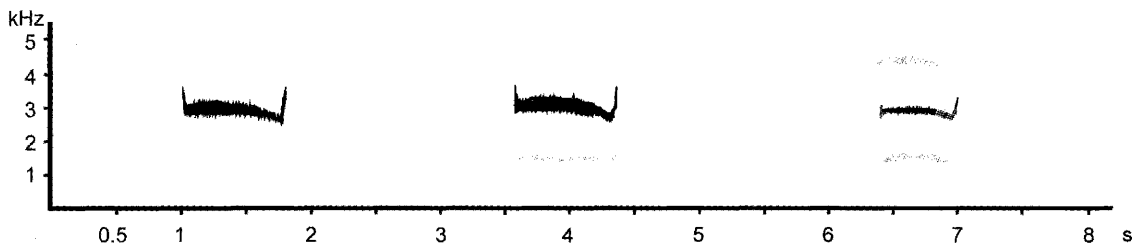


Fig. 3. Sonogram of the "teeu-it" call of the Baird's Sandpiper. Recorded by PST at Turquoise Lake, 14 May 1999. Sonogram digitally enhanced.

latter contained a damaged egg suggesting the clutch had suffered partial predation prior to our finding it. Mean measurements for 9 eggs were: length $32.9 \text{ mm} \pm 1.7 \text{ SD}$ (range 30.9–35.1); breadth $23.8 \text{ mm} \pm 0.4 \text{ SD}$ (range 23.3–24.4 mm). Two nests were lined mostly with dry leaves of *Dryas octopetala* and some lichen; the third nest was lined with dry leaves of *Vaccinium uliginosum*.

Hatch during all three years (Fig. 5) spanned a 23-day period between 14 June and 6 July with a suggested peak in mid-June (median date 16 June for combined years). At about this same period each year (18–19 June) we first observed adults that did not appear to be associated with either an area or mate and presumed these to be birds that had abandoned broods (see following).

Both parents tended broods until chicks were about four days of age; thereafter only a single adult was present. In two instances involving single adults, males were the attending parents based on analysis of blood samples (see methods). In the one unusually late nesting effort (estimated hatch on 6 July), the brood was tended by a single adult beginning the day after hatch. When chicks were about 4–7 days old, marked adults began to move broods away from nest sites (many to upper slopes; Fig. 1) where they formed loose, ephemeral aggregations with up to four broods present in a 1-km² area. Such directed movements ranged in distance from several hundred to over a thousand metres from the nest site. The mean elevation ($1,131 \text{ m} \pm 103 \text{ SD}$, $n = 8$) at which nests and broods <3 days old were found was significantly lower ($p = 0.001$, $t = 3.62$, $df = 23$) than the mean elevation ($1,303 \text{ m} \pm 114 \text{ SD}$, $n = 17$) at which broods >5 days old were observed (Fig. 1).

We have three records of adults still alarm-calling from nesting areas when their chicks were between 19 and 21 days old; the first independent young on these areas were noted on 12 July 1998 and 10 July 1999.

Departure

During the third week of June adults, presumably those that had abandoned broods and/or failed breeders, began to flock and by the second week of July the overall number of birds on the high plateaus had decreased markedly. When we departed each year (16–18 July) a few adults but many fledged juveniles were still present. A single observation of a non-vocal adult and fledged juvenile away from nesting habitat along a gravel shore near Turquoise Lake on 17 July 1997 likely represented non-local breeders moving through the area.

None of four adults or 21 pulli ringed in 1997 and 1998 was seen there in a subsequent season.

Distribution in relation to landscape characteristics

In spring, we initially recorded Baird's Sandpipers near lake level and throughout the Mulchatna River drainage where they fed along the mostly gravel lakeshore or on sparsely vegetated portions of terminal moraines. We do not know if these birds were passage migrants or if they eventually moved to local nesting areas, but within a week or two of our first observations we began to find birds on the upper plateaus of the lake basin where they were regularly seen on snow-free areas of mostly gravel (not rocks), especially at the base of snow-covered slopes with emerging meltwater. Once birds appeared on upper slopes and plateaus they were usually found there throughout the nesting period. Exceptions occurred during the occasional spring storms that blanketed the entire basin in snow and then Baird's Sandpipers, along with several other species of shorebirds, would visit the lake's outfall – the only snow-free habitat – where they fed among algae-covered rocks (e.g., on 23 May 1998). All nesting records (3 nests, 22 broods and/or broody adults, and one

