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Environmental and physiological constraints in the life history of a northerly-wintering shorebird

Daniel Ruthrauff

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of a northerly-wintering shorebird

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On the frozen edge

Environmental and physiological constraints in the life history of a northerly-wintering shorebird

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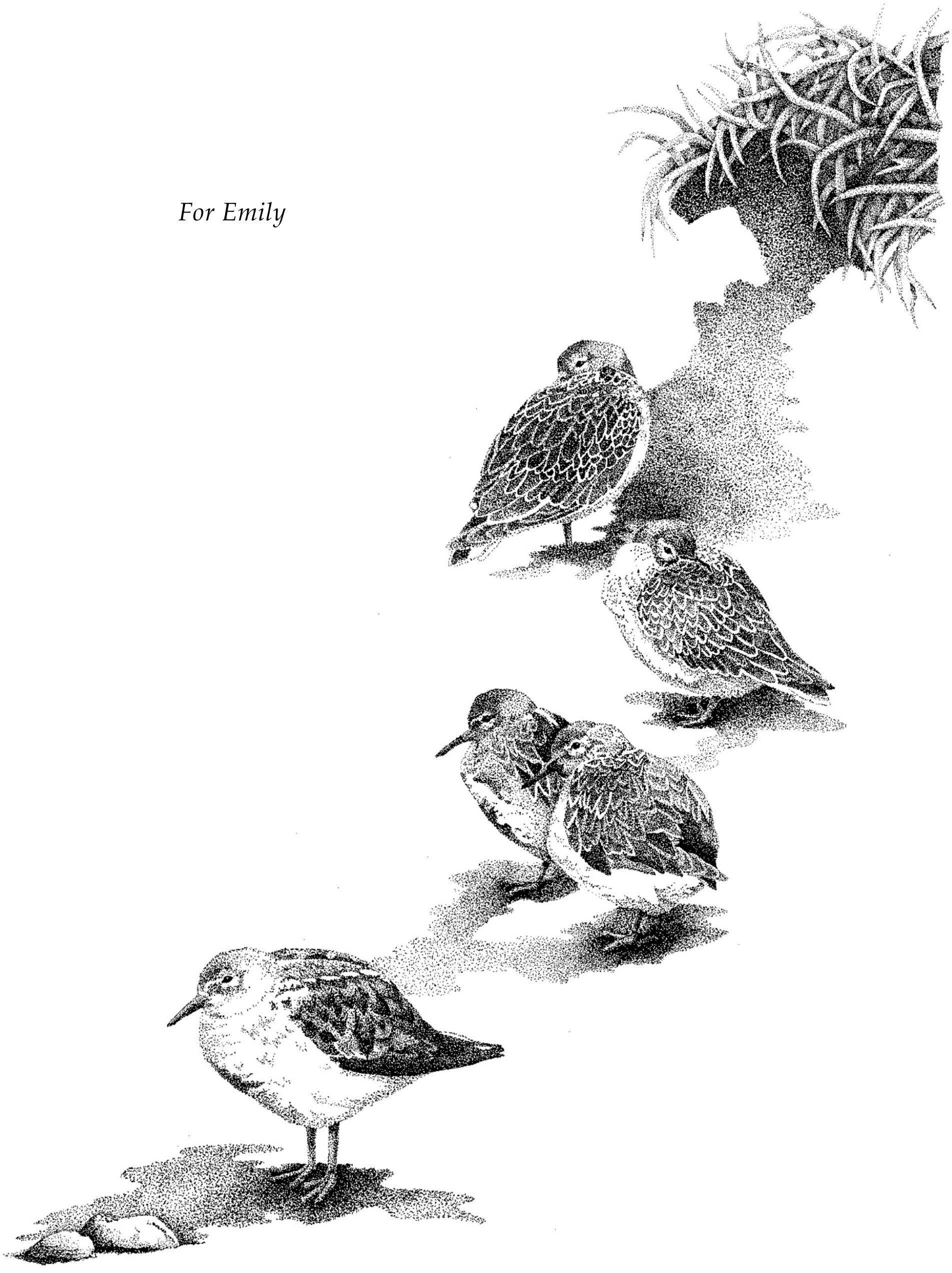

Contents

CHAPTER 1

Introduction

Daniel R. Ruthrauff

Introduction

Humans continue to marvel at 'unbelievable' occurrences in the natural world: Methuselah-like plants (Ferguson 1968) and animals (George et al. 1999), serial sex-swapping fish (Sunobe and Nakazono 1993), and heat-tolerant deep sea organisms (Cary et al. 1998) are just a few examples that alter our perceptions of the natural world. Birds, too, have long fascinated humans, and despite an extensive history of dedicated ornithological research, new and astonishing aspects of avian natural history continue to redefine our appreciation of this animal group. For instance, our ideas concerning physiological limits are tested when we learn that male Emperor Penguins *Aptenodytes forsteri* fast for up to 9 weeks at temperatures approaching -50° C in the normal course of their reproductive efforts (Le Maho 1977), or that Bar-tailed Godwits *Limosa lapponica baueri* annually conduct 11,000-km-long non-stop flights lasting nearly 10 days (Gill et al. 2009).

Nonbreeding shorebirds (Charadriiformes, suborders Charadrii and Scolopaci) also hold a place among such 'unbelievable' natural phenomena. Shorebirds peck and probe for surface- and subsurface-active prey, food items accessible only under ice-free conditions. Many species of shorebird live exposed to the chill of northern environments and so tend to have relatively high energetic demands (Kersten and Piersma 1987). When coupled with their reliance on predictably accessible food sources, shorebirds are susceptible to starvation during stochastic periods of deep cold (Marcström and Mascher 1979, Dietz and Piersma 2007). Consequently, factors related to their high energetic demands and relatively specialized foraging ecologies limit the nonbreeding distribution of most shorebirds to sites that rarely, if ever, experience freezing temperatures (Piersma 1996). Thus, a natural history dependent upon relatively benign environmental conditions generally defines the seemingly nondescript world of shorebirds in winter.

A handful of shorebird species, however, spends the nonbreeding season at high-latitude sites, and these species exhibit marked phenotypic changes in response to prevailing environmental conditions. The most obvious changes are those concerning the regulation of body fat. Fat stores in northerly-wintering shorebirds increase across the winter season, usually culminating in a winter peak constituting 4–15% of body mass (Davidson and Evans 1982, Evans and Smith 1975, McEwan and Whitehead 1984, Pienkowski et al. 1979). This peak usually coincides with the period of lowest temperatures (Davidson 1979, McEwan and Whitehead 1984, Pienkowski et al. 1979, Scott et al. 1994), suggesting that fat stores primarily provide energy during periods of high metabolic demand and low food intake (Blem 1990). As winter conditions ameliorate and the threat of food shortage wanes, fat stores slowly decrease. Comparatively little is known about the regulation of lean body components (e.g., organ and muscle groups) in northerly wintering shorebirds, but work on Purple Sandpipers (*Calidris maritima*) by Summers et al. (1998) indicates that lean tissues also change to accommodate process-specific metabolic demands. In the case of

Purple Sandpipers near the northern extent of their nonbreeding range, Summers et al. (1998) hypothesized that a hypertrophy of liver and intestine reflected an increased emphasis on digestive processes due to higher energetic demands at colder, more northerly sites.

Purple Sandpipers are the shorebird with the most northerly winter distribution, and are found along rocky shores of the North Atlantic Ocean from about 35°N to beyond the Arctic Circle as far as 71°N in Norway (Payne and Pierce 2002, Summers et al. 1990). This is well north of any other shorebird species, but due to the moderating influence of the Gulf Current, atmospheric advection patterns, and the prevailing maritime conditions, coastal regions of western Europe experience milder winter climates compared to other regions of the world at similar latitudes (Seager et al. 2002). Such relatively benign environmental conditions result in lowered energetic demands and, importantly, ensure predictable, ice-free access to food resources (Summers et al. 1992, 1998). In the event of severe cold weather, the rocky coastal habitats preferred by Purple Sandpipers are less likely to be affected by ice than low-salinity intertidal estuaries. These factors enable Purple Sandpipers to maintain relatively low winter fat stores at sites across their nonbreeding range (~5%; Summers et al. 1992, 1998).

In the Pacific Basin, Rock Sandpipers (*C. ptilocnemis*) are the ecological counterpart and sister taxon (Conover 1944, Gibson and Baker 2012, Pruett and Winker 2005) of Purple Sandpipers (see Species Overview). Rock Sandpipers are common during winter along the east Pacific coast (Gill et al. 2002), but the northern limits of their nonbreeding range had not been well documented until surprisingly recently (Gill and Tibbitts 1999). Rock Sandpipers had frequently been observed at locations like Prince William Sound, Alaska (~60.75° N; Isleib and Kessel 1973), typically using rocky intertidal habitats less prone to freezing. But a chance observation collected in an unanticipated location led to the description of the northern limit of the species' nonbreeding range (Erikson 1977). In the course of surveys to document the distribution of marine birds in Cook Inlet, Alaska, Alaska Department of Fish and Game employee David Erikson noted shorebirds ('probably Rock Sandpipers') on the mudflats of Tuxedni Bay (~61° N) in February 1976 (Erikson 1977). In contrast to sites at similar latitudes in Prince William Sound, the winter environment in upper Cook Inlet is considerably colder and characterized by the extensive presence of sea and shore-fast ice (Poole and Hufford 1982). The importance of Cook Inlet's mudflat habitats to migrating shorebirds was already recognized, but given the region's extreme cold and annual accumulation of extensive sea and shore-fast ice, it was simply assumed that no shorebirds spent the winter at this cold, dark, and icy site.

Erikson's observations went largely unnoticed, however, and subsequent observations of flocks of small shorebirds in the upper Cook Inlet region in late fall and early spring (W. Eldridge pers. comm., Butler and Gill 1987) were assumed to represent migrating birds. In the late 1990s, however, Bob Gill and Lee Tibbitts of the US Geological Survey received funding from the (then) Minerals Management Service to determine the seasonal use of intertidal habitats of Cook Inlet (Gill and Tibbitts 1999). This work supported surveys that began to systematically document the occurrence of Rock Sandpipers during winter in Cook Inlet. As the project progressed, it became clear that the occurrence of Rock Sandpipers in the region during winter was a regular, winter-long phenomenon. Additional observations demonstrated that these birds employed unique behavioral adaptations, like foraging in mud scours behind receding icebergs (Gill 1997) and roosting on sea ice (Ruthrauff and Eskelin 2009), and endured severe environmental conditions (Ruthrauff and Eskelin 2009) during winter in upper Cook Inlet. As these studies progressed, the extent to which this nonbreeding life history differed from all other shorebirds deepened, and the curiosity of researchers grew.

Thus, although birds regularly winter in colder climates, to the best of our knowledge upper Cook Inlet represents the world's coldest nonbreeding location used by a wading bird. The land/water interface is especially costly from an energetics perspective due to water's high conductance compared to air (Marsh and Dawson 1989, de Vries and van Eerden 1995). Wading and foraging at the land/water interface exposes Rock Sandpipers in upper Cook Inlet to the constant risk of frozen foraging substrates, and even the accumulation of ice on plumage and body (Ruthrauff and Eskelin 2009). In wading birds, such body icing typically occurs only during stochastic weather events, events that often lead to death due to starvation or exposure (Davidson and Clark 1985, Ticehurst and Hartley 1948, Ticehurst and Witherby 1940).

The Structure of this Dissertation

What elsewhere are considered stochastic weather conditions thus define the normal winter environment of upper Cook Inlet, Alaska, and Rock Sandpipers apparently contend quite successfully with what would otherwise be considered dangerously cold conditions for a wading bird. This naturally raised questions about whether these birds possessed unique adaptations that facilitated this unusual nonbreeding distribution. It seemed likely that any such adaptations would be physiological (e.g., increased thermogenic capacity) or behavioral (e.g., foraging behaviors) in nature. But because the very occurrence of Rock Sandpipers in upper Cook Inlet itself remained to be properly documented and described, such an investigation could not focus solely on the underlying mechanisms supporting this uncommon winter ecology. Both describing the phenomenon and investigating the underlying adaptations that support it became the dual avenues of inquiry that formed the foundation of this dissertation.

In addition to questions relating solely to the winter occurrence of Rock Sandpipers in upper Cook Inlet, this study also presented a unique opportunity to assess this nonbreeding life history strategy in a laboratory setting. Such an opportunity was fortuitous logistically as well: the long-term average daily temperature in January in the upper Cook Inlet region is about –9.5°C, making the site cold not only for Rock Sandpipers, but also for researchers attempting to study them. Despite our best efforts, collecting field observations in upper Cook Inlet during winter proved to be extremely challenging. Furthermore, the cost and logistical difficulty of accessing the isolated locations where Rock Sandpipers spend the winter made field observation largely impractical. For these reasons, we determined that experimental work in a laboratory setting could provide insights that would be impossible to gather in a natural setting.

We further decided that a comparative approach would potentially provide greater insight than a single-species approach. To this end, we availed ourselves of the co-occurrence of two Rock Sandpiper subspecies as sites in western Alaska during fall migration, and established a captive flock of Rock Sandpipers at the Royal Netherlands Institute for Sea Research. This flock comprised individuals of the nominate subspecies and the *tschuktschorum* subspecies, a comparison between the Rock Sandpiper subspecies with the most-northerly (*C. p. ptilocnemis*) and most-southerly (*C. p. tschuktschorum*) nonbreeding distributions (see Species Overview). We also seized upon previously published work on Purple Sandpipers (e.g., Summers et al. 1992, 1998) for a comparison of how these closely-related species adaptively regulate stores of lean and lipid body components in response to prevailing environmental conditions. In this way we made comparisons between and within the most-northerly wintering shorebird species.

The outline of this dissertation reflects the process of defining this unusual life history strategy and identifying the relevant physiological and behavioral factors that support it. In Chapter 2, my co-authors and I attend to the 'who?' of the story. As our work in Cook Inlet progressed, it became evident that the Rock Sandpipers occurring in the region during winter were almost exclusively *C. p. ptilocnemis* individuals. The breeding range of this subspecies is restricted to four relatively small islands in the Bering Sea, and colleagues and I designed, implemented, and conducted range-wide breeding surveys of *C. p. ptilocnemis* to accurately determine the size of this subspecies' population. Knowing the size of this subspecies' population is not only invaluable for basic conservation planning purposes (see Species Overview), but it also provides an important context for the winter use of sites in upper Cook Inlet. In Chapter 3, my co-authors and I provide this context by describing the abundance and distribution of Rock Sandpipers in upper Cook Inlet during winter. With the population estimate of the subspecies in hand, we now know that upper Cook Inlet occasionally supports essentially the entire population of this subspecies during winter. I next describe some of the physiological attributes of these birds in winter. There is a dearth of information on variation in lean and lipid components in nonbreeding shorebirds, and Chapter 4 explores how Rock Sandpipers adaptively regulate lean and lipid components from autumn to winter. This chapter also documents how these patterns differ from those of their northerly-wintering congener, the Purple

Sandpiper, and how contrasting environmental conditions between upper Cook Inlet and sites in the north Atlantic determine these differences.

The final chapters describe the experimental approaches we used to assess potential adaptations that the nominate subspecies of Rock Sandpiper employs in upper Cook Inlet during winter. These experiments compare nominate subspecies individuals to *tschuktschorum* individuals, and focus on basic physiological processes and foraging behaviors as the likely mechanisms by which the two subspecies maintain largely distinct nonbreeding distributions. In Chapter 5 my co-authors and I examine evidence for intrinsic differences between the two subspecies in basal metabolic rate, metabolic response to cold, and thermal conductance. Shorebirds are paragons of metabolic flexibility (e.g., Piersma 2011, Piersma et al. 1996), and previous work has demonstrated their ability to accommodate discrete metabolic adjustments via acclimatization to cold temperatures (e.g., Vézina et al. 2006, 2011). The contrast between the two subspecies' nonbreeding life histories provides a strong comparison whereby evidence for intrinsic physiological differences can be assessed under identical captive holding conditions.

To assess evidence for other intrinsic differences between the two subspecies, we next performed experiments to determine how the two subspecies exploit available food resources. For molluscivorous shorebirds, the act of crushing and digesting hard-shelled prey represents a digestive bottleneck (van Gils et al. 2005a, van Gils et al. 2005b). Given the high metabolic demands exacted by Cook Inlet's cold winter environment, this likely poses a serious constraint to Rock Sandpipers during winter, and in chapter 6 I compare the foraging ecologies of the two subspecies. Specifically, we measure differences between the subspecies in prey size selection, their maximum intake rates as a function of prey size, and their intake rates with respect to prey density and prey size. We use the small bivalve *Macoma balthica* as prey in all the trials; both subspecies feed on *Macoma* during spring and fall migration, but this prey species constitutes almost the entirety of the nominate subspecies' winter diet. The focused breadth of this diet may be expressed in a specialized foraging ecology that more effectively exploits these abundant food resources.

These various lines of inquiry are synthesized in Chapter 7. I summarize the physiological and behavioral adaptations that allow Rock Sandpipers to exploit Cook Inlet during winter. It is often the case that the most interesting questions in science remain unanswered, and in this context I also speculate as to why this subspecies' winter ecology stands in such stark contrast to other northern-breeding shorebirds. All shorebirds that breed at high northern latitudes (i.e., >60°N) are migratory, and nearly all conduct long north-south migrations between breeding and nonbreeding locations. Rock Sandpipers, however, essentially conduct a latitudinal, east-west migration between breeding sites in the Bering Sea (56°–60°N) and their more northerly, primary nonbreeding site, upper Cook Inlet (61°N). The historical biogeography of Rock Sandpipers was defined by periods of glacial advancement and retreat across Beringia during the late Pleistocene, and it is believed that relatively recent

(≤ 240,000 ypb) use of persistent glacial refugia shaped patterns of genetic differentiation within the species (Pruett and Winker 2005). Fossil marine bivalves suggest that upper Cook Inlet was most recently glacier-free about 11,000–15,000 years ago at the onset of the Holocene epoch (Schmoll et al. 1972, 1999). Given the dynamic conditions under which this nonbreeding life-history evolved, I speculate on the establishment and future persistence of upper Cook Inlet as the primary nonbreeding site used by the nominate subspecies of Rock Sandpiper.

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Rock Sandpiper species overview: a review of intraspecific variation

Daniel R. Ruthrauff

The following section owes a huge debt of gratitude to Robert Gill, Jr., Pavel Tomkovich, and Brian McCaffery, the three authors of the excellent Birds of North America species account for Rock Sandpipers (Gill et al. 2002). This exhaustive compilation provided much of the information detailed below, and also served as a constant touchstone throughout the course of this dissertation. Rock Sandpipers have rarely been the subject of dedicated scientific study, but the Birds of North America species account is a thorough distillation of over seventy years of the authors' collective knowledge regarding the natural history of Rock Sandpipers. As such, Gill et al. (2002) is frequently (and reverently) cited throughout this dissertation, for which I offer sincere thanks to these three researchers. I also thank the numerous photographers who generously shared images of the various subspecies included below.

Rock Sandpipers (*Calidris ptilocnemis*) are a shorebird species unique to the North Pacific Basin. The regions encompassing much of Alaska, northeastern Siberia, and the Bering Strait region are collectively termed 'Beringia', and Rock Sandpipers are the only endemic Beringian bird with recognized subspecies (Pruett and Winker 2005). Believed to number about 155,000 birds in total (Andres et al. 2012, Lappo et al. 2012), genetic evidence indicates that the species is most closely related to the Purple Sandpiper (*C. maritima*; Gibson and Baker 2012) and that the two species diverged near the beginning of the Pleistocene about 1.5 million years ago (Pruett and Winker 2005). Within the species group, intraspecific phylogenies suggest historic population isolation in glacial refugia with relatively recent (≤ 240,000 ybp) subspecific divergence times (Pruett and Winker 2005). Although analysis of mitochondrial DNA has provided inconclusive evidence of phylogenetic structure within the Rock Sandpiper clade (Pruett and Winker 2005), four subspecies are currently recognized based on appearance and morphology (American Ornithologists' Union 1957, Gibson and Kessel 1997). A putative fifth subspecies, *C. p. kurilensis*, describes birds breeding at the tip of the Kamchatka Peninsula (Lobkov 1986, 2001) and wintering on the Japan Archipelago (Ornithological Society of Japan 2000), but a paucity of specimens (Yamashina 1929a, b) and a poorly described distribution hinders accurate subspecific assignment of birds from this region (Gill et al. 2002). Within each subspecies, females are slightly larger than males; among the subspecies, individuals of the nominate subspecies are largest, followed by *C. p. tschuktschorum*, *C. p. couesi*, and *C. p. quarta*. Variation in size between the subspecies in measures of wing length, culmen, and tarsus ranges from 5–11% (see Appendix 2, Gill et al. 2002).

Rock Sandpipers breed at near-shore habitats ringing the Bering Sea (Figure 1.1), and the subspecies exhibit differential migration patterns (Table 1.1, Figure 1.2). It is believed that two subspecies, *C. p. couesi* (Gill et al. 2002) and *C. p. quarta* (Lappo et al. 2012), are essentially non-migratory, moving primarily between upland breeding sites and coastal nonbreeding sites. The population estimates for *C. p. couesi* and *C. p. quarta* are 75,000 (Brown et al. 2001) and 10,000 individuals (Y. Artukhin, in Gill et al. 2002), respectively. The nominate subspecies (population size about 20,000; this

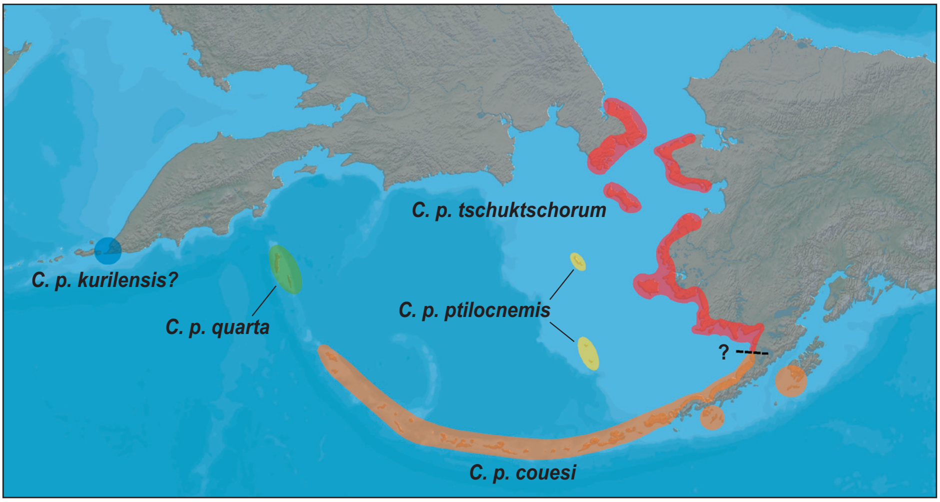

Figure 1.1. The Beringian breeding distribution of Rock Sandpipers *Calidris ptilocnemis*.

Table 1.1. Breeding and nonbreeding ranges of the four recognized subspecies of Rock Sandpiper (summarized from Gill et al. 2002). See Figure 1.2 for location of place names.

Subspecies and Colloquial Name	Breeding Range	Nonbreeding Range
C. p. couesi, "Aleutian Sandpiper"	Throughout Aleutian Archipelago west to Alaska Peninsula (at least Ugashik); Shumagin and Kodiak Archipelagoes. Extent into western Alaska and overlap with *C. p. tschuktschorum* unknown	Same as breeding range; birds breeding on Alaska Peninsula likely move to more southerly locations on Alaska Peninsula during winter
C. p. quarta, "Commander Sandpiper"	Commander Islands, Russia	Same as breeding range
C. p. ptilocnemis, "Pribilof Rock Sandpiper"	Pribilof, St. Matthew, and Hall Islands	Primarily Cook Inlet and Alaska Peninsula; no known large concentrations outside these regions, but occurs as far south as Alexander Archipelago, Alaska
C. p. tschuktschorum, "Northern Rock Sandpiper"	Northern Bristol Bay north along mainland Alaska to central Seward Peninsula; St. Lawrence and Nunivak Islands; east to Chukotskiy Peninsula, Russia. Extent into southern Bristol Bay and overlap with *C. p. couesi* unknown	Southcentral Alaska to northern California; occasionally Pribilof Islands

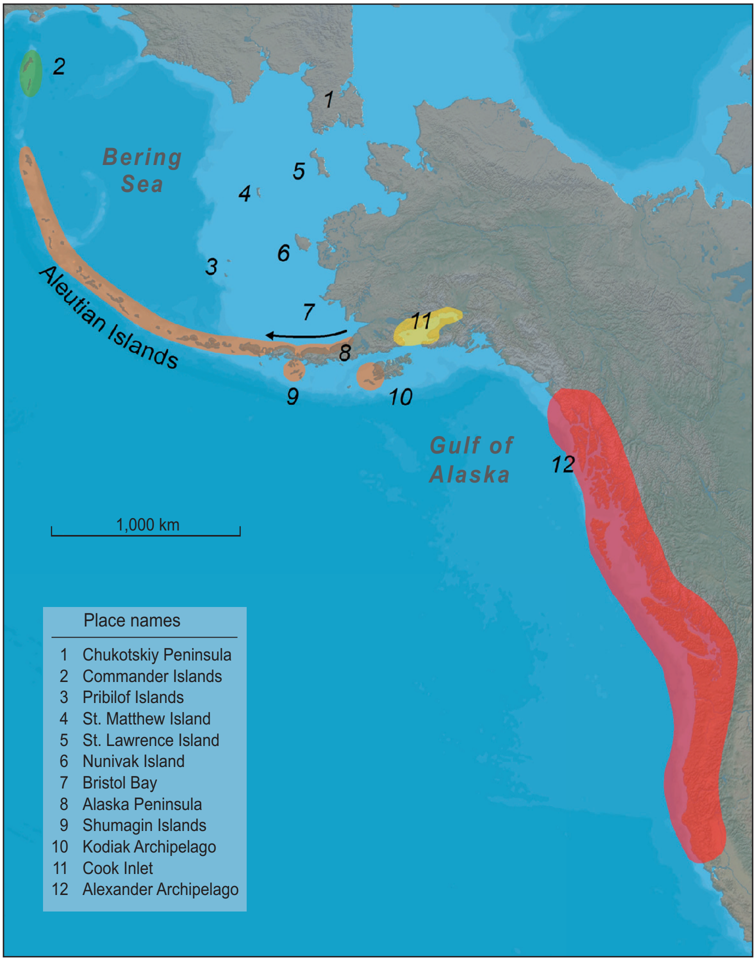

Figure 1.2. Primary nonbreeding distribution of Rock Sandpipers. See Figure 1.1 for key to subspecies-specific colors; place names refer to locations mentioned in text and Table 1.1.

thesis) moves intermediate distances (≤ 1,500 km) between breeding and nonbreeding sites (Gill et al. 2002), and the fourth subspecies, *C. p. tschuktschorum* (North American breeding population estimate 50,000 individuals, Brown et al. 2001; Chukotskiy Peninsula, Russia, breeding population estimate 10,000–20,000 individuals, Delany and Scott 2006), migrates comparatively long distances (~ 4,000 km). The subspecies exhibit distinct plumage patterns of the wing and mantle (see below; Gill et al. 2002), and these traits, in conjunction with a handful of band recoveries, helped to delineate each subspecies' nonbreeding range. Subspecies likely overlap at the limits of their respective nonbreeding ranges, but in general the subspecies have allopatric winter ranges. This subject requires additional study.

Figure 1.3. Rock Sandpiper *C. p. ptilocnemis* in basic plumage. Photo taken by Daniel Ruthrauff at Homer, Alaska, on 18 March, 2011.

Like most calidridine sandpipers, the appearance of Rock Sandpipers varies seasonally based on annual patterns of molt (Prater et al. 1977), and molt cycles and subspecific appearances are described in detail by Gill et al. (2002). In brief, basic plumage is maintained from approximately October through late March and alternate plumage from mid-April through August. Only individuals of the nominate subspecies have a diagnostic basic plumage (Figure 1.3). Birds of the nominate subspecies have light grey crowns, napes, and mantles, and the grey wraps to form a discrete collar with small grey streaks partway down the breast and flanks. The breast, belly, flanks, and undertail are pure white, as are feathers at the base of the bill and the lores. The scapulars and tertials are slightly darker than the mantle, with dark grey centers to each feather, while the greater coverts and primaries are darker still. In contrast, the basic plumage of the three other subspecies includes muted shades of dark grey rather than light grey (Figs. 1.4–6). The nonbreeding plumage of these three subspecies closely resembles that of Purple Sandpipers (Figure 1.7). The extent of dark grey streaking along the breast and flanks is much more extensive in these three subspecies than the nominate subspecies, and typically terminates mid-breast (as opposed to slightly below the throat in *C. p. ptilocnemis*) and at the undertail coverts (as opposed to mid-flank in *C. p. ptilocnemis*). All subspecies have dull yellow / greenish legs and feet, and the bill is typically yellow / green at the base and black at the tip. The bill, legs, and feet tend to darken in individuals of both sexes during the breeding season.

Figure 1.4. Rock Sandpiper *C. p. couesi* in basic plumage. Photo taken by Kristine Sowl at Kinzarof Lagoon, Alaska, on 28 September, 2008.

Figure 1.5. Rock Sandpipers *C. p. quarta* in basic plumage. Photo taken by Yuri Artukhin, Cape Nepropusk, Bering Island, Russia, on 20 March, 1993.

Figure 1.6. Rock Sandpiper *C. p. tschuktschorum* in basic plumage. Photo taken by Jared Hughey at Humboldt Bay, California, on 21 February, 2013.

Figure 1.7. Purple Sandpiper *C. maritima* in basic plumage. Purple Sandpipers are very similar in size and appearance to Rock Sandpipers, and the species' close relation is confirmed by phylogenetic analyses. Photo taken by Gerrit Vyn in Barnegat Light, New Jersey, on 16 February, 2006.

The alternate plumage of all subspecies is characterized by mantles, scapulars, and crowns with rusty and rufous highlights, a smudgy, indistinct black patch on the lower breast, and dark brown auricular patches. Subtle differences in alternate plumage exist between the subspecies (Figs. 1.8–11), primarily relating to the color and extent of edging on mantle feathers, extent of breast patch, and definition of the auricular patch (see Appendix 1, Gill et al. 2002). Unlike in basic plumage, Rock Sandpiper sexes differ in alternate plumage. In males of all subspecies, whitish plumage around the eyes contrasts with their auricular patch, while the face of female birds tends to have more mottled browns and reds, creating a uniform, less contrasting appearance to their heads (Figure 1.12). Males also tend to have a more clearly defined breast patch than females. Nevertheless, there is considerable variation in the appearance of the alternate plumage within each subspecies, especially with respect to the extent and density of mottling on the breast patch. As such, the photos included herein are not intended to serve as diagnostic images of each subspecies, but instead represent a range of the natural variation within each subspecies.

Figure 1.8. Rock Sandpiper *C. p. ptilocnemis* in alternate plumage. Plumage characteristics indicate that this bird is likely a male. Photo taken by Doug Gochfeld on St. Paul Island, Alaska, on 5 June, 2013.

Figure 1.9. Rock Sandpiper *C. p. couesi* in alternate plumage. Plumage characteristics and the relatively large bill indicate that this bird is likely a female. Photo taken by Kristine Sowl at Cold Bay, Alaska, on 6 July, 2008.