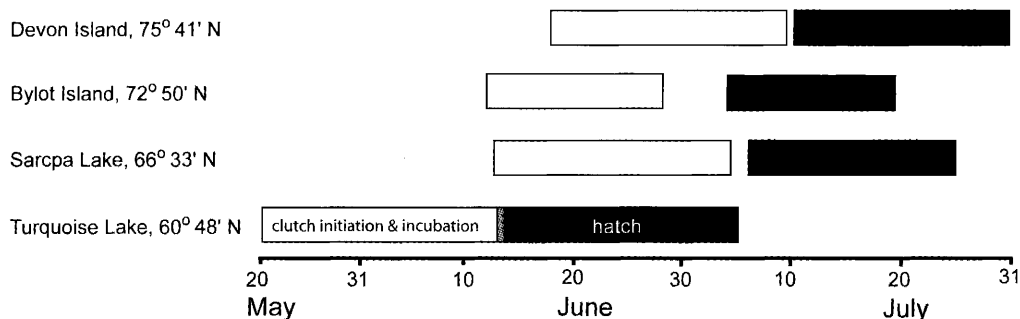


Fig. 4. Temporal difference in stages of nesting chronology between Arctic and subarctic breeding sites of Baird's Sandpiper. Sarcpa Lake data from Montgomerie *et al.* (1983) and Moskoff & Montgomerie 2002; Bylot Island from Drury (1961); Devon Island from Hussell & Holroyd (1974).



female with an obvious egg in its lower oviduct) were located on the plateaus above the lake between 990 and 1,450 m elevation (Fig. 1), with the north plateau hosting about four times as many pairs as the south plateau.

Nesting Baird's Sandpipers were most abundant on gently sloping southern aspects above the upper limit of tall shrubs (Figs 1 & 2) and appeared to avoid steep slopes and rock fields. Actual nests were placed in the first snow-free patches available and often near rivulets of melt-water. Nesting substrate was usually mosaics of bare ground and patches of tundra with rich lichen cover (*Alectoria*, *Cetraria*, *Cladonia*, *Thamnolia* spp.), sparse low shrubs and heath (*Dryas* sp., *Diapensia lapponica*, *Vaccinium uliginosum*, *V. vitis-idea*, *Loiseleuria procumbens*, *Salix* sp., *Betula nana*, *Empetrum nigrum*), and scattered herbs (grasses {Gramineae}, *Carex*, *Arnica*, *Anemone* spp.). Broods were found in similar habitats but also in areas with more gravel and less tundra, usually at the base of terraces in wet, mossy areas at the edge of receding or recently melted snow.

Density

Over the 65 km² of montane-tundra that we regularly visited we recorded a minimum density of about 0.2 pairs/km². Within the 12-km² area where birds were most concentrated (north and south plateaus; Fig. 1), the minimum nesting density (not accounting for nest loss during incubation) was about 0.9 pairs/km² in both 1997 and 1999.

DISCUSSION

Chronology

Even though nesting at Turquoise Lake was restricted to high elevations that retained some snow cover into June, the arrival of *bairdii* in early- to mid-May coincided with the usual arrival of most coastal-nesting shorebirds throughout southwestern and western Alaska, which was 2–5 weeks ahead of that reported for *bairdii* nesting in coastal areas of the Arctic (Dixon 1917, Drury 1961, Parmelee *et al.* 1967, Norton 1972, 1973, Hussell & Holroyd 1974, Bergman *et al.* 1977, Witts 1981, Lehnhausen & Quinlan 1982, Freedman & Svoboda 1982, Montgomerie *et al.* 1983, Tomkovich 1985, Johnson & Herter 1989, Kessel 1989, Moskoff & Montgomerie 2002; but see Irving 1960 for interior montane nesting). This advanced chronology was maintained through the nesting period (Fig. 4). Egg laying started about 2–3 weeks ahead of that in Arctic areas, and peak hatch occurred 2–4 weeks earlier; modal egg laying in Arctic regions typically occurs in mid-June and modal hatch in mid-July (Drury 1961, Parmelee *et al.* 1967, Norton 1973, Hussell & Holroyd 1974, Patterson & Alliston 1978, Witts 1981, Montgomerie *et al.* 1983, Reid & Montgomerie 1985, Kessel 1989, Lepage *et al.* 1998, Moskoff & Montgomerie 2002). Only from regions of Beringia (eastern Chukotka, Wrangel Island, and Seward Peninsula) are there records of *bairdii* hatching during the third and fourth weeks of June (Dixon 1917, Gabrielson & Lincoln 1959, Tomkovich 1985, Kessel 1989, Stishov *et al.* 1991). Two records of fledglings on 4 and 13 July in Nunavut, Canada, suggest on rare occasions hatch can occur in June in the Canadian Arctic (McEwen in Johnson & Herter 1989, Lepage *et al.* 1998).