Figure 1.10. Rock Sandpipers *C. p. quarta* in alternate plumage. Plumage characteristics and the relatively small bills indicate that these birds are likely males. Photo taken by Thomas Van Pelt at Nikolskoye, Bering Island, Russia, on 15 July, 2006.

Figure 1.11. Rock Sandpiper *C. p. tschuktschorum* in alternate plumage. Plumage characteristics and relatively small bill indicate that this bird is likely a male. Photo taken by Luke DeCicco on the Seward Peninsula outside Nome, Alaska, on 25 June, 2012.

Figure 1.12. Rock Sandpiper *C. p. tschuktschorum* in alternate plumage. The more extensive mottling on throat and neck, less distinct breast patch, and relatively large bill indicate that this bird is likely a female. Photo taken on 28 June, 2012 by Luke DeCicco at the same site on the Seward Peninsula as Figure 1.11.

Figure 1.13. Characteristic wing patterns of three subspecies of Rock Sandpipers. All birds were collected during the breeding season (University of Alaska Museum collections, Fairbanks). From top to bottom, *C. p. couesi* exhibits limited white on the leading edge of the primaries, none of which reaches the rachis. Individuals of this subspecies exhibit extensive dark grey coloring in the tips of their secondaries; in this individual, dark grey is present in secondaries 1–9. In the middle specimen (*C. p. tschuktschorum*), white is present on the leading edge of the first five primaries, and reaches the rachis on primaries one and two. The extent of dark grey on the secondaries is more limited in this individual, barely reaching secondaries seven and eight. In the bottom specimen (*C. p. ptilocnemis*), the light grey coverts contrast with the darker coverts of the other two specimens. Additionally, the primaries show more extensive white on the leading edges, reaching the rachis on the first three primaries. Dark grey in the secondaries is limited to feathers 1–5 in this individual. *C. p. quarta* (not pictured) exhibits wing patterns most similar to that of *C. p. couesi* Photo by Robert Gill, Jr.

Rock Sandpiper subspecies exhibit diagnostic wing patterns, however, a trait which was exploited in this dissertation to differentiate between otherwise indistinguishable *C. p. ptilocnemis* and *C. p. tschuktschorum* birds captured at a fall staging site. Specifically, the subspecies display predictable patterns in the amount of white on the leading edge of the primaries and extent of white on the secondaries (Figure 13; Gill et al. 2002). The nominate subspecies has the most white on primaries and secondaries, and *C. p. quarta* the least; *C. p. tschuktschorum* and *C. p. couesi* fall between these extremes, with *C. p. tschuktschorum* exhibiting slightly more white in these traits than *C. p. couesi*.

Rock Sandpipers are socially monogamous (Pitelka et al. 1974) and typically breed at low elevation sites with low-lying dry or moist habitats (Gill et al. 2002). The nominate subspecies commonly occurs in upper Cook Inlet, Alaska, during winter where it is found exclusively on mudflat habitats, while it is believed that the other three subspecies prefer rocky intertidal habitats (Gill et al. 2002). Birds forage on a variety of intertidal invertebrates, but molluscs, crustaceans, and polychaete worms likely dominate the diet during the nonbreeding season (Gill et al. 2002). The two most migratory subspecies (*C. p. ptilocnemis* and *C. p. tschuktschorum*) tend to move south later in the fall (October–November) and return back north to breeding areas earlier (mid- to late April) than most other sympatric shorebird species (Gill et al. 2002).

The population status of Rock Sandpipers is unknown but assumed to be stable. Due to their small population size and limited breeding and nonbreeding ranges, however, the nominate subspecies of Rock Sandpiper is considered a subspecies of high conservation concern in both the United States Shorebird Conservation Plan (Brown et al. 2001) and the Alaska Shorebird Conservation Plan (Alaska Shorebird Group 2008). Following the same criteria, the *quarta* subspecies similarly merits recognition as a subspecies of high conservation concern, while both the *couesi* and *tschuktschorum* subspecies are currently considered subspecies of moderate conservation concern (Brown et al. 2001, Alaska Shorebird Group 2008).

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Observations of body-icing on Rock Sandpipers during winter in upper Cook Inlet, Alaska

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Wader Study Group Bulletin 116:88–90. 2009

The effects of severe winter weather on birds are well documented and include forced migration (Dobinson and Richards 1964, McIlhenny 1940), reduced physiological condition (Davidson and Evans 1982, Dugan et al. 1981, Piersma et al. 1994), and direct mortality (Dobinson and Richards 1964, Scott 1937, Ticehurst and Hartley 1948). Direct mortality is typically manifested through starvation or hypothermia; birds lacking sufficient energy reserves to emigrate may succumb to starvation or cold if food resources are depleted or inaccessible (Davidson and Evans 1982, Piersma et al. 1994). Less commonly, mortality may be due to ice accumulation, often reported as the consequence of ice accretion on auxiliary markers (e.g., nasal saddles, neck collars [Byers 1987, Greenwood and Bair 1974, Zicus et al. 1983]), typically on waterfowl species. Markers can become heavily laden with ice, hindering a bird's ability to feed, swim, or fly, often resulting in death. Less commonly, others have reported the effects of icing on unmarked birds. Ticehurst and Witherby (1940) and Ticehurst and Hartley (1948) reported instances of numerous bird species (including shorebirds) suffering body-icing during severe winters in Britain. In general, however, observations of body-icing on unmarked birds are rare, and all reports mention obvious negative impacts due to the icing (e.g., inability to fly, loss of plumage, death).

On the dates 14 March 2006, 20 November 2006, and 17–19 December 2007, we observed numerous individual Rock Sandpipers *Calidris ptilocnemis* with extensive body-icing on their plumage and/or tarsi (Figures 1.14 and 1.15). Birds were observed near the mouth of the Kasilof River, upper Cook Inlet, Alaska (60.390°N, 151.297°W). Approximately 6300, 6000, and 7000 Rock Sandpipers were present at the site on 14 March 2006, 20 November 2006, and 17–19 December 2007, respectively. Although we were unable to systematically assess the prevalence of icing due to the sandpipers' rapid feeding movements and their attempts to shelter their legs under their plumage, we estimated that approximately 5% of birds were affected with body-icing. Due to the high number of birds present at the site and their frenetic feeding activity, it was impossible to follow any one individual for prolonged observation. Nonetheless, all of the iced birds that we observed behaved normally and fed actively side by side with unaffected birds. We did not note any lethargic, listless, or otherwise obviously impacted birds, nor did we note any dead birds. Furthermore, we did not observe any of the iced birds attempting to dislodge the ice from their bodies. The fact that only approximately 5% of all birds were afflicted, however, may indicate a selective predisposition that reflects an individual's 'quality' (e.g., body condition, thermogenic capacity, etc.).

Our observations indicate that Rock Sandpipers do not appear to be obviously impacted by body-icing, and we are unaware of similar observations for other shorebird species. The persistence of such icing is unknown and likely affects the overall severity of the condition. For instance, it may be that the ice only forms while birds are relatively inactive (e.g., while roosting) but quickly melts once the birds increase metabolic activity (e.g., while flying, feeding, or simply wading back into the water).

Figure 1.14. Two Rock Sandpipers exhibiting body-icing observed near the mouth of the Kasilof River, Alaska, 18 December 2007. The bird to the right has its left tarsus encased in ice and the bird to the left exhibits limited plumage icing on its lower right breast (photo D. Ruthrauff).

Figure 1.15. Rock Sandpipers roosting at high tide near the mouth of the Kasilof River, Alaska, 19 December 2007. Birds bathe in the splash zone while others roost on frozen ground. Numerous individuals exhibit plumage-icing (red arrows), and two individuals also exhibit icing on their left tarsi (red circles; photo D. Ruthrauff).

Alternatively, the icing may endure or even increase for as long as cold weather conditions persist, and birds that endure longer periods of body-icing are likely incurring increased thermogenic costs. Severe icing may also increase predation risk due to the diminished flight capabilities of heavier birds. Rock Sandpipers average approximately 100 g during winter in upper Cook Inlet (Gill et al. 2002), and extensive icing (e.g., Fig. 1.14) could conceivably increase a bird's mass by 2–4%, predisposing an iced individual to increased predation risk compared to non-iced conspecifics (e.g., Burns and Ydenberg 2002, Lima 1986). As with the previously mentioned waterfowl markers, leg bands may predispose banded individuals to ice accumulation, and Rock Sandpipers in upper Cook Inlet may thus be especially susceptible to negative band-related impacts. Rock Sandpipers wintering in upper Cook Inlet are almost exclusively individuals of the nominate race (Gill et al. 2002), and less than 200 individuals of this race of approximately 25000 birds (Alaska Shorebird Group 2008) have been marked with leg bands. We detected no banded birds during the aforementioned observation periods, but subsequently observed banded Rock Sandpipers during other more benign periods in upper Cook Inlet. Thus, banding may not necessarily predispose Rock Sandpipers in upper Cook Inlet to increased negative impacts related to body-icing, but this threat should be acknowledged and more rigorously assessed by researchers in the future.

Our observations coincided with periods of severe, but not unprecedented, cold. The minimum temperatures recorded at Kenai, Alaska, a coastal town approximately 18 km north of the Kasilof River was –23°C, –17°C, and –22°C for March 2006, November 2006, and December 2007, respectively (unless otherwise noted, all meteorological information from National Oceanic and Atmospheric Administration 2009). In contrast, we did not encounter any iced birds during recent observations of approximately 4000 Rock Sandpipers at the same location from 4–5 and 18–20 February 2009 when the coldest temperatures recorded at Kenai were –19°C and –15°C, respectively. These temperatures were sufficiently cold to freeze standing water on the exposed mudflats (brackish water at this site freezes at approximately –2°C), but not cold enough to cause the accumulation of ice on the birds. When feeding, the Rock Sandpipers often stand in water as deep as their bellies, but the water apparently does not freeze to the bird unless the air temperature is considerably lower than –2°C (e.g., approaching –20°C).

Studies of marine structures indicate that as sea temperatures approach freezing the main factors contributing to ice accretion are air temperature and wind speed (Pease and Comiskey 1985). Like many other bird species, Rock Sandpipers likely rely upon countercurrent circulation to minimize heat loss through their legs (Johansen and Bech 1983), and during extreme cold the temperature of the feet and tarsi of Rock Sandpipers likely approaches 0°C. Similarly, Rock Sandpiper plumage is clearly an extremely effective insulator, and the temperature of outer plumage layers are essentially at ambient temperature. Thus, in cold, windy conditions, legs and plumage are suitably cold structures upon which ice can accumulate. While air temperature is likely the most significant factor promoting this phenomenon, a combination of wind and near-freezing water seems to be required to produce body-icing as evidenced by the absence of iced birds during calm, –19°C conditions from 4–5 February 2009.

Our observations are unique and intriguing, but may not necessarily be uncommon. Rock Sandpipers are present at sites throughout upper Cook Inlet during winter (Gill et al. 2002), and weather conditions similar to those that induced the body-icing described above are common throughout the winter. For instance, the average daily minimum temperature in Kenai during January and February is –15°C and –13°C, respectively (Western Regional Climate Center 2009). Additionally, Kenai has an average of 48 days where minimum temperatures are –18°C or lower, and annual extremes <–30°C are not uncommon, demonstrating that the cold temperatures that promote body-icing can occur throughout the winter. The fact that this phenomenon has gone unreported is not surprising, however, because during the winter most Rock Sandpipers in Cook Inlet occur at sites unfrequented by humans. At the few locations where Rock Sandpipers co-occur with humans, the weather conditions that induce body-icing on birds are the same weather conditions that typically encourage humans to stay indoors. Hence, few observers are present to note the occurrence of this phenomenon. However common the accretion of body-ice on Rock Sandpipers may be, the survival implications of this phenomenon are fascinating, especially in the broader context of the species' ability to survive long, dark, cold winters in upper Cook Inlet, Alaska.

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CHAPTER 2

Small population size of the Pribilof Rock Sandpiper confirmed through distance-sampling surveys in Alaska

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Abstract

The Rock Sandpiper (*Calidris ptilocnemis*) is endemic to the Bering Sea region and unique among shorebirds in the North Pacific for wintering at high latitudes. The nominate subspecies, the Pribilof Rock Sandpiper (*C. p. ptilocnemis*), breeds on four isolated islands in the Bering Sea and appears to spend the winter primarily in Cook Inlet, Alaska. We used a stratified systematic sampling design and line-transect method to survey the entire breeding range of this population during springs 2001–2003. Densities were up to four times higher on the uninhabited and more northerly St. Matthew and Hall islands than on St. Paul and St. George islands, which both have small human settlements and introduced reindeer herds. Differences in density, however, appeared to be more related to differences in vegetation than to anthropogenic factors, raising some concern for prospective effects of climate change. We estimated the total population at 19 832 birds (95% CI 17 853–21 930), ranking it among the smallest of North American shorebird populations. To determine the vulnerability of *C. p. ptilocnemis* to anthropogenic and stochastic environmental threats, future studies should focus on determining the amount of gene flow among island subpopulations, the full extent of the subspecies' winter range, and the current trajectory of this small population.

Introduction

The Rock Sandpiper (*Calidris ptilocnemis*) is the only polytypic bird species endemic to Beringia (Pruett and Winker 2005), with all four subspecies breeding in coastal habitats ringing the Bering Sea (Gill et al. 2002). It is among the least migratory of all calidridine sandpipers and remains at high latitudes throughout its annual cycle (Gill et al. 2002). The nominate form, *C. p. ptilocnemis* (Coues, 1873), was considered a distinct species by Ridgway (1919) and originally named the "Pribilof Sandpiper" from the location of the type specimen. Its current taxonomic position has been confirmed originally on the basis of plumage and morphology (Conover 1944) and more recently by genetic analyses (Pruett and Winker 2005).

The core breeding range of the Pribilof Rock Sandpiper (hereafter Pribilof Sandpiper) seems certain. As summarized by Conover (1944), the Pribilof Sandpiper nests primarily on four Bering Sea islands (St. Paul, St. George [together the Pribilof Islands], St. Matthew, and Hall; Fig. 2.1). Questions remain as to whether it also breeds on two other nearby Bering Sea islands (Nunivak and St. Lawrence, Fig. 2.1; see Gill et al. 2002), but Conover (1944) and Gibson and Kessel (1997) concluded that the Rock Sandpipers at these two locations belong to the subspecies *C. p. tschuktschorum*. For this study we followed these conclusions and consider the breeding range of the Pribilof Sandpiper as shown in Fig. 2.1.

The winter range of the Rock Sandpiper in North America extends from the coasts of the Aleutian Islands and Gulf of Alaska and south to northern California (in Gill et al. 2002), but the ranges of each subspecies are poorly described. Among the four subspecies of the Rock Sandpiper, the Pribilof Sandpiper is the only one with a distinctive basic plumage (Conover 1944, Gill et al. 2002), enabling easy discrimination from the three other subspecies. There are several reports (Gill and Tibbitts 1999, in Gill et al. 2002) of large numbers of Rock Sandpipers from the Gulf of Alaska in winter, but none mentions subspecies. Erikson (1977) reported about 3400 birds in early February in Cook Inlet, Alaska. Small numbers of Rock Sandpipers were subsequently reported through the early 1990s (Gill and Tibbitts 1999) from both upper and lower Cook Inlet in winter, but not until specimens were collected in upper Cook Inlet in February 1997 was it determined that these included Pribilof Sandpipers (Daniel Gibson, pers. comm.; Gill, unpubl. data). Recent field work in lower Cook Inlet in winter has revealed a mixture of subspecies, most a darker form (likely *C. p. tschuktschorum*) but also including some Pribilof Sandpipers (Ruthrauff, unpubl. data). Concurrent aerial and ground surveys of upper Cook Inlet in winter have revealed many thousands of Rock Sandpipers, almost all of the Pribilof subspecies (Gill and Tibbitts 1999; Gill and Ruthrauff, unpubl. data). Given the subspecies' extremely limited breeding range, the paucity of winter records elsewhere, and the large number of birds recorded in upper Cook Inlet through most winters, we hypothesized that this area hosts the majority of the Pribilof Sandpiper's population during winter (Gill and Tibbitts 1999, Gill et al. 2002).

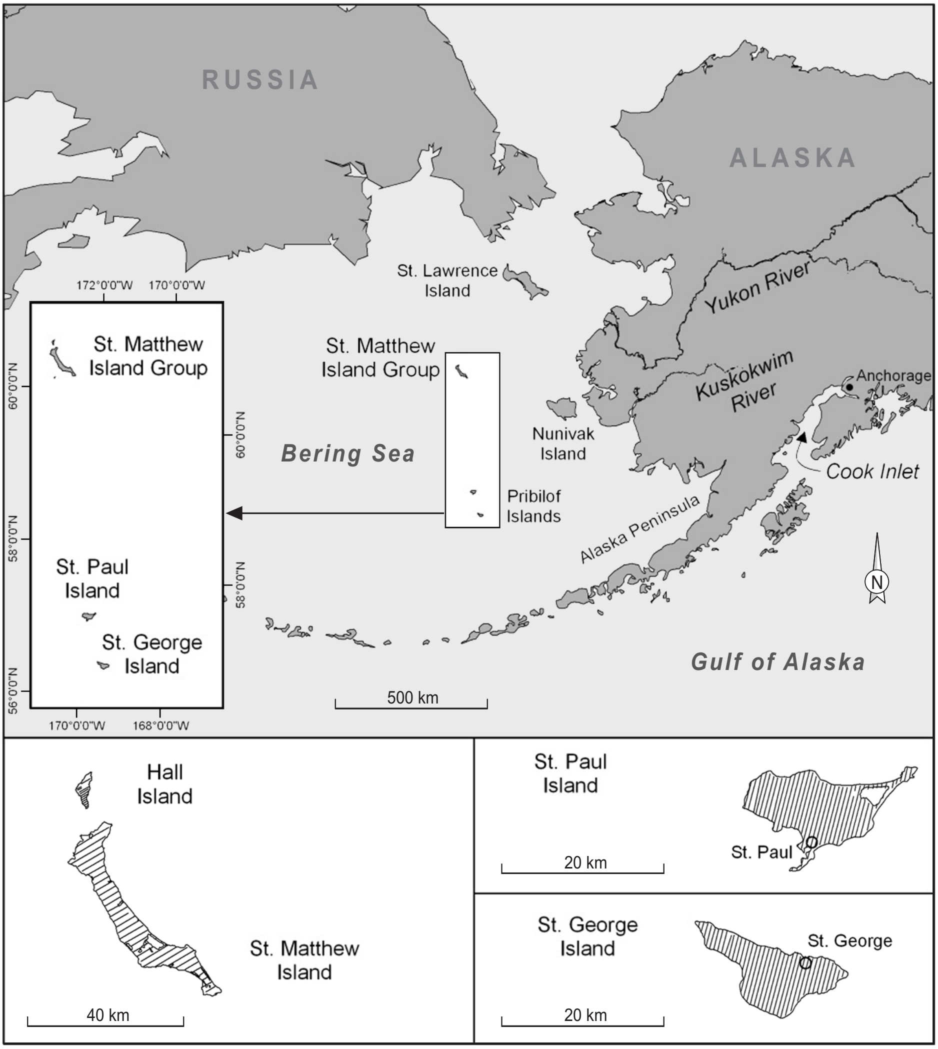

Figure 2.1. The Bering Sea region showing the breeding range of the Pribilof Rock Sandpiper, *Calidris p. ptilocnemis* (inset boxes, upper panel), and the layout of transects on each island (lower panels). Additional site names refer to locations mentioned in the text.

Small, geographically restricted populations are inherently more vulnerable to population-level perturbations (Pimm et al. 1988, Davidson et al. 2009). As such, the Rock Sandpiper is one of only three North American shorebird species included on the "Red List" of global conservation concern by National Audubon Society's WatchList program (Butcher et al. 2007). For similar reasons, the Pribilof Sandpiper has been designated as a subspecies of high conservation concern in both the U.S. Shorebird Conservation Plan (Brown et al. 2001) and the Alaska Shorebird

Conservation Plan (Alaska Shorebird Group 2008). Effective conservation of any wildlife population requires an understanding of its population trajectory, and an accurate estimate of population size provides a baseline against which change may be measured. On the basis of winter counts in Cook Inlet, Gill and Tibbitts (1999) and Gill et al. (2002) estimated the Pribilof Sandpiper's population at 20 000–25 000 individuals. Despite uncertainty about the subspecific composition of the Rock Sandpipers wintering in Cook Inlet (Gill et al. 2002), this figure has been employed for conservation planning (Morrison et al. 2006, Alaska Shorebird Group 2008).

To address uncertainties about the subspecies' population size, we designed and implemented a survey across its breeding range to obtain an accurate, baseline population estimate. The four remote and rugged islands that encompass the breeding area differ in size, latitude, and terrain and also have varied histories of habitation by humans and introduced reindeer (*Rangifer tarandus*). Thus our study represents a rare opportunity not only to systematically survey a bird population of conservation concern across its entire breeding range but also to investigate variation in its density with respect to anthropogenic and environmental factors.

Methods

Study Areas

We surveyed each island in the Bering Sea where the Pribilof Sandpiper breeds: St. Paul (109 km^2) and St. George (90 km^2), and the more northerly St. Matthew (314 km^2) and Hall (16 km^2) islands (Fig. 2.1). All islands are either wholly or partially included within the Alaska Maritime National Wildlife Refuge, managed by the U.S. Fish and Wildlife Service. The Pribilof Islands support two villages with populations of 437 and 125 on St. Paul and St. George, respectively (U.S. Census Bureau 2011); St. Matthew and Hall islands are uninhabited. All four islands are characterized by rocky shorelines, massive sea cliffs, and gently rolling terrain topped by rocky uplands. St. Paul has the lowest mean elevation (38 m), followed by St. Matthew (94 m), St. George (102 m), and Hall (182 m); maximum elevations range from 201 m on St. Paul to 507 m on Hall. Predominant habitats on all islands include low-lying meadows, dwarf-shrub heath tundra dominated by *Empetrum nigrum*, thick lichen mats, and sparsely vegetated rocky uplands (Preble and McAtee 1923, Rausch and Rausch 1968, Byrd and Norvell 1993, Talbot et al. 2001). The more southerly Pribilof Islands also contain extensive regions of forb tundra dominated by *Lupinus nootkatensis* and *Angelica lucida*.

Introduced ungulates can greatly alter vegetation cover (Klein 1987), and these Bering Sea islands have varied histories of large-mammal introductions. Reindeer were introduced to the Pribilof Islands in 1911 as an additional food source for the islands' residents (Osgood et al. 1915), and the size of each herd has fluctuated greatly since introduction (Swanson and Barker 1992). Reindeer were introduced to

St. Matthew Island in 1944, but the population collapsed 20 years later following years of near-exponential population growth (Klein 1968); the last reindeer died there in the early 1980s (Klein 1987). Reindeer have never been introduced to Hall Island.

Survey Design

We conducted line-transect surveys (Buckland et al. 2001) to estimate the breeding densities and population size of the Pribilof Sandpiper. Gill et al. (2002) suggested that all individuals of the subspecies, including nonbreeders, reside on these islands during the breeding season. We designed the surveys to assure that all critical assumptions of distance sampling (Buckland et al. 2001) were met: (1) transect lines were placed randomly relative to the distribution of the birds, (2) birds directly on the transect line were always detected, (3) birds were detected at their initial location, prior to any movement in response to the observer, and (4) distances to the birds were measured accurately. Using a randomly chosen start, we selected a systematic sample of line transects parallel to the short axis of each island. This design facilitated access via the coast and ensured transect lengths (<10 km) that could reasonably be surveyed by foot in a day. We spaced transects at 0.5-km intervals on St. Paul (n = 38), St. George (n = 39), and Hall (n = 15) islands and at 1.5-km intervals on the much larger St. Matthew Island (n = 35; Fig. 2.1). On Hall Island three transects were not surveyed and two others were only partially completed because of time constraints; on St. Matthew one transect was not surveyed because of dangerous terrain. We did not survey sections of transects that crossed large lakes (≥1 km^2), and we excluded these areas from density calculations. Large lakes excluded (18.7 km^2), the breeding range totaled 510.5 km^2.

We timed our surveys in each area to coincide with the establishment and maintenance of breeding territories, a period during which breeding pairs (and males in particular) are very active and highly detectable (Gill et al. 2002). During this period the males engage in conspicuous flight displays and give an array of distinctive, context-specific vocalizations. We surveyed St. Paul from 1 to 19 May 2001, St. George from 4 to 16 May 2002, St. Matthew from 29 May to 29 June 2003, and Hall on 21 June 2003. Surveys at St. Matthew and Hall took place 3–4 weeks later than at the Pribilof Islands to coincide with the delayed breeding season at these higher-latitude sites. We believe interannual movement of individuals between islands to be minimal because studies of *C. p. tschuktschorum* have shown the birds to be strongly site-faithful (Tomkovich 1994, Johnson et al. 2009). Thus we assumed that each island's survey represented an independent sample.

The probability of detection of shorebirds nesting in the subarctic, unlike that of passerines, varies little through the day (Nebel and McCaffery 2003), so to maximize sampling we surveyed throughout daylight. We surveyed only when conditions were suitable (i.e., wind <25 km hr^{-1}, >500 m visibility, no precipitation); if they deteriorated during a survey, we repeated it when conditions improved and discarded the original results. A total of eight observers participated, one in all three years, three in two years, and four in only one of the years. We assigned observers randomly to the transects surveyed each season. Prior to field work, observers were trained in distance estimation and in recognition and interpretation of Pribilof Sandpiper behavior and vocalizations. In a complementary study, observers on St. Matthew and Hall simultaneously surveyed for McKay's Bunting (*Plectrophenax hyperboreus*) (Matsuoka and Johnson 2008).

Observers used a GPS to locate each transect's starting point and to navigate to the end point on the opposite shore. Observers used a laser rangefinder to measure the perpendicular distance from the transect line to the initial location of each bird seen (or flock center for ≥2 birds). For birds heard but not seen, observers used the rangefinder to estimate the distance to the approximate location of the bird. There were 184 aural-only detections (9.3% of total) of birds whose distances were estimated in this way. Observers recorded flock size for each detection and any behavior or vocalizations that would help determine a bird's sex and status (territorial or transient). The Pribilof Sandpiper is sexually dimorphic (Gill et al. 2002), but differences in size and plumage are subtle and not easily discerned at a distance. Therefore, in addition to morphological cues, observers relied on sex-specific behaviors (e.g., the male's flight displays and nest-scraping behaviors) and vocalizations (e.g., the male's songs, "cricket" calls, rhythmically repeated calls; Miller et al. 1988, Gill et al. 2002) to determine the bird's sex.

Statistical Analyses

The brevity of our visit to each island and our need to survey whenever weather permitted constrained our ability to randomize surveys by time of season and time of day. In a post-hoc assessment of potential temporal effects on detection probability, we calculated the number of birds detected per linear kilometer and evaluated transects on each island for evidence of seasonal (except Hall Island, surveyed on one day) and diurnal trends in detection rates. The number of detections per kilometer did not vary by date (linear regression; all islands $P > 0.05$) or by the time of the survey's start (<12:00 hr AST, 12:01–16:00 hr, >16:00 hr; ANCOVA, $P = 0.62$). Therefore, we excluded season and time of day as covariates in our subsequent modeling.

We used the Multiple Covariates Distance Sampling (MCDS) engine in program Distance 6.0, release 2 (Thomas et al. 2010), to model the potential effects of sex, island, and island group on detection probability. We defined sex (male, female, or unknown) according to the sex-specific aural, visual, and behavioral cues that we used to detect each individual or group. For instance, if we first detected a male aurally by its male-specific vocalization and subsequently observed it interacting with a bird identified as a female by bill morphology and plumage, we recorded the presumed sex of both birds in the field (male and female, respectively). In analysis of detection probability, however, we coded both birds as male-type detections. We included the four individual islands as covariates in order to account for island-specific factors related to survey design (e.g., year, observers, seasonal timing) and physiography (e.g., general habitat, elevation). In an alternative set of models we included a covariate for island group (Pribilofs vs. St. Matthew and Hall) to test for latitudinal effects on detection probability and potential influences of increased survey duties at Hall and St. Matthew, where observers simultaneously surveyed for McKay's Bunting. Although some studies have shown that cluster size can affect detection probability (Drummer and McDonald 1987, Marques and Buckland 2003), we did not include it as a covariate because only 2% of the birds were detected in groups larger than two.

Our initial step in the analysis was to assess the data for the best truncation distance (150 m) and intervals for pooling (equal intervals of 10 m) to improve the models' fit (Buckland et al. 2001). We excluded all observations of birds in straight-line overflight (i.e., transient birds passing through the survey area) to minimize positive bias in density estimates arising from movement of birds. Using this reduced data set, we assessed the fit of hazard-rate and half-normal key detection functions with and without series-adjustment terms (cosine and simple polynomial for hazard-rate, cosine and hermite polynomial for half-normal; Buckland et al. 2001). Our candidate set included 12 models, 6 for each detection function: (1) no covariates, (2) sex, (3) island, (4) island group, (5) sex + island, and (6) sex + island group. We did not include island and island group in the same models because of their redundancy, and we did not include any interactions because we expected the effect of sex-specific behaviors on detection probability to be consistent across the breeding range. We used Akaike's information criterion adjusted for small sample sizes (AIC_c) and Akaike weights (w_i) to assess the relative support for each of the candidate models considered (Burnham and Anderson 2002). We classified the four islands as separate strata and calculated point estimates of density and population size for each, along with associated bootstrap-generated 95% confidence intervals (Buckland et al. 2001). We weighted these by each island's area (determined with ArcGIS 9.2 at mean sea level) to estimate overall density and population size.

Results

We detected a total of 2376 Pribilof Rock Sandpipers in 1967 groups on 123 transects encompassing 575.9 km across the four Bering Sea islands on which they breed (Fig. 2.1, Table 2.1). The truncated sample used for estimation of densities included 2114 sandpipers in 1738 groups. Mean group size was 1.22 ± 0.01 (SE) birds; almost all birds were detected as singles (86%) or in groups of two (12%), and the largest group was of six birds. Using a combination of cues, observers identified 940 sandpipers as males (45% of total), 321 as females (15%), 364 associating as breeding pairs (17%), and the remaining 489 as individuals of unknown sex (23%). Across all four islands, the effective half-width of a strip was 60.6 m (58.3–63.0, 95% confidence interval),

Table 2.1. Density and estimated size of the populations of the Pribilof Rock Sandpiper by island relative to area, sampling effort, and number of individuals detected within each stratum during line-transect surveys across the subspecies' entire breeding range in Alaska, 2001–2003. Stratified point estimates and bootstrap-generated 95% confidence intervals (CI) are based on the best-fitting model (half-normal detection function with two-term cosine adjustment fitting the covariates sex and island group; see Table 2.2). Areas of large lakes were excluded from surveys and calculations of density; birds detected >150 m from the observers were truncated during the analysis (see Methods).

		Transects			Density (birds km^{-2})		Population size	
Island	**Area (km^2)**	***n***	**km**	**Individuals detected**	**Mean**	**95% CI**	**Estimate**	**95% CI**
St. Paul	109	38	205.1	396	11.78	9.50–14.11	1226	988–1469
St. George	90	39	170.6	770	29.08	24.05–33.71	2607	2155–3022
St. Matthew	314	34	180.5	1104	50.82	44.83–57.50	15 280	13 480–17 289
Hall	16	12	19.8	106	44.73	34.14–57.70	719	549–928
Combined	529	123	575.9	2376	38.83	34.97–42.96	19 832	17 853–21 930

indicating that we surveyed an effective area of about 70 km^2, or 14% of the total breeding range.