Because we departed our study area in mid-July each year when both juveniles and some adults were still present, we

do not know the extent to which the species lingers on the area or the timing of its departure on migration. Elsewhere in Alaska we have seen fledged juveniles away from breeding habitat on 20 July 1998 (Anchorage) and flocks of juveniles in alpine tundra (Eagle Summit, 65°30'N, 145°30'W) on 22 July 1998. These observations, coupled with those at Turquoise Lake of flocking adults beginning the third week of June, independent young in early July, and migrant juveniles in mid-July, suggests birds are capable of departure in the first half of summer. Given the comparatively advanced schedule of Turquoise Lake birds (Fig. 4), and if juveniles from there and other subarctic nesting areas move south rapidly as indicated in other populations of *bairdii* (Jehl 1979, Paulson 1983), these southern alpine breeding areas may be the source of early and mid-summer birds, particularly juveniles, reported from the Pacific Northwest south to Baja (Paulson 1983, 1993, Campbell *et al.* 1990, AOU 1998). Conversely, we can not assume that birds produced in south-central Alaska, British Columbia, or possibly southern Yukon are restricted to a coastal migration route. Mid-summer records of juveniles within and east of the Rocky Mountains (Paulson 1983) could represent birds from any of these locations that migrated east and then south along the species' main mid-continent migration corridor (Jehl 1979, Campbell *et al.* 1990). Lastly, Jehl (1979: 63) felt there was no evidence to support the idea of a major autumn movement of *bairdii* along the Rocky Mountain Cordillera. Given information since Jehl (1979) that suggests *bairdii* are not uncommon at alpine sites during southward migration (Campbell *et al.* 1990, W. Campbell pers. comm., our study), we feel Jehl's assessment needs to be revisited.

Investigators studying the breeding biology of *bairdii* at northern latitudes (e.g., Barrow, Melville Peninsula) have speculated that the compressed and highly synchronous breeding schedule all but precludes a re-nesting attempt or for that matter even a replacement clutch for a nest lost early in incubation (Norton 1973, Reid & Montgomerie 1985, Moskoff & Montgomerie 2002). Given the comparatively early nest initiation period at Turquoise Lake and the potential length of the season, we became intrigued with the idea that the species could not only replace lost clutches, well into late incubation, but even be double-brooded (serially polygamous). Our data, however, suggest neither is likely. The span of hatch dates at Turquoise Lake (23 days) is only slightly longer than reported elsewhere (Fig. 4). This could represent a combination of both initial and replacement clutches, but the latter only for a few pairs failing early during incubation. The non-overlapping of clutch initiation periods on southern

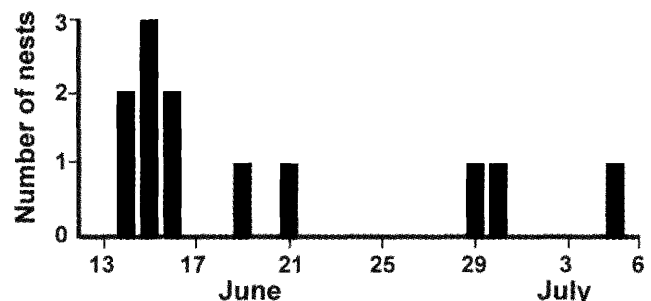


Fig. 5. Chronology of hatching in Baird's Sandpipers at Turquoise Lake, 1997–1999.



and northern breeding areas (Fig. 4) suggests it may also be possible for failed nesters from southern areas such as Turquoise Lake to move north before laying replacement clutches, as suspected by Norton (1973) for two birds nesting at Barrow, Alaska. While this speculation can only be proven with marked birds, it is clear to us that regardless of nesting latitude, the chronology of nesting and patterns of parental care constrain *bairdii* to a single brood each year.

Vocalization

Most breeding vocalizations of *bairdii* have been recorded and described (Drury 1961, Miller *et al.* 1988, Moskoff & Montgomerie 2002). The “teeu-it” call we recorded is obviously structurally related to the “laugh” described by Miller *et al.* (1988) but yet with several marked differences. Contextual differences between the two vocalizations, however, are not as clear. “Laughs” are generally considered a form of warning, either to inform potential predators that they have been detected or to alert mates or chicks, and are readily elicited by humans approaching one or both mates (Miller *et al.* 1988, Moskoff & Montgomerie 2002, our observations). We noted “teeu-it” calls during prenesting, in a “lek-like” situation (Myers *et al.* 1982) where birds were spaced widely apart, and also following instances of three-bird chases. To us this suggests the vocalization is associated with mate acquisition, but we can not exclude its being given as a warning even though we were often a considerable distance from the birds.

Density

From all reported values of nesting density (pairs or nests/km²) that we could find ($n = 28$; Appendix) most sites are represented within a range of 0.1 and 10.0 pairs/km² (median 1.2), including the 0.9 pairs/km² we found at Turquoise Lake. However, for a few sites in mid-Arctic latitudes (68–73°N) of the central Canadian Archipelago and northern coastal Alaska, reported densities are well above this norm, exceeding 20–93 pairs/km². These sites include narrow beach ridges at Barrow, Alaska (Norton 1973, Myers *et al.* 1977, 1982), dry ridges on eastern Bylot I., Canada (Van Tyne & Drury 1959, Drury 1961), and vegetated “oases” among vast areas of less suitable habitat on Victoria Island and Melville Peninsula, Canada (Parmelee *et al.* 1967, Montgomerie *et al.* 1983). We do not question that in some areas *bairdii* nest in unusually high densities, but from the literature we reviewed (Appendix) it is not clear if these unusually high densities are related to unique or limited habitat features or are possibly due to the timing and method of assessment. For example, projecting densities from information collected during either early or late breeding might produce inflated values – during pre-nesting if focal birds are from “lek-like” situations (Parmelee *et al.* 1967, Myers *et al.* 1982) before they disperse to nest, and during brood-rearing when widely dispersed nesting pairs move their broods to localized areas (e.g., Lanctot *et al.* 1995, Soloviev & Tomkovich 1998, this study).