Our model-selection process for detection probability yielded strong support (w_i = 0.85) for a single model over the other 11 in the candidate set; this model included sex and island group as covariates and fit a half-normal key function with a two-term cosine series adjustment (Table 2.2, Fig. 2.2; AIC_c = 8582.1). The second-

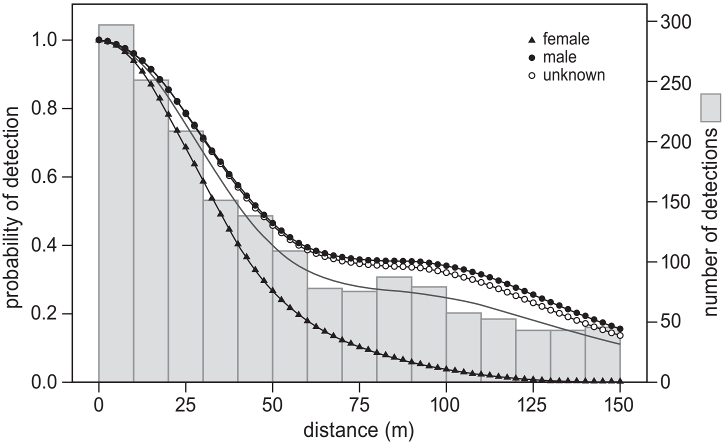

Figure 2.2. Probability of detection of the Pribilof Rock Sandpiper by sex-related behavior (female, male, and unknown sex) relative to distance from the transect line. Marginal-detection curves are derived from the output of the model in Table 2.2 and control for the effect of island-specific variation in probability of detection. Histogram represents actual survey detections (scale on right axis) binned by 10-m intervals; the solid line without symbols represents the overall fitted detection function.

Table 2.2. Coefficients of the best-supported model for probability of detection of the Pribilof Rock Sandpiper, which included covariates for sex (female, male, and unknown [reference level]) and island group (Pribilof Islands vs. St. Matthew and Hall islands [reference level]). Data are from line-transect surveys from 2001–2003 on the four islands constituting the subspecies' breeding range. The data were best fit by a half-normal key function with a two-term cosine series adjustment; the log likelihood of this model was –4285.04.

Parameter	**Estimate ± SE**
Scale parameter	68.75 ± 1.30
Female	–0.65 ± 0.09
Male	0.04 ± 0.09
Pribilof Islands	0.26 ± 0.05
Second-order adjustment term	0.25 ± 0.04
Third-order adjustment term	0.11 ± 0.04

ranked model carried the remainder of the weight (w_i = 0.15, ΔAIC_c = 3.42) and differed from the top model only in that it fit individual islands as covariates instead of island group. These models yielded nearly identical values for the estimates of the sex covariate, so we did not average models and hereafter present only the results of the best-supported model. Detection probability was lowest for female-type detections, declining rapidly and steadily with distance from the observer, and was marginally higher for male-type detections than for birds of unknown sex (Fig. 2.2). Detection probability was higher on the Pribilof Islands than on St. Matthew and Hall islands (Table 2.2).

Of the four islands, St. Matthew supported the highest density (50.82 birds km^{-2}) and greatest number (15 280) of sandpipers; density on the nearby but much smaller Hall Island was similar (Table 2.1). Although almost equal in size to its neighbor St. Paul Island, St. George supported over twice as many sandpipers (2607 birds) as St. Paul (1226 birds), and densities on St. Paul (11.78 birds km^{-2}) were only a quarter of those on St. Matthew (Table 2.1). Across the entire breeding range, Pribilof Sandpipers occurred at an average density of 38.85 birds km^{-2}, yielding an overall population estimate of 19 832 birds (17 853–21 930 95% confidence interval; Table 2.1).

Discussion

Our population estimate of about 20 000 birds places the Pribilof subspecies of the Rock Sandpiper among the smallest 25% of the 70 North American shorebird populations treated by Morrison et al. (2006). Although relatively small by these standards, this population size is not necessarily small in the context of population viability, where minimum populations of 2000–7000 animals are considered essential to ensure persistence (see summary in Reed et al. 2003). Small populations are subject to decreased genetic diversity, lower fitness, and increased susceptibility to environmental perturbations (Shaffer 1981, Lande 1993, Reed and Frankham 2003). If gene flow among the island subpopulations is limited, the effective population size of the Pribilof Sandpiper may be smaller than 20 000, and the subspecies may be vulnerable to some of these factors. Almost 80% of the population breeds on one (St. Matthew) of the four islands on which the subspecies breeds, and each of the other three islands hosts fewer than 3000 individuals. We do not know the extent of interchange between the four islands, and evidence of genetic mixing between Rock Sandpiper subspecies is inconclusive (Pruett and Winker 2005). Given these uncertainties, the high site fidelity of *C. p. tschuktschorum* documented by both Tomkovich (1994) and Johnson et al. (2009) suggests gene flow between and within the four subspecies is limited. Additional genetic analyses of birds from adjacent areas of potential breeding would help resolve uncertainties about any gene flow outside the known range of the Pribilof Sandpiper.

The Pribilof Sandpiper's breeding distribution surely ranks as one of the most restricted of any North American shorebird's, and its concentration on four small islands totaling less than 530 km^2 renders the subspecies vulnerable to local and stochastic effects. The marked difference in population density between the Pribilof Islands and the more northerly St. Matthew and Hall islands may indicate such local effects, but without definitive historical data we can only speculate about the factors responsible. St. Matthew and Hall islands have never been inhabited, but permanent human settlements were established on the Pribilof Islands in the late 1700s (Osgood et al. 1915). Historically, residents of the Pribilof Islands hunted Pribilof Sandpipers heavily (Osgood et al. 1915), but hunting pressure has been negligible since the early 1900s (Hanna 1921). The current footprint of human infrastructure is small on both St. Paul and St. George, and at the time of our study vegetation cover on both islands appeared largely unaffected by human habitation .

A further distinction between the two island groups that may have contributed to the difference in population density is the history of reindeer introductions. The Pribilof Islands support the only reindeer herds remaining in the sandpiper's breeding range. Large ungulates may reduce reproduction and recruitment of ground-nesting birds directly through trampling of nests (Wright 1979) and consumption of eggs (Abraham et al. 1977) or indirectly through habitat alteration (Klein 1987). Rock Sandpipers typically nest in dry upland tundra dominated by lichens and ericaceous shrubs (Gill et al. 2002), and excessive reindeer grazing tends to promote graminoids and mosses at the expense of lichen-dominated upland habitats (Klein 1987). Swanson and Barker (1992) attributed much of the fluctuation in reindeer populations on the Pribilof Islands to range degradation, and habitat alteration may account, at least in part, for the difference in the sandpiper's density between the Pribilofs and the currently reindeer-free St. Matthew and Hall islands. It should be noted, however, that anecdotal observations (Hanna 1921, Preble and McAtee 1923) made shortly after reindeer were introduced on the Pribilof Islands in 1911 suggest that during the early 20th century relative densities of sandpipers breeding on the four islands were similar to those we documented: lowest on St. Paul, higher on St. George, and highest on St. Matthew. It is unlikely that the small reindeer populations present then (25 on St. Paul and 15 on St. George; Osgood et al. 1915) had yet adversely affected the islands' habitats.

Differences due to a combination of the islands' physiography and latitude may have a greater effect on vegetation cover than do either direct anthropogenic or reindeer-induced effects. The Pribilof Islands are about 425 km south of Hall and St. Matthew islands, and the mean elevation of St. Paul is considerably lower than that of the other islands (38 m, compared to 94–182 m). Concomitantly, on St. Paul the cover of graminoids is greater and the dry upland tundra Pribilof Sandpipers prefer for nesting is less extensive (Tibbitts, unpubl. data). Accurate land-cover maps and more detailed information on the Rock Sandpiper's habitat preferences would help clarify the relative contributions of physiography, latitude, human settlement, and reindeer introductions on the sandpiper's population densities on the four islands. Given that our results concur with historical observations (see above), we believe that variation in vegetation types is the most likely cause of island-specific variation in the density of breeding Pribilof Sandpipers.

Understanding the relationship between reproductive success and microhabitat structure would help elucidate potential effects of climate-mediated changes on this small population. There is strong evidence that the marine ecosystem of the Bering Sea region has already experienced a major shift of climatic regime (Hare and Mantua 2000). Studies elsewhere in Alaska have documented how the structure of terrestrial vegetation has been changing dramatically in response to climatic change (Sturm et al. 2001, Hinzman et al. 2005, Tape et al. 2006), with a general trend toward increasing herbaceous and shrub cover and decreasing dwarf shrub/upland tundra habitats. There is no information on how vegetation might be changing on the four Bering Sea islands where the Pribilof Sandpiper breeds, but climate models predict relatively rapid and extensive habitat alteration across high latitudes (Rupp et al. 2000, Euskirchen et al. 2009), changes that may alter current habitat structures throughout the Pribilof Sandpiper's range.

Having established an accurate baseline for the size of this vulnerable population, focus should now turn to determining its trajectory. Our point estimate for the Pribilof Sandpiper's population was similar to the previous approximation of ~20 000–25 000 (Gill et al. 2002). This figure was based primarily on winter surveys of upper Cook Inlet, which employed photography to verify counts of large flocks and a partial correction factor based on observer bias in estimating flock size (Gill and Ruthrauff, unpubl. data). Uncertainty remains, however, about what proportion of the population winters in the region surveyed. Surveys of the entire breeding range have greater inferential power than potentially incomplete surveys of the wintering grounds but ground surveys of the breeding range are costly and logistically difficult. Winter surveys may serve as a relatively inexpensive population-monitoring tool once the winter range of the subspecies has been refined. Similarly, if Pribilof Sandpipers are confirmed breeding on Nunivak and St. Lawrence islands, future studies will need to identify the extent of breeding on these islands and integrate counts from these sites into a revised population estimate.

Our findings confirm the need for accounting for differences in detection probability during bird surveys, as has been found in many other studies (see Thompson 2002 for review). As expected, our analysis indicated strong sex-specific differences in detection probabilities, an important consideration when shorebird surveys are designed and their results are analyzed. We found that the probability of detection was considerably higher through male-specific than through female-specific behaviors, which is consistent with the species' breeding ecology (see Study Design). The similarity of detection-probability curves for males and birds of unknown sex suggested a preponderance of males in the latter category.

Why detection probability varied by island group is less clear. The probabilities of detection were lower on Hall and St. Matthew islands than on the Pribilof Islands, and this trend persisted whether the islands were grouped by latitude or assessed individually. There are no obvious differences between the islands in factors that commonly influence detection probability. For instance, it is unlikely that island-specific habitats affected the detection process because all of the islands support relatively simple, prostrate vegetation structures. Similarly, two of five observers surveyed both the Pribilof Islands and Hall and St. Matthew islands, making it unlikely that a systematic difference in observer skill accounted for these discrepancies. A systematic difference in bird behavior, however, is a potential cause of the lower probabilities of detection at Hall and St. Matthew. We intentionally surveyed Hall and St. Matthew 2 to 5 weeks later than we did the Pribilof Islands to account for later breeding at the more northerly sites, but there is evidence that we sampled sites at different stages of the breeding cycle and that birds on Hall and St. Matthew had progressed further in the breeding cycle than had birds on the Pribilof Islands. On the Pribilofs, 41% of all detections were of singing males, compared with 32% on St. Matthew and Hall. Similarly, 22% of birds detected on the Pribilofs were in flight display, compared with 9% of birds on St. Matthew and Hall. Males behaving so conspicuously were detectable at greater distances and likely contributed to increased detection probability on the Pribilof Islands.

Interestingly, detection probabilities were inversely related to bird density. Observers on St. Matthew and Hall islands may have been "swamped" by sandpipers at close distances at the expense of detecting those at greater distances. Simultaneous surveys for McKay's Bunting on St. Matthew and Hall may have further exacerbated this effect, resulting in a probability of detection less than that on the Pribilof Islands. During this effort, the density of McKay's Bunting was estimated at 95.7 birds km^{-2} (Matsuoka and Johnson 2008), nearly double that estimated for the Pribilof Sandpiper at these sites. Thus a combination of differences in breeding phenology, birds' higher densities, and observers' increased duties likely accounted for the lower probability of detection at these sites than on the Pribilof Islands. It should be noted, however, that analysis of distance-sampling data accounts for such differences in detection probabilities and that estimates of density on the different islands are robust to such variation, provided the assumption of perfect detection on the transect line itself is met (Buckland et al. 2001).

Many migratory birds have a restricted distribution during one phase of their annual cycle, but those with year-round restricted distributions face increased threats (IUCN 2011). Our population estimate from the Pribilof Sandpiper's breeding range serves as an effective foundation upon which its trajectory can be monitored and future research can be established. Because the Pribilof Sandpiper's population is effectively a geographically closed system, it provides researchers the opportunity to isolate meaningful biological measures and enact practical conservation measures. Specifically, we recommend detailed comparative and experimental studies of the effects of habitat structure on reproductive success and recruitment across the breeding range to help elucidate current and past potential anthropogenic and reindeer-induced effects, as well as projected effects of climate change. Additionally, genetic samples that fill geographic gaps identified by Pruett and Winker (2005), along with measures of adult survival and inter-island movements, would enable a more complete assessment of metapopulation dynamics and vulnerability to stochastic factors.

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CHAPTER 3

Coping with the cold: An ecological context for the abundance and distribution of rock sandpipers during winter in upper Cook Inlet, Alaska

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Abstract

Shorebirds are conspicuous and abundant at high-northern latitudes during spring and summer, but as seasonal conditions deteriorate few remain during winter. To the best of our knowledge, Cook Inlet, Alaska (60.6° N, 151.6° W), is the world's coldest site that regularly supports wintering populations of shorebirds and is also the most northerly nonbreeding location for shorebirds in the Pacific Basin. During the winters of 1997–2012, we conducted aerial surveys of upper Cook Inlet to document the spatial and temporal distribution and number of rock sandpipers (*Calidris ptilocnemis*) using the inlet. The average survey total was 8191 ± 6143 (SD) birds and the average of each winter season's highest single-day count was 13 603 ± 4948 (SD) birds. We detected only rock sandpipers during our surveys, essentially all of which were individuals of the nominate subspecies (*C. p. ptilocnemis*). Survey totals in some winters closely matched the population estimate for this subspecies, demonstrating the region's importance as a nonbreeding resource to the subspecies. Birds were most often found at only a handful of sites in upper Cook Inlet, but shifted their distribution to more southerly locations in the inlet during periods of extreme cold. Two environmental factors allow rock sandpipers to inhabit Cook Inlet during winter: 1) an abundant bivalve (*Macoma balthica*) food source, and 2) current and tidal dynamics that keep foraging substrates accessible during all but extreme periods of cold and ice accretion. *C. p. ptilocnemis* is a subspecies of high conservation concern for which annual winter surveys may serve as a relatively inexpensive population-monitoring tool that will also provide insight into adaptations that allow these birds to exploit high-latitude environments in winter.

Introduction

Birds exemplify many of the adaptations that have enabled animals to inhabit high-latitude regions year-round. Many species have evolved behavioral and physical adaptations that promote survival during winter at high northern latitudes when food becomes scarce and environmental conditions are at an extreme. For example, marine birds (e.g., spectacled eider *Somateria fischeri*, thick-billed murre *Uria lomvia*) occupy isolated but seasonally predictable areas free of sea ice where they feed on lipid-rich prey (Gaston and Hipfner, 2000; Lovvorn et al., 2003), while frugivorous and granivorous passerines (e.g., pine grosbeak *Pinicola enucleator*, black-capped chickadee *Poecile atricapillus*) exhibit behavioral adaptations such as irruptive movements in search of food (Newton, 2006), food caching (Hitchcock and Sherry, 1990), and communal cavity roosting (Cooper, 1999).