Also to emerge from this compilation of density data (Appendix) was the marked inter-annual fluctuation in density values occasionally recorded at the same site or between adjacent sites. Such differences could have resulted from different environmental conditions between years, but they would also be expected in a species that exhibits low breed-

ing site fidelity as appears to be the case with Baird’s Sandpiper (Norton 1973, Tomkovich 1985, Moskoff & Montgomerie 2002, our study).

Distribution in relation to landscape characteristics

Three themes emerged from our analysis of nesting distribution: 1) nesting by Baird’s Sandpipers south of high- to mid-Arctic latitudes is almost exclusively restricted to montane areas, 2) the montane component of the breeding range is much more extensive than previously known and is likely to include much of subarctic Alaska and the Yukon of Canada, and 3) nesting throughout the species’ range is strongly tied to disturbed landscapes, especially the montane component and landscapes affected by glaciation.

Over the mid- to high Arctic portions of the species’ range throughout the Canadian Archipelago and northern Alaska, Baird’s Sandpipers can be characterized as largely coastal breeders with nests placed over barren or sparsely vegetated areas such as beach ridges, eskers, river terraces, outwash plains, upland plateaus, rocky hillsides, and even anthropogenically-altered areas (Drury 1961, Parmelee *et al.* 1967, Hussell & Holroyd 1974, Witts 1981, Montgomerie *et al.* 1983, TERA 1994, Johnston *et al.* 2000, Appendix). In the low- and sub-Arctic portions of its range the species continues to nest over sparsely vegetated habitats that are largely restricted to the alpine zone of prominent mountain ranges. For example, in the Endicott Mountains (68°N) of the central Brooks Range, 250 km south of the Beaufort Sea coast, Baird’s Sandpipers nest at elevations between 400 and 1,200 m (Irving 1960, R. Gill unpubl.), while 600 km farther southeast (65°N) in the Ogilvie Mountains of the Yukon (Frisch 1987, Sinclair *et al.* 2003) and 600 km due south in the Talkeetna Mountains of interior Alaska (Kessel *et al.* 1982), nesting occurs at 1,500 and 1,300 m elevation, respectively (Fig. 6). At the southern limit of the breeding range in the Cassiar Mountains of northern British Columbia (56–59°N) nesting has been reported at elevations between 1,900 and 2,400 m (R. W. Campbell, *in litt.*).

Indeed, we are aware of over 4-dozen nesting records of *bairdii* outside the Canadian Archipelago and coastal northern Alaska and Chukotka, and all but two come from montane areas (see below). Conversely, many montane areas in this region apparently do not host nesting Baird’s Sandpipers. This enigma, but also the overall selection of nesting habitat throughout the species’ range, appears related to disturbance that has operated at two disparate temporal scales: 1) paleogenic processes that produced glaciated landscapes throughout most of the Nearctic, and 2) ongoing natural processes (see above) that act not only on previously glaciated areas such as most of the Canadian Arctic, but also on glacial refugia such as the coastal plain of the Beaufort Sea coast of Alaska and Canada.

How strong is this association between nesting and glaciation? In essence, it entails the majority of the species’ range (Moskoff and Montgomerie 2002), including the core nesting area of the Canadian Archipelago and adjacent mainland that were almost entirely blanketed by the Laurentide ice sheet as recently as 18,000 years ago (Pielou 1991). The only nesting area not affected by glaciation is extreme northern Alaska where the species is common along the immediate coast west to Barrow, but increasingly uncommon farther south along the Chukchi Sea coast (Connors 1985, Connors & Connors 1985; see beyond). It is just south of there, how-