Such adaptations are the exception, however. Most northern-breeding birds instead migrate south in response to the onset of deteriorating conditions in autumn. This pattern is particularly evident in arctic-nesting shorebirds (order Charadriiformes, suborders Scolopaci and Charadrii) which have relatively high daily energy requirements and mostly forage by probing in soft substrates (Kersten and Piersma, 1987; Piersma et al., 1996; Piersma et al., 2003). The onset of winter at high latitudes greatly reduces food resources, and freezing conditions preclude shorebirds from probing for food in preferred wetland and estuarine habitats.

A few species of small sandpipers, however, have overcome these limitations, most notably the purple sandpiper (*Calidris maritima*) which in Norway occurs in winter as far as 71° N (Summers et al., 1990) under prolonged periods of complete darkness, cold temperatures, and steady wind (Summers et al., 1998). Because of advection patterns and the moderating influence of the Gulf Stream current (Seager et al., 2002), marine intertidal substrates along the northeast Atlantic coast seldom freeze, allowing purple sandpipers predictable access to intertidal food resources (Summers et al., 1998).

In the North Pacific, the counterpart to the purple sandpiper is the closely related rock sandpiper (*C. ptilocnemis*; Conover, 1944; Pruett and Winker, 2005). Rock sandpipers have the most-northerly nonbreeding distribution of any shorebird in the Pacific Basin, and the species is common in Alaska throughout the winter as far north as 61° N (Gill et al., 2002). These nonbreeding sites, though farther south than sites used by purple sandpipers in Norway, experience more severe winter conditions, including periods of extreme cold, persistent sea ice, and snow and ice that regularly cover intertidal habitats (Poole and Hufford, 1982; Gallant et al., 1995).

Given such conditions, it was not until relatively recently that rock sandpipers were even suspected of occurring in south-central Alaska in winter. In February 1976, Erikson (1977) observed "several large flocks of . . . probably rock sandpipers" in Tuxedni Bay, Cook Inlet. A decade passed before biologists again observed small sandpipers on partially frozen mudflats during aerial surveys in late fall and early spring (W. Eldridge pers. comm.; Butler and Gill, 1987). Building on these observations, work was initiated in the late 1990s to determine the seasonal status of shorebirds occurring in upper Cook Inlet, Alaska (Gill and Tibbitts, 1999). These studies involved aerial surveys and ground observations of birds and sampling of potential foods (consisting primarily of the bivalve *Macoma balthica*) on intertidal areas (Gill and Tibbitts, 1999; Gill et al., 2002).

In this paper we summarize data collected over a 16-year period (1997–2012) to assess the seasonal distribution and abundance of rock sandpipers during winter in upper Cook Inlet. We also summarize benthic invertebrate collections and long-term climatological information to describe the behavioral, biotic, and abiotic factors that influence the occurrence of rock sandpipers at the northern extreme of their wintering range.

Methods

Study Area and Winter Setting

We studied rock sandpipers in Cook Inlet, Alaska (60.6° N, 151.6° W; Fig. 3.1), a ~280-km-long by 20–70-km-wide estuary fed by glacially-derived rivers. The Inlet is characterized by extensive mudflats interspersed with rocky coastline and high bluffs, and tidal amplitudes that can exceed 10 m (Oey et al., 2007). Circulation patterns in Cook Inlet are driven by river runoff (Kyle and Brabets, 2001). Currents of up to 1 m s^{-1} sweep strongly south along the western edge of the Inlet and flow more gently to the north along the eastern shores, inducing a general counter-clockwise flow (Johnson, 2008).

Average daily high temperature for the city of Anchorage, in upper Cook Inlet (Fig. 3.1), is ≤0°C between early November and mid-March (Fig. 3.2). The daily temperature in January, the coldest month, averages –9.4°C (National Climatic Data Center, 2012). The coldest period of winter also coincides with the period of shortest day lengths (U.S. Naval Observatory, 2012; Fig. 3.2): at the winter solstice, the day length at 61°N is 5 hours and 27 minutes (Fig. 3.2). The formation of sea ice in upper Cook Inlet is driven primarily by air temperature (Poole and Hufford, 1982) and coincides with sub-zero temperatures that typically causes significant sea ice to form beginning in late November (Poole and Hufford, 1982). Shore-fast ice and stranded bergs can persist through mid-April in upper Cook Inlet.

Data Collection

We assessed the seasonal distribution and abundance of rock sandpipers using aerial surveys. We conducted surveys each year from February 1997–March 2012, typically flying at least one survey per month between October and April. We routinely surveyed six segments of upper Cook Inlet shoreline: 1) the Susitna Flats from Pt. MacKenzie to Beluga (~58 km of shoreline), 2) Trading Bay (~28 km), 3) Redoubt Bay

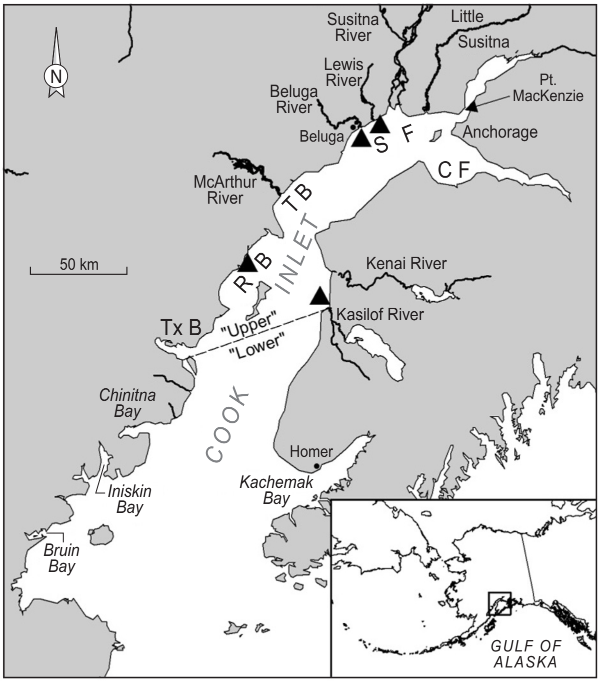

Figure 3.1. Primary survey sites of Cook Inlet, Alaska. Upper Cook Inlet was the location of aerial shorebird surveys conducted during winters 1997–2012. Abbreviated site names (clock-wise, from top): SF = Susitna Flats, CF = Chickaloon Flats, TxB = Tuxedni Bay, RB = Redoubt Bay, TB = Trading Bay. Sites of benthic sampling are marked by triangles; place names are mentioned in the text.

(~41 km), 4) Tuxedni Bay (~37 km), 5) the mouths of the Kasilof and Kenai rivers, and 6) Chickaloon Flats (~23 km; Fig. 3.1). These segments are composed primarily of intertidal mudflats and sandflats connected to adjacent segments by steep bluffs with rocky cobble intertidal habitats. Because we never detected shorebirds on these rocky connecting sections during the initial years of the study, we often overflew these areas in later years. On 19 December 2001 we also conducted a survey of Bruin, Chinitna, and Iniskin bays in lower Cook Inlet (Fig. 3.1). The importance of certain sites to rock sandpipers (e.g., the mouths of the Kasilof and Kenai rivers) did not become known to us until 2006, but were surveyed regularly thereafter.

We were unable to survey all segments of the main study area on all occasions due to unsafe flying conditions. We conducted surveys during diurnal periods and timed our route to maximize observation conditions based on tide cycle, but other factors also affected survey timing, including the marked change in day length during winter and the varying length and breadth of mudflats among segments. We nevertheless tried to fly surveys when mudflats were only partially exposed to mini-

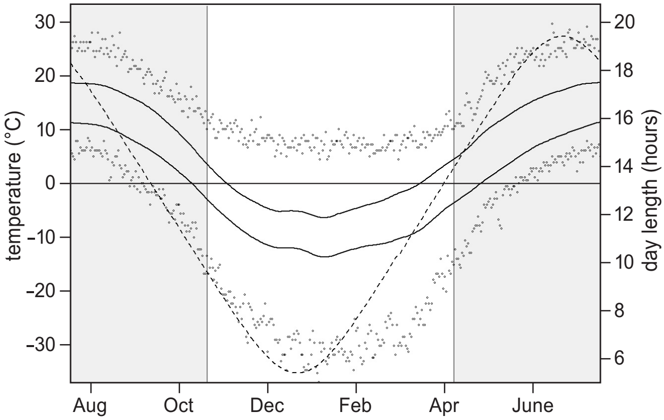

Figure 3.2. Average daily high and low temperatures (solid lines) and extreme values (dots) recorded from 1952–2012 in Anchorage, Alaska. Day length (dotted line) is plotted on right axis. The non-shaded portion depicts the approximate period of occurrence of rock sandpipers in upper Cook Inlet, Alaska.

mize search time and increase the likelihood of detecting shorebirds. Surveys were conducted by one observer in single engine, fixed-wing aircraft flown at 185 km/h indicated air speed and at an altitude of about 50 m above sea level; pilots assisted with detecting birds, but only observers estimated flock sizes. Observers recorded the size and location of each flock on a gridded topographic map (cell width 1 km), and took photographs of large flocks (about ≥500 birds) whenever possible in order to correct flock-size estimates. After surveys, flock locations were transferred to a geospatial database, and flock size estimates were photo-corrected. For the sake of our summaries, single birds constituted flocks of one bird.

We opportunistically conducted ground-based observations independently of aerial surveys to determine the identification of birds recorded on aerial surveys. Because it was difficult to access most sites in winter, on-ground assessment was limited to the mouths of the Beluga, Kasilof, and Kenai rivers, and portions of Kachemak Bay near Homer (Fig. 3.1). To distinguish subspecies of rock sandpipers seen on the ground we followed criteria described in Gill et al. (2002) to separate the lighter nominate form (*C. p. ptilocnemis*) from the two darker forms (*C. p. couesi* and *C. p. tschuktschorum*) that might also occur in the area (Gill et al., 2002). The non-breeding distributions of these three subspecies are heretofore not well defined (Gill et al., 2002), and subspecies may overlap at the extremes of their ranges.

We also assessed the potential foods available to rock sandpipers. We sampled the diversity and abundance of intertidal benthos along transects at four sites in upper Cook Inlet. At each site we randomly spaced a series of transects (0.18–1.80 km) parallel to each other and oriented perpendicular to shore; these included three transects each near the Beluga and Lewis rivers at Susitna Flats, three at Redoubt Bay, and two at the Kasilof River (Fig. 3.1). We divided the mudflats into 250-m-wide parallel zones that extended seaward from the vegetated shoreline (four zones at Susitna Flats and Redoubt Bay, three zones at the smaller Kasilof River). Along each transect we randomly allocated five sampling locations per zone per transect. At each location we collected a 10-cm- diameter by 20-cm-deep core sample from the substrate. Samples were stored in plastic bags and sorted as soon as possible after collection by flushing the contents with water over a 1-mm sieve.

Analysis

AERIAL SURVEYS

We summarized the survey results to determine the winter residency period of shorebirds in upper Cook Inlet, as well as seasonal, interannual and geographic patterns of occurrence. The minimum period of residency was determined to encompass the first and last surveys on which birds were detected during each winter period.

We assumed that observers detected all flocks in the surveyed areas and correctly counted the numbers of individuals in flocks of ≤100 birds (n = 713 flocks, 57% of all flocks). However, we assumed that errors likely occurred in estimating sizes of large flocks. To estimate the magnitude of observer bias, the two primary observers in this study each photographed a subsample of flocks (REG, n = 70; DRR, n = 26) during several surveys to compare with their estimated flock sizes. Using these, we constructed a no-intercept linear model of actual photo-counts as a function of estimated flock size and observer, after first log-transforming actual and estimated flock sizes to meet the assumptions of normality and constancy of error variances. Because estimation bias differed significantly between observers ($P < 0.05$), we derived separate models for the two observers. Actual flock sizes were typically larger than those estimated: the ratio for REG was 1.0005 ± 0.0035 SE and for DRR was 1.02 ± 0.01 SE. To derive model-corrected values for flocks >100 birds that were not photographed, we multiplied log-transformed estimates by these observer-specific parameters and back-transformed the results. TLT conducted one survey on which no photo-verification images were collected so this survey's estimates were not adjusted. Unless otherwise noted, reported values represent mean ±SD.

CLIMATOLOGICAL AND ENVIRONMENTAL SUMMARIES

We identified benthic specimens to the lowest practical taxonomic level, and measured the length of all bivalve shells to the nearest 1.0 mm (see Dekinga and Piersma, 1993). We determined the density (individuals/m^2 ± SE) of prey items per transect per site and calculated each site's overall mean using a two-stage sampling estimator. Because we made our benthic collections during four different months over 11 years, we did not compare invertebrate densities between sites using formal statistical analyses.

We summarized temperature information over the period 1952–2012 from Anchorage, Alaska, to describe the winter environment of the upper Cook Inlet region. We deployed temperature loggers in two winter seasons (1998–1999, 1999–2000) at the Ivan River and Trading Bay (Fig. 3.1) to determine how Anchorage winter temperatures compared to sites where shorebirds were detected. Average daily temperatures recorded by data loggers during the 1998–1999 and 1999–2000 winter periods at the Ivan River and Trading Bay were highly correlated with average daily temperatures in Anchorage ($R \geq 0.94$ for both sites), and temperatures were slightly colder in Anchorage. The average difference between Anchorage and the Ivan River and Anchorage and Trading Bay was 0.1 ± 2.8 °C and 0.9 ± 2.8 °C, respectively.

We calculated the extent of mudflat at survey sites in upper Cook Inlet using National Oceanic and Atmospheric Administration (NOAA) Environmental Sensitivity Index (ESI) geographic information system (GIS) shapefiles (NOAA, 2012). During aerial surveys, we noted the presence of sea ice and shore-fast ice and used these observations to delimit the period of sea ice presence in the study area. We used digitized NOAA / National Ice Center (NIC) ice analysis GIS products derived from satellite imagery of Cook Inlet to estimate the extent of shore-fast ice that had accreted on mudflats (NIC, 2012). We restricted our analysis to the period 27 January 2006–16 March 2012 (the date of our last survey) to coincide with a period of methodological consistency and greater accuracy of the NIC products. We have assumed that data from this period is representative of average annual ice dynamics in upper Cook Inlet throughout the study period. We used the last (i.e., latest in month) image from each month per year to estimate the areal extent of shore-fast ice, and compared site-specific monthly values of shore-fast ice during winter to ice-free totals calculated from the NOAA ESI shapefiles to determine the proportion of ice-covered mudflat unavailable to sandpipers.

Results

Aerial Surveys and Ground Observations

We conducted 99 aerial surveys over 16 winter seasons from February 1997–March 2012. Surveys were conducted as early as 28 August and as late as 1 May. During each of the 16 winters we flew an average of 6.2 ± 3.6 SD surveys (range 1–14). Seasonal survey effort was similarly comprehensive, averaging 6.2 ± 2.8 SD surveys (range 1–10) during each two-week period across all years combined (Fig. 3.3). The earliest we detected shorebirds on surveys was 6 October (2001) while the latest detection occurred on 13 April (2002). We did not detect any birds on 11 surveys (11.1%); 9 of these were surveys that occurred either early ($n = 3$) or late ($n = 6$) in the winter season when we were trying to determine periods of arrival and departure (Fig. 3.3). The two mid-season surveys during which no birds were detected (19 January 2004 and 22 February 2006) were both unavoidably conducted during high tides. The lack of birds on these surveys was likely due to suboptimal survey condi-

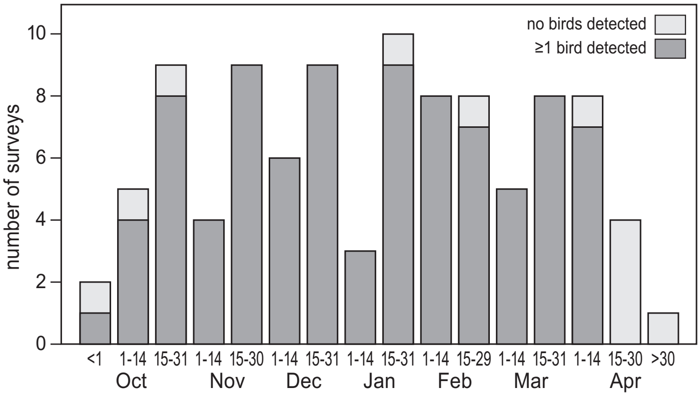

Figure 3.3. Timing of aerial shorebird surveys (*n* = 99) of upper Cook Inlet, Alaska, by two-week interval during winter. The light grey bars represents the number of surveys on which no birds were detected; the dark grey bars surveys on which ≥1 bird was detected.

tions (i.e., birds may have been roosting along shore and gone undetected) and not necessarily to their absence from the study area. In order to focus our findings on the period of winter residency in upper Cook Inlet, all results presented hereafter (unless otherwise noted) concern surveys during which ≥1 bird was detected.

Birds were detected primarily on mudflats and sandflats, or, less commonly, roosting along shores or on sea ice. We did not detect any birds along rocky or cobble shorelines. Based on size, flight behavior, and dorsal wing patterning, all birds seen on aerial surveys were tentatively identified as rock sandpipers. Ground observations confirmed that only rock sandpipers occurred in upper Cook Inlet during

Table 3.1. Ground-based identification of rock sandpiper subspecies sampled in winter at sites in Cook Inlet, Alaska.

Site	Date	Percent Dark-plumage Rock Sandpipers[1]	# Birds in Sample Pool
Beluga River	26 Feb. 2004	3.2 ± 0.4 SE[2]	5000
Kasilof River	18 Dec. 2007	≤1[3]	7500
	19 Dec. 2007	≤1[3]	4400
	5 Feb. 2009	≤1[3]	3884
Homer	18 Mar. 2011	81.6 ± 1.7 SE[4]	3648

[1] See Gill et al. (2002) for plumage characteristics used to distinguish subspecies.
[2] Value represents average of 52 subsamples from flock (group size 8–50 rock sandpipers).
[3] ≤Five dark-plumage individuals observed each day.
[4] Value represents average of 13 subsamples from flock (group size 9–69 rock sandpipers).

winter and that nearly all belonged to the nominate subspecies, *C. p. ptilocnemis* (Table 3.1). Farther south (e.g., Homer; Fig. 3.1), dark-plumage birds (*C. p. couesi* or *C. p. tschuktschorum*) predominated (Table 3.1).

Rock Sandpiper Abundance

Model corrections increased REG and DRR's flock size estimates by an average of 0.31 ± 0.05% and 12.7 ± 2.5%, respectively. Hereafter, all results report model-corrected counts. We detected 1258 flocks of rock sandpipers during the surveys. The average flock size was 573 ± 1311 birds (range 1–12 904; median = 75). The highest single-day count (22 913 birds) occurred on 4 March 1998 (Fig. 3.4), and the lowest season-high count (4453 birds) occurred on 23 January 2010 (Fig. 3.4). Across the entire study period, the average survey total (not including surveys when no birds were detected) was 8191 ± 6143 rock sandpipers and the average of each winter season's highest single-day count was 13 603 ± 4948 rock sandpipers.

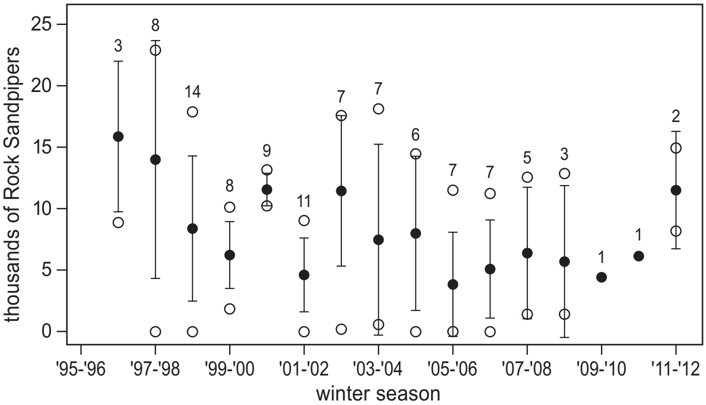

Figure 3.4. Winter aerial survey results, upper Cook Inlet, Alaska, 1997–2012. Filled circle is the average number of rock sandpipers detected per winter season, whiskers are SD, and hollow circles represent seasonal maximum and minimum counts. Plotted values include only surveys on which rock sandpipers were detected; numbers represent the total number of surveys flown each winter season, including those on which when no birds were detected. Values are corrected for errors in observer estimation of flock size (see Methods).

Site Preference and Movements

Rock sandpipers consistently used specific locations both between and within seasons (Fig. 3.5). Rock sandpipers were most often encountered at Susitna Flats (85.2% of all surveys conducted there), Trading Bay (71.2%), and the Kasilof River (44.4%; Fig. 3.5). The greatest proportion of birds recorded during surveys occurred at Susitna Flats (mean of survey totals = 58.9%), followed by the Kasilof River (29.5%), and Trading Bay (28.6%; Fig. 3.5). Birds were also detected on a high propor-

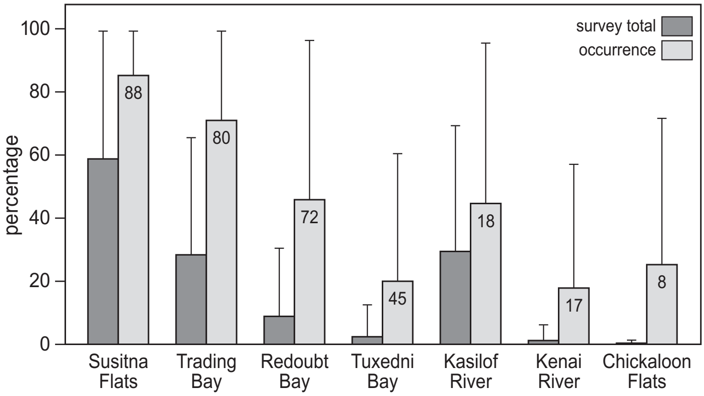

Figure 3.5. Occurrence of rock sandpipers at primary winter aerial survey sites in upper Cook Inlet, Alaska, 1997–2012. Only frequently-surveyed sites are represented, and only surveys (*n* = 88) when birds were detected are shown. Dark grey bars represent each site's average (± SD) percent of survey total, and light grey bars represent each site's average (± SD) percent occurrence. For instance, shorebirds counted at Susitna Flats constituted an average of 59% of survey totals, and shorebirds were detected at this site on 85% of surveys. Numbers represent the number of times each site was surveyed, including surveys when birds were not detected at that particular site. Not all sites were visited during each survey (see text).

tion of surveys at Redoubt Bay (45.8%), but typically in low numbers overall (average proportion of survey total = 9.0%; Fig. 3.5).

Rock sandpipers also exhibited preferential use for sites within each of the major survey segments. For example, of the 416 188 total birds recorded at Susitna Flats, most (56.8%) were detected along a 7-km-long stretch (~12% of the segment total) of intertidal flats between the Lewis and Beluga rivers (Fig. 3.1). The same stretch, when assessed in terms of the overall proportion of surveys on which birds were recorded, revealed a similar rate of occurrence (65.9%). The next most-used site was a 5-km-long portion (~18% of the segment total) near the mouth of the McArthur River in Trading Bay (Fig. 3.1), where 46.3% of all rock sandpipers observed at Trading Bay (*n* = 190 891 birds total) were detected. Birds were observed at this site on 37.5% of surveys.

On two occasions the occurrence and distribution of rock sandpipers in upper Cook Inlet appeared to be influenced by prolonged periods of deep cold. In the first instance, documented over five consecutive surveys from December 1998–March 1999, numbers of birds fluctuated from 12 595 birds on 21 December 1998 to a low of 3194 on 2 February 1999 and returned to late-December levels of 11 938 birds on 4 March 1999. The mean high (–17.9°C) and low (–26.5°C) temperatures from 29 January–13 February 1999, the period when the fewest birds were recorded, represented deviations of as much as 20°C from long-term average temperatures. The lowest temperature recorded during this period was –33.3°C. The second occasion, on 19 December 2001, also coincided with a period of unusual cold, with temperature deviations up to 13°C below normal. As with the aforementioned example, survey numbers declined in concert with the period of deep cold and rebounded as temperatures normalized. We also surveyed sites on the east side of the lower portion of Cook Inlet (e.g., Bruin, Chinitna, and Iniskin bays, Fig. 3.1) on 19 December. We did not detect any shorebirds in this region, indicating that many rock sandpipers had likely departed the Cook Inlet region entirely.

Rock sandpipers also appeared to move from north to south within upper Cook Inlet during these two cold periods. Across the five surveys encompassing December 1998–March 1999, the percent of survey totals comprised by Susitna Flats and Trading Bay dropped from 100% (21 December 1998) to 0% (8 February 1999), and increased back to 100% once temperatures normalized (4 March 1999). Concordantly, the percent of survey totals at Redoubt and Tuxedni bays rose from 0% (21 December 1998) to 99.2% (36.7% at Redoubt, 62.5% at Tuxedni; 8 February 1999), and then declined back to 0% (4 March 1999). The 19 December 2001 survey was also characterized by a similar displacement of birds from Susitna Flats and Trading Bay to Redoubt and Tuxedni bays. These two periods of unusual cold were the only occasions during which we detected >1000 rock sandpipers in Tuxedni Bay.

Benthic Prey Diversity and Abundance

We collected benthic samples at 60 locations along transects at Drift River, 57 at Beluga River, 49 at Lewis River, and 30 at Kasilof River ($n = 196$ total; Table 3.2). About 7% ($n = 14$) of selected sample locations could not be accessed due to tide or ice conditions. The bivalve *Macoma balthica* was the dominant prey item in all samples, present at 169 (86.2%) locations. Polychaete worms occurred in 137 samples (81.1%), but specimens were minute and fragile and were typically destroyed in the sieving process, precluding accurate species identification or measurement. *Macoma* ($n = 2087$) ranged in size from 0.8–20.0 mm (Table 3.2). Across all sampling periods the average density of *Macoma* ranged from 424.4 ± 68.3 (SE) individuals/m^2 at the Kasilof River to 3145.1 ± 201.6 (SE) individuals/m^2 at the Beluga River (Table 3.2). Average *Macoma* ranged in size from 4.4 ± 0.1 (SE) mm at the Beluga River to 12.2 ± 0.4 (SE) mm at the Kasilof River (Table 3.2).

Table 3.2. Density (individuals/m^2) and size (mm) of the bivalve *Macoma balthica* collected at sites in upper Cook Inlet, Alaska, 1998–2009.

Segment	Site[1]	No. Transects (Samples)	Density (mean ± SE)	Shell Length (mean ± SE; *n*)
Susitna Flats	Beluga River	3 (57)	3145.1 ± 201.6	4.4 ± 0.1; 1408
	Lewis River	3 (49)	511.9 ± 56.2	7.5 ± 0.2; 197
Redoubt Bay	Drift River	3 (60)	810.6 ± 128.8	9.1 ± 0.3; 382
Kasilof River	Kasilof River	2 (30)	424.4 ± 68.3	12.2 ± 0.4; 100

Mudflat Extent and Winter Ice Formation

The upper Cook Inlet study area included approximately 610 km^2 of intertidal habitat (primarily mudflats, but also sandflats). Prior to the formation of sea ice, rock sandpipers roosted on shoreline habitats, but once sea ice formed birds were more commonly detected roosting on sea ice. Persistent cold slowly caused shore-fast ice to accrete across the study area. Estimates of the extent of shore-fast ice derived from remote imagery indicated that as much as 82% (e.g., March 2007) of intertidal habitats can be covered by accreted shore-fast ice. The mean extent of shore-fast ice covering intertidal habitats in upper Cook Inlet exhibited a marked seasonal flux. Shore-fast ice began forming in November (101.8 ± 136.4 km^2; 16.7% of total), peaked in January (353.9 ± 102.3 km^2; 58.0% of total), declined through March (250.2 ± 141.5 km^2; 41.0% of total), and by April each year was gone.

Shore-fast ice was less prevalent at certain sites, and these sites overlapped with the occurrence of rock sandpipers. For example, the commonly occupied 7-km-long section between the Beluga and Lewis rivers (see Site Preference and Movements above) did not consistently accrete shore-fast ice. We analyzed 28 GIS shapefiles that documented shore-fast ice in upper Cook Inlet, and this region accumulated shore-fast ice on 11 occasions (39.2%). In contrast, an adjacent 20-km-long section running from the mouth of the Susitna River to the Little Susitna River (Fig. 3.1) accreted shore-fast ice on 26 occasions (92.9%), and we detected over 50% fewer rock sandpipers (1082 322 birds, 26.0% of Susitna Flats' total) along this nearly three-times longer section.

Discussion

To the best of our knowledge, the environmental conditions in upper Cook Inlet, Alaska, are the coldest documented within the nonbreeding range of any shorebird, demonstrating the ability of shorebirds to tolerate extreme cold. Our previous understanding of cold tolerance in shorebirds came from purple sandpipers wintering in the Atlantic Basin (Summers et al., 1998). There birds occur at more northerly latitudes where day lengths are shorter compared to conditions experienced by rock sandpipers in upper Cook Inlet. However, the average temperature during January, the coldest month at each location, is appreciably warmer in Norway (–2.7°C at Vardo, Norway; Summers et al., 1998) than in Anchorage, Alaska (–9.4°C; this study). Moreover, due to the Gulf Current, purple sandpipers use ice-free rocky intertidal habitats at high northern latitudes (Summers et al., 1998), while rock sandpipers in upper Cook Inlet forage exclusively on mudflats and sandflats, habitats that diminish in extent across the winter season due to the accretion of shore-fast ice. In addition to shore-fast ice, upper Cook Inlet annually accumulates sea ice that deposits bergs and floes along mudflats at low tide, further reducing foraging habitat. Finally, the upper layers of the Inlet's mudflats often freeze upon exposure to sub-freezing air temperatures during low tides.

Spending the winter at cold northern latitudes places high energetic demands on shorebirds (Wiersma and Piersma, 1994). Ruthrauff et al. (2013) estimated that the maintenance metabolism of rock sandpipers in upper Cook Inlet during December was 2.55 Watts, a figure over three times greater than their basal metabolic rate at normothermic temperatures. High metabolic rates likewise require high rates of energy intake, and rock sandpipers thus avail themselves of an abundant food resource, the bivalve *Macoma balthica*. Although the region's cold restricts access to *Macoma* via the accretion of shore-fast ice and, less commonly, stochastic periods of deep cold when the top surface of mudflats flash-freeze, this food resource is in such abundance that rock sandpipers can evidently satisfy their energetic demands during winter. Our benthic sampling documented high *Macoma* densities (424–3145 *Macoma*/m^2; Table 3.2) at all sites, and field observations and analysis of stomach contents (Gill et al., 2002) indicate that rock sandpiper diets in upper Cook Inlet during winter are comprised almost exclusively of *Macoma*. Thus, *Macoma* are a critical winter food resource for rock sandpipers, a trait shared with other molluscivorous shorebirds (e.g., common redshank [*Tringa totanus*], bar-tailed godwit [*Limosa lapponica*], red knot [*C. canutus*]; Goss-Custard et al., 1977; Piersma et al., 1993).