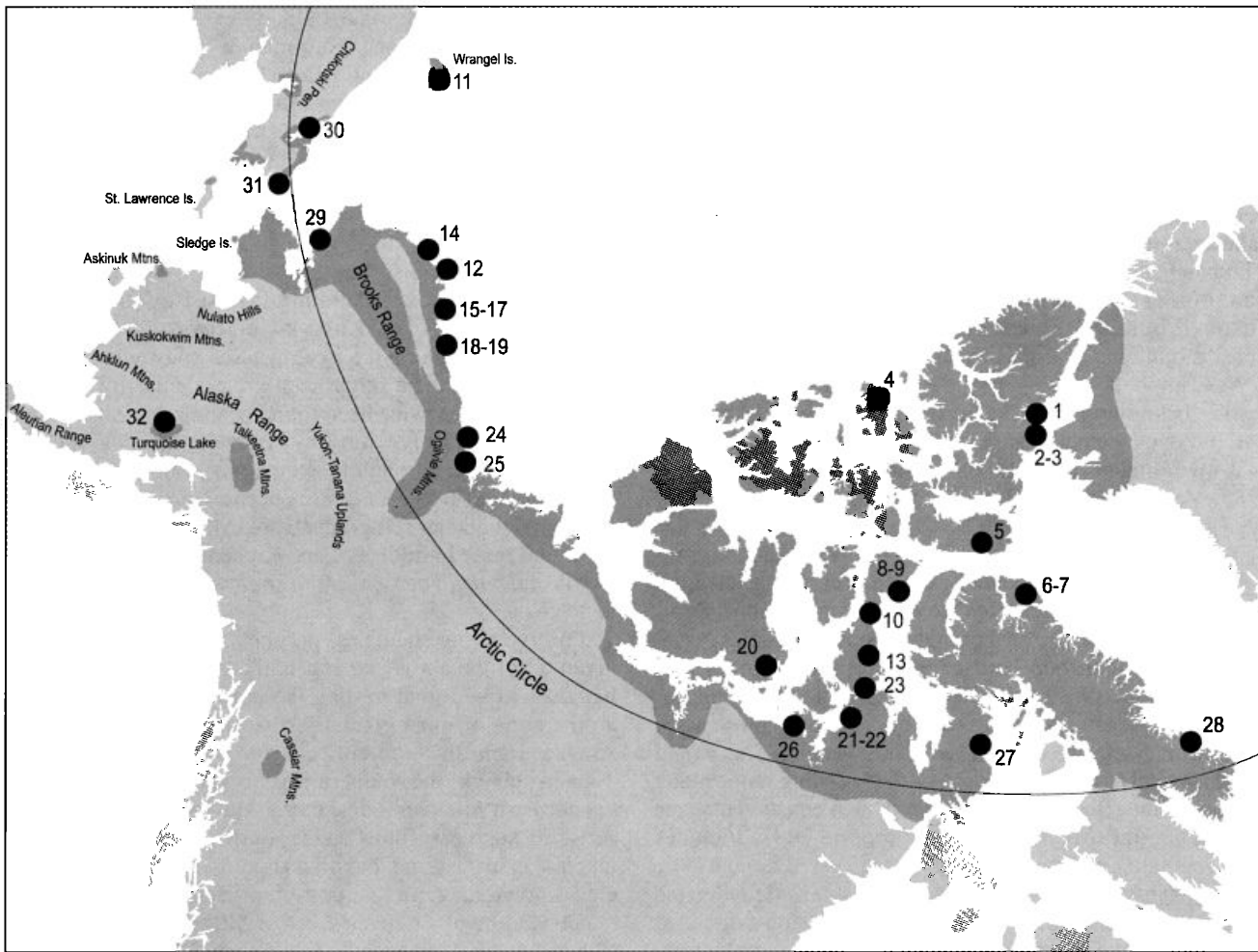


Fig. 6. Breeding range (dark shading) and sites reporting nesting densities (filled circles) of Baird's Sandpipers. Range modified from Moskoff & Montgomerie (2002); numbers correspond to sites listed in Appendix.

ever, in the most northerly montane regions of Alaska – the Baird, DeLong, Endicott, and Philip Smith mountains of the Brooks Range and the York and Kigluaik mountains of the Seward Peninsula – that *bairdii* again becomes a relatively common nesting species but only in high alpine habitats (Bailey 1943, Irving 1960, Kessel 1989, Gill *et al.* 2002, Tibbitts *et al.* 2003, R. Gill unpubl., UAM unpubl.). Interestingly, one attribute these montane sites share with the Canadian Archipelago portion of the range is that they all have well-documented glacial records (Coulter *et al.* 1965, Péwé 1975, Hamilton 1986, Kaufman & Hopkins 1986, Manley & Kaufman 2002).

Moving south and southwest of the Brooks Range-Seward Peninsula region there is an apparent 350- to 500-km-wide gap in the species' breeding distribution (Fig. 6). This area encompasses several prominent mountain ranges from which there are no confirmed breeding records, including the Nulato Hills of western Alaska (B. McCaffery pers. comm.) and the Yukon-Tanana uplands of eastern Alaska (*contra* Moskoff & Montgomerie 2002). However, the latter area is the only one among them that was affected by Pleistocene to Holocene glacial episodes (Weber 1986, Duk-Rodkin *et al.* 2001) and for which there are summer (mid-June to August) but no spring records of *bairdii* (Swanson & Nigro 2003, UAM unpubl., D. Gibson pers. comm.).

South of this gap, the species is again recorded nesting, but to date only at five widely dispersed sites: St Lawrence Is., two sites on the west-central Yukon-Kuskokwim Delta (Askinuk Mountains and Hooper Bay coast), the Talkeetna Mountains and portions of the northern Alaska Range, and now Turquoise Lake (Fig. 6). Nesting by *bairdii* on St Lawrence I. is known only for the extreme northwestern portion (UAM unpubl.), the only part of the island affected by Pleistocene glacial advances from Chukotka (Coulter *et al.* 1965). Similarly, the only portion of the expansive Yukon-Kuskokwim Delta to be affected by glaciation was the relatively small and isolated Askinuk Mountains where *bairdii* have also been found nesting (Gabrielson & Lincoln 1959, B. McCaffery pers. comm.).

From the Askinuk Mountains south and east to the Alaska Range we found no nesting records of *bairdii*, including from the completely glaciated Ahklun Mountains, the patchily glaciated Kuskokwim Mountains, and the heavily glaciated Aleutian Range (Coulter *et al.* 1965, Kline & Bundtzen 1986, Manley & Kaufman 2002). This does not, however, preclude *bairdii* from nesting there. Petersen *et al.* (1991) investigated the avifauna of the Kilbuck and Ahklun mountain region, but their efforts focused on marine and lacustrine habitats with comparatively little time spent in the higher montane areas (M. Petersen pers. comm.), while information on the avi-



fauna of the Kuskokwim Mountains is acknowledged as being among the poorest for any portion of Alaska (D. Gibson pers. comm.).

Lastly, the only other montane site in Alaska where *bairdii* are known to nest is the extensively glaciated Alaska Range (Manly & Kaufman 2002), specifically the Talkeetna Mountains (Kessel *et al.* 1982, UAM unpubl.), probably in Denali National Park (UAM unpubl.), and in the Turquoise Lake area (this study). Montane nesting by *bairdii* in Canada is known from two sites, both formerly glaciated (Prest 1984, Hamilton *et al.* 1986): the Ogilvie Mountains of northern Yukon (Frisch 1987, Sinclair *et al.* 2003) and the Cassiar and Coast mountains of northern British Columbia (56–59°N; R.W. Campbell, *in litt.*). In the Asian portion of its range, nesting is known from 12 sites on the Chukotski Peninsula – all but two (see below) are montane areas with glacial history, including several sites on Wrangel Island (Tomkovich 1985, Velichko *et al.* 1987, Stishov *et al.* 1991, Dorogoi 1997).

While the above clearly details not only a montane component to the breeding range of *bairdii* but also a selection of areas shaped by glaciation, we did find exceptions. Scrutiny of these, however, further highlighted the species' association with disturbed landscapes (see also Drury 1961, Parmelee *et al.* 1967), whereby in all instances natural ongoing processes of a smaller scale, but similar to those associated with glacial events, shaped nesting habitat. This would apply particularly to that portion of the breeding range along the immediate Beaufort and Chukchi Sea coasts. Here the nesting habitat (Moskoff & Montgomerie 2002) includes both vegetated and unvegetated sites affected annually by frost boils; by freeze–thaw cycles on polygonized tundra and slopes that produce solifluction; by water-erosion associated with alluvial plains, runoff streams, river bluffs, and immediate coastal sites affected by storm-driven tides; and by winds that constantly shape sparsely vegetated coastal dunes. Indeed, this penchant for nesting on disturbed substrates, particularly in northern Alaska, is highlighted by the fact that *bairdii* is the only Nearctic sandpiper to regularly nest on human-altered landscapes such as gravel substrates associated with roads, airport runways, storage areas, parking lots, and pads constructed for oil and natural gas extraction (Parmelee *et al.* 1967; TERA 1994; B. McCaffery, D. Derksen and D. Troy pers. comm.).

But what about those instances alluded to earlier where *bairdii* has been found nesting in non-glaciated montane or coastal sites other than northern Alaska? Again, disturbance appears to be critical. For instance, Ear Mountain, an isolated monolith only 30 km from the eastern extent of the York Mountain glaciation on the eastern Seward Peninsula (Kaufman & Hopkins 1986) was presumably never glaciated but yet *bairdii* nest there (R. Gill & J. Pearce unpubl.). Here ongoing erosion accounts for the disturbed, boulder-strewn landscape at the toe slope of the mountain (D. Kaufman, *in litt.*) that in turn affords surface habitats similar to those of young- to moderate-aged moraines such as at Turquoise Lake (Fritschen 1995) and throughout preferred nesting sites in the central Brooks Range (Kaufman & Hopkins 1986). Another montane site just off the southern Seward Peninsula on which *bairdii* have nested (Cade 1952) is Sledge Island (Fig. 6), a 100- to 150-m-tall volcanic plateau about 10 km off the coast. The island appears to have just escaped the advance of the Nome River glacial drift, but erratics recovered from offshore dredge hauls suggest the terminal posi-

tion of older-age ice tongues likely extended beyond (and possibly over) the island (Kaufman & Hopkins 1986).