The consistent occurrence of rock sandpipers at certain discrete sites provides insight into how abiotic conditions facilitate the reliable exploitation of upper Cook Inlet's abundant *Macoma* resources. We regularly observed rock sandpipers near the mouths of the Beluga and McArthur rivers (Figs. 3.1, 3.5; see Results), and we attribute this to an overlap between areas of high *Macoma* density and little or no shore-fast ice accretion. Ice formation in Cook Inlet is primarily a function of air temperature (Poole and Hufford, 1982), but shore-fast ice accretion and berg deposition are strongly affected by currents and tides. The region between the Beluga and Lewis rivers is strongly swept by freshwater outflow (Johnson, 2008), likely inhibiting the accumulation of shore-fast ice. Similarly, Cook Inlet's great tidal fluctuations also probably flush sea ice from high tide regions adjacent to areas with strong currents. In contrast, regions like those between the Susitna and Little Susitna rivers receive less current scouring (Johnson, 2008), and these regions more frequently accrete shore-fast ice. This in turn limits foraging access to mudflats, and ultimately inhibits rock sandpiper occupancy at such sites.

Thus, an interaction of biotic (high *Macoma* abundance) and abiotic (ice-inhibiting currents and tides) factors enables rock sandpipers to occupy upper Cook Inlet during winter. Rock sandpipers also exhibit unusual behavioral adaptations to the region. For instance, we frequently observed rock sandpipers roosting on sea ice, a behavior that likely decreases the risk of predation by both avian and mammalian predators. Additionally, REG and TLT (Gill, 1997) have observed rock sandpipers foraging during falling tides on freshly-exposed *Macoma* turned over by the scouring action of receding icebergs. And given that day lengths decrease to less than 5.5 h during winter solstice in upper Cook Inlet (Fig. 3.2), rock sandpipers must undoubtedly forage outside of daylight periods.

Nearly all rock sandpipers within upper Cook Inlet belong to the nominate subspecies (Table 3.1), and their reliance on upper Cook Inlet during winter has important conservation implications. The nominate subspecies of rock sandpiper is considered a species of high conservation concern in numerous conservation planning documents (e.g., Brown et al., 2001; Butcher et al., 2007; Alaska Shorebird Group, 2008), and surveys conducted across the subspecies' breeding range during the summers of 2001–2003 yielded a population estimate of 19 832 (95% confidence interval 17 853–21 930) individuals (Ruthrauff et al., 2012). Maximum counts for the winter periods 2001–2002, 2002–2003, and 2003–2004 were 9084, 17 586, and 18 186 birds (Fig. 3.4), respectively, indicating that in at least some winters nearly the entire subspecies' population occurs in upper Cook Inlet. Although survey totals varied within each of these winter seasons, upper Cook Inlet annually serves as a critical wintering area for the subspecies. This is further emphasized by the long-term average annual maximum count (13 603 birds) encompassing nearly 70% of the population estimate. Since *C. p. ptilocnemis* breeds only on remote islands in the Bering Sea (Gill et al., 2002) that are difficult and costly to survey, winter surveys in upper Cook Inlet may serve as an informative and cost-effective population monitoring tool (e.g., Brown et al., 2005). Determining the patterns and causes of within-region movements as well as documenting the subspecies' winter distribution outside of upper Cook Inlet would strengthen the inferential power of future surveys.

Our surveys document the unusual occurrence of rock sandpipers at sites in Cook Inlet, Alaska, during winter. Due to their high metabolic rates (Kersten and Piersma, 1987) and reliance on aquatic food resources (Piersma, 1996), northerly-wintering shorebirds are highly susceptible to starvation induced by periods of severe cold (Dugan et al., 1981; Davidson and Evans, 1982; Dietz and Piersma, 2007). Rock sandpipers, however, stand in contrast to these examples: average winter conditions in upper Cook Inlet surpass the severity of the stochastic conditions described during the aforementioned starvation events. Roosting on sea ice, foraging in ice scours, the likely occurrence of nocturnal foraging, novel observations of body- and plumage-icing (Ruthrauff and Eskelin, 2009), and recent physiological experiments revealing a less-severe metabolic response to extreme cold than other shorebird species (Ruthrauff et al. 2013) are evidence that rock sandpipers are adapted to regularly exploit sites in upper Cook Inlet during winter. The unanticipated discovery of rock sandpipers at these sites during winter extends the known environmental limits to which shorebirds are adapted, and make the species a unique addition to the winter avifauna of high-northern latitudes.

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CHAPTER 4

Ecological correlates of variable organ sizes and fat loads in the most northerly-wintering shorebirds

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Abstract

Shorebirds at northern latitudes during the nonbreeding season typically carry relatively large lipid stores and exhibit an up-regulation of lean tissues associated with digestion and thermogenesis. Intraspecific variation in these tissues across sites primarily reflects differences in environmental conditions. Rock (*Calidris ptilocnemis* (Coues, 1873)) and Purple (*Calidris maritima* (Brünnich, 1764)) Sandpipers are closely-related species having the most northerly nonbreeding distributions among shorebirds, living at latitudes up to 61°N in Cook Inlet, Alaska, and up to ~71°N in northern Norway, respectively. Cook Inlet is the coldest known site used by nonbreeding shorebirds, and the region's mudflats annually experience extensive coverage of foraging sites by sea and shore-fast ice. Accordingly, Rock Sandpipers increase their fat stores to nearly 20% of body mass during winter. In contrast, Purple Sandpipers exploit predictably ice-free rocky intertidal foraging sites and maintain low (<6.5%) fat stores. Rock Sandpipers increase the mass of lean tissues from fall to winter, including contour feathers, stomach, and liver components. They also have greater lean pectoralis and supracoracoideus muscle and liver and kidney tissues compared to Purple Sandpipers in winter. This demonstrates a combined emphasis on digestive processes and thermogenesis, whereas Purple Sandpipers primarily augment organs associated with digestive processes. The high winter fat loads and increased lean tissues of Rock Sandpipers in Cook Inlet reflect the region's persistent cold and abundant but sporadically unavailable food resources.

Introduction

Avian body composition has been extensively studied in numerous contexts, demonstrating that birds adaptively regulate fat and protein stores in conjunction with a diversity of life-history stages (Blem 1990; Lindström and Piersma 1993; Piersma and Lindström 1997). Variation in fat stores is most marked in migratory birds, both with respect to the demands of migratory fueling (Odum 1960; Battley et al. 2001) and reproductive activities (e.g., egg production [Hobson 2006] and incubation [Croxall 1982; Schmutz et al. 2006]). Stores of protein (i.e., lean tissue mass) generally do not fluctuate as much as lipid stores, but variation in protein is likewise common, including muscle groups associated with exercise (Biebach 1998; Lindström et al. 2000) and digestive organs (Hume and Biebach 1996; Battley and Piersma 2005). Such within-individual variation in lean and fat stores is a category of phenotypic plasticity labeled phenotypic flexibility (Piersma and Drent 2003; Piersma and van Gils 2011).

Shorebirds of the family Scolopacidae are typically highly migratory and have high energetic demands (Kersten and Piersma 1987; Piersma et al. 1996; Piersma 2002). As a result, shorebirds show clear patterns of accumulation and depletion of fat stores (Piersma and Gill 1998; Battley et al. 2001; Landys-Ciannelli et al. 2003) and exhibit hypertrophy and atrophy of lean body components across their annual cycle (Lindström et al. 2000; Battley and Piersma 2005; Dietz et al. 2007). These phenotypic responses to annual life-history stages are sometimes predictable, and usually rapid and reversible (Piersma and Lindström 1997; Dekinga et al. 2001). This makes shorebirds good subjects to study how environmental conditions affect phenotypes (Piersma and van Gils 2011).

During the boreal winter, shorebirds are distributed primarily at temperate and tropical latitudes (Piersma 1996), but a small number of species remain at colder, more northerly latitudes (Cramp and Simmons 1983; Davidson and Clark 1985; Summers et al. 1990b). Studies of northerly-wintering shorebirds indicate that fat stores increase to a winter peak typically coinciding with the period of lowest temperatures (Davidson 1979; Pienkowski et al. 1979; McEwan and Whitehead 1984; Piersma et al. 1994; Scott et al. 1994). This suggests that fat stores primarily provide energy during periods of high metabolic demand and low food intake, a role underscored by the lack of lipid stores and small organs in starved shorebirds (Marcström and Mascher 1979; Davidson and Evans 1982; Dietz and Piersma 2007). Peak fat stores expressed as lipid index ([fat mass / body mass] × 100) in shorebirds wintering at northerly latitudes (e.g., Dunlin [*Calidris alpina* L., 1758], Redshank [*Tringa totanus* L., 1758], Eurasian Oystercatcher [*Haematopus ostralegus* L., 1758], and Bar-tailed Godwit [*Limosa lapponica* L., 1758]) range from 4–15% (Evans and Smith 1975; Pienkowski et al. 1979; Davidson and Evans 1982; McEwan and Whitehead 1984), but can be as high as 24% in Eurasian Golden Plovers (*Pluvialis apricaria* L., 1758; Davidson 1981; Piersma and Jukema 2002). As the most energetically demanding period of winter passes, metabolic stresses decrease as food resources become more reliably accessible, conditions that are correlated with decreases in fat stores (Evans and Smith 1975; Summers et al. 1992).

Purple Sandpipers (*Calidris maritima* (Brünnich, 1764)), distributed along rocky shores of the North Atlantic Ocean from about 35°N to beyond the Arctic Circle as far as 71°N in Norway, are the shorebird with the most northerly winter distribution (Summers et al. 1990b; Payne and Pierce 2002). Due to the moderating influence of the Gulf Current, atmospheric advection patterns, and the prevailing maritime conditions, coastal regions of western Europe experience milder winter climates compared to other regions of the world at this latitude (Seager et al. 2002). Such relatively benign environmental conditions result in lowered energetic demands and ensure predictable, ice-free access to food resources (Summers et al. 1992, 1998). Purple Sandpipers feed primarily on small (≤ 5 mm) littorinids and mussels (Strann and Summers 1990; Summers et al. 1990a), abundant and predictable food resources in their preferred rocky intertidal habitats (e.g., Feare 1966). In the event of severe cold weather, the rocky coastal habitats of Purple Sandpipers are less likely to be affected by ice than low-salinity intertidal estuaries. It has been argued that these factors enable Purple Sandpipers to maintain relatively low winter fat stores (~5%, Summers et al. 1992).

In the Pacific Basin, Rock Sandpipers (*Calidris ptilocnemis* (Coues, 1873)) are the ecological counterpart and sister taxon of Purple Sandpipers (Conover 1944; Pruett and Winker 2005; Gibson and Baker 2012). Rock Sandpipers are common during winter along the east Pacific coast from about 37°–61°N (Gill et al. 2002). The northern extent of the Rock Sandpiper nonbreeding range (upper Cook Inlet, Alaska; 61°N, 151°W; Fig. 4.1) is the coldest experienced by any shorebird species. The average temperature in January, the region's coldest month, is –9.4°C (Ruthrauff et al. 2013b), compared to –2.7°C at Vardo, Norway, near the northern extent of the Purple Sandpiper range (Summers et al. 1998). These conditions result in 30% higher estimated maintenance metabolic rates for Rock Sandpipers (2.6 W; Ruthrauff et al. 2013a) compared to Purple Sandpipers in Varangerfjord, Norway, at 70°N (1.7 W; Summers et al. 1998). Upper Cook Inlet's cold winter conditions also create unpredictable access to foraging habitats. The Rock Sandpiper's primary food resource in upper Cook Inlet is the Baltic tellin (*Macoma balthica* L., 1758), with densities of up to 3,145 individuals m^{-2} recorded at these sites (Ruthrauff et al. 2013b). These abundant prey resources are not reliably available, however, as seasonal accretion of thick shore-fast ice on upper Cook Inlet's mudflat foraging habitats diminishes their accessibility to Rock Sandpipers (Ruthrauff et al. 2013b).

Thus, although Rock and Purple Sandpipers are closely related species, they face markedly different environmental conditions across their nonbreeding ranges. This provides a strong contrast for assessing the hypothesis that shorebirds wintering at high northern latitudes regulate lean and lipid body components in response to prevailing environmental conditions. We compared the winter body composition of

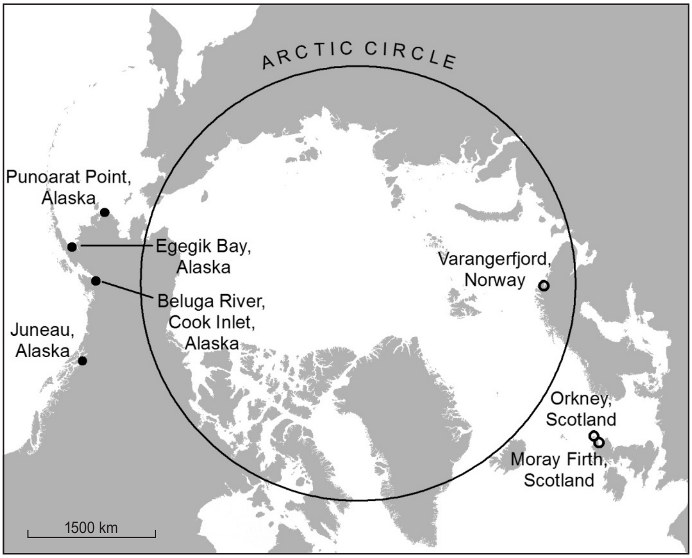

Figure 4.1. Rock (Alaska, solid circles; *Calidris ptilocnemis*) and Purple (Norway and Scotland, open circles; *Calidris maritima*) Sandpiper sample locations. All samples were collected from November–March ('winter'), with the exception of samples from Punoarat Point and Egegik, Alaska, which were collected in August or September ('fall').

Rock Sandpipers from the northern extent of their nonbreeding range (upper Cook Inlet, Alaska) to Purple Sandpipers from two locations (Scotland and close to the northern limit of their nonbreeding range in northern Norway). Given Cook Inlet's colder winter climate, we predicted that Rock Sandpipers would exhibit an up-regulation of organs and muscle groups associated with food processing (e.g., gizzard, intestine, liver, and kidney) and thermoregulation (e.g., pectoralis and supracoracoideus muscles, liver). Because food is periodically inaccessible during parts of the winter in upper Cook Inlet, we also predicted that Rock Sandpipers in upper Cook Inlet would carry increased fat stores compared to Purple Sandpipers exploiting epifauna on ice-free rocky shorelines in Scotland and Norway. To put the values in a seasonal context, we also compared the body composition of Rock Sandpipers in winter to that in fall. We predicted that Rock Sandpipers would carry lower lean and fat stores during fall than winter, a reflection of the mild temperatures and predictable access to food resources that characterize their fall staging sites (Gill and Handel 1990; Gill et al. 2009; Lindström et al. 2011).

Material and methods

Study specimens

We collected 20 Rock Sandpipers (all *Calidris p. ptilocnemis* (Coues, 1873); hereafter '*ptilocnemis*') near the mouth of the Beluga River in upper Cook Inlet, Alaska (61.19°N, 150.95°W; Fig. 4.1), on 28 December 1996 ($n = 7$) and 15 January 1997 ($n = 13$). Upper Cook Inlet is the most-northerly nonbreeding location used by the subspecies (Gill et al. 2002), and at times supports nearly the entire subspecies' population (Ruthrauff et al. 2013b). All other specimens were otherwise healthy birds accidentally killed during capture efforts. These included 10 specimens (all *Calidris p. tschuktschorum* (Portenko, 1937); hereafter '*tschuktschorum*') from Egegik Bay, Alaska (58.19°N, 157.53°W; Fig. 4.1), in September 2005 ($n = 1$) and 2006 ($n = 9$), from Punoarat Point, Alaska (61.31°N, 165.79°W; Fig. 4.1), on 30 August 2007 ($n = 3$), and one *tschuktschorum* bird from near Juneau, Alaska (58.3°N, 134.44°W; Fig. 4.1), on 17 November 2009 ($n = 1$). Purple Sandpipers