Lastly, it is worth mentioning a couple of coastal sites that do not fit the patterns we have outlined. Most interesting is a nesting record (Brandt 1943) from coastal dunes of the central Yukon-Kuskokwim Delta, only 20 km south of the Askinuk Mountains where *bairdii* also nest (see above). And while it appears to be an exception to the pattern, three things stand out about this site: 1) it is an area naturally disturbed by winds and storm surges, 2) it is the only such pocket of habitat along almost 1,000 km of coast from the southern Seward Peninsula to the Kuskokwim River, and 3) it closely resembles areas along the Beaufort Sea coast where *bairdii* commonly nest. The other such area occurs in Chukotka where birds have twice been found nesting on gravel bars at coastal sites in Kolyuchin Bay (Belyaka Spit and Yuzhny Island {one pair in one of seven years} and at Rekokaver Cape in one of two years). This portion of the bay was part of a narrow glacial refugium (Hopkins 1984) and occurs at about the same latitude as Cape Krusenstern where, at least in Alaska, *bairdii* cease nesting southward along the immediate coast.

Forgive us our shameless prophetic pronouncements, but given all of the above we expect that with additional effort *bairdii* will be found nesting in appropriate habitats in the alpine zone of most glacially-disturbed montane areas of Alaska, including the entire Brooks Range, the Yukon-Tanana uplands, the southern Kuskokwim Mountains, likely the northern Aleutian Range of the Alaska Peninsula, and the Alaska Range east into Canada. Further inventory of montane areas in eastern Chukotka should also expand the species' known range in that portion of Beringia. With further understanding of the species' range will come a need to identify and understand specific features that define the nesting and brood-rearing habitat of *C. bairdii* as well as adaptations within the species that have allowed it to occupy a niche defined by seasonally xeric, sparsely vegetated substrates.

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Appendix. Sites where densities (of birds, pairs or nests) of Baird's Sandpipers have been reported.

No. ^a	Site	Location ^b	Birds per km ²	Pairs/nests per km ²	Habitat used	Source	Years of study	Comments
1	Ellesmere Island (Esayoo Bay)	81°N, 82°W		2.0	Braided, <i>Dryas</i> -dominated river bed at coast	Whitfield & Brade 1990	1	Minimum estimate based on broods and hatching success on 22-km ² area
2	Ellesmere Island (Alexandra Fiord)	79°N, 76°W		0.4–0.8 ^c	Peri-glacial outwash plain	Freedman & Svoboda 1982	2	Based on nests or broods; study area about 12 km ²
3	Ellesmere Island (Princess Marie Bay)	79°N, 76°W		0.3	Poorly vegetated gravel of braided river beds and terraces within 5 km of coast	Witts 1981	1	Based on nests and calculated from Fig. 4D, 82-km ² study area
4	Ellef Ringnes Island	79°N, 102°W		0.03		Savile in Freedman & Svoboda 1982	1	Study area 10.25 km ²
5	Devon Island	76°N, 85°W		0.5	Beach ridge and dwarf shrub heath-moss among granitic outcrops	Pattie 1977	1	Value calculated by Freedman & Svoboda (1982) and based on June 1971 count of birds on transects; study area 43 km ²
6	Bylot Island	73°N, 79°W		9.7 93.0	Mostly barren tundra and beach ridges within 1000 m of coast	Van Tyne & Drury 1959, Drury 1961 Moskoff & Montgomerie 2002	1	Based on 25 pairs in 1-mi ² study area
7	SW Bylot Island	73°N, 80°W		1.9		Lepage <i>et al.</i> 1998	6	Data of Drury 1961 recalculated from Fig. 3 for 30 ha of 'suitable' habitat Study area 73 km ²
8	Somerset Island (Creswell Bay)	73°N, 93°W	0.7			Crockford in Johnston <i>et al.</i> 2000	1	From transects on study plot
9	Somerset Island	73°N, 93°W	5.4		Evergreen dwarf shrub, sedge meadow	Latour in Johnston <i>et al.</i> 2000	1	Conducted 16 June–4 July
10	SE Somerset Island	72°N, 93°W	5.7		Evergreen dwarf shrub, sedge meadow	Patterson & Alliston 1978	1	Conducted 5–14 July; densities calculated by Johnston <i>et al.</i> 2000
11	Wrangel Island	71°N, 180°W		0.2 0.4–2.5	All nests in heavily eroded low mountains 0.3–7.0 km from coast	Patterson & Alliston 1978	1	Conducted 5–14 July; densities calculated by Johnston <i>et al.</i> 2000
12	Barrow, Alaska	71°N, 157°W		20.7 8.0	Highest densities from most disturbed plots From 2 plots also run by Norton (1973)	Stishov <i>et al.</i> 1991; pers. comm. Stishov <i>et al.</i> 1991; pers. comm. Norton 1973	1 3	Mapping of alarming adults in June–July over 35-km ² area From transects at various sites
13	S. Boothia Pen. (Sanagak L.)	71°N, 95°W	16.4		Evergreen dwarf shrub, sedge meadow	Myers <i>et al.</i> 1982	4	Average value over 6 plots during 4 years; range on plots 10–33
14	Icy Cape, Alaska	70°N, 162°W	2.0			Patterson & Alliston 1978	5	Average in prime habitat over 5 years, but to 18 pairs/km ² in some years
15	Storkersen Pt., Alaska	70°N, 149°W	0.0–4.0		All 6 nests found on frost boils near coast Mostly human-disturbed areas within 0.5 km of coast	Lehnhausen & Quinlan 1982 Bergman <i>et al.</i> 1977	1 5	Conducted 5–14 July; densities calculated by Johnston <i>et al.</i> (2000) From 8 plots of 0.32 km ² within 5 km of coast, 13–24 June Range for biweekly counts, June 1971–1975

(Appendix continued)

No. ^a	Site	Location ^b	Birds per km ²	Pairs/nests per km ²	Habitat used	Source	Years of study	Comments
16	Milne Point, Alaska	70°N, 149°W		8.0	Tundra on immediate mainland	Johnson & Richardson 1981	1	Projected from values on single 0.25-km ² plot
17	Jones Islands, Alaska	70°N, 149°W		4.4	Tundra on barrier islands	Johnson & Richardson 1981	1	Derived from 4 plots totalling 1.8 km ²
18	Prudhoe Bay, Alaska	70°N, 148°W		5.5 3.5 2.5	Dry coastal tundra, rare and localized Vegetated coastal meadows Nonsaline coastal tundra	TERA 1994 TERA 1994 TERA 1994	2 2 2	Derived from 10 plots of 10 ha each Derived from 10 plots of 10 ha each Derived from 10 plots of 10 ha each
19	Prudhoe Bay, Alaska	70°N, 148°W	6.0		Highly polygonized, dry, elevated tundra	Jones <i>et al.</i> 1980		Study area 75 ha; 5–8 km from coast; value averaged— from transects at 5-day intervals, 1 June–1 July
20	Victoria Island	70°N, 105°W		50–60	Dry tundra from coast to 20 km inland	Parmelee <i>et al.</i> 1967	2	1960, 1962; “. . . estimated at 20–25 pairs per 100 acres of suitable habitat.”
21	Rasmussen Lowlands	69°N, 93°W		4.0 1.1 0.6	Mostly beach ridge/esker Interrupted tundra High-center polygons	Johnston <i>et al.</i> 2000 Johnston <i>et al.</i> 2000 Johnston <i>et al.</i> 2000	2 2 2	1.05 km ² sampled (9 plots); 16 June–13 July 2.03 km ² sampled (15 plots); 16 June–13 July 2.14 km ² sampled (15 plots); 16 June–13 July
22	Rasmussen Lowlands	69°N, 93°W	0.2			McLaren <i>et al.</i> 1977	2	Conducted 30 June–17 July
23	S. Boothia Pen. (Middle L.)	69°N, 93°W	2.8		Evergreen dwarf shrub, sedge meadow	Patterson & Alliston 1978	1	Conducted 5–14 July; densities calculated by Johnston <i>et al.</i> (2000)
24	Stokes Point, Yukon	69°N, 139°W	0.4		Wet sedge-patterned ground 0.5–3.0 km from coast	Dickson <i>et al.</i> 1988	1	26–28 June; total of 2 birds seen on transect
25	Phillips Bay, Yukon	69°N, 138°W	0.3		Wet sedge-patterned ground 0.0–5.0 km from coast	Dickson <i>et al.</i> 1988	1	26–27 June; based on single bird on transect
26	Adelaide Peninsula	68°N, 98°W	3.1		Inland on dry stony ridges, outcrop/boulder plains, barren areas Within 6.5 km of coast	MacPherson & Manning 1959	1	June–September
			0.8			MacPherson & Manning 1959	1	June–September
27	Melville Peninsula	68°N, 83°W		4.0–7.0	Dry <i>Dryas</i> -lichen ridges 30 km from coast	Montgomerie <i>et al.</i> 1983	2	Two-year range for “maximum nest density” on any 1-km ² area of 13-km ² study area.
28	Baffin Island	68°N, 68°W		0.4	In 40-ha area of dry grassland and boulders 25 km from coast	Watson 1957	1	Based on a single pair of birds seen mid-June to mid-July
29	Cape Krusenstern, Alaska	67°N, 163°W		0.0–13.0	All on dry ericaceous shrub tundra	Schroeder 1995	3	From 30 plots of 5 ha; birds present on plots on only 1 of 3 years
30	Kolyuchin I., north Chukotski Peninsula	67°N, 175°W		1.2	Plateau on island with rock fields and forb meadows	Kondratyev 1982	1	“at least 6 broods at an island of 5 km ² in size”
31	Dezhnev Cape, Chukotski Peninsula	66°N, 170°W		0.1–0.3	Dry montane tundra <0.5–7.0 km from coast	Myers <i>et al.</i> 1982, Tomkovich 1985	3	Three year range; mapping of nests and broods on 32–35-km ² area
32	Turquoise Lake, Alaska	61°N, 154°W	0.9		Dry <i>Dryas</i> -lichen/bare ground on lateral moraines 100 km from coast	This study	2	Value for 12.0-km ² area of most suitable habitat

^a Numbers correspond to sites noted on Fig. 5; ^b Sites arranged by order of decreasing latitude; ^c Mid-point of ranges used in calculation of median density. See text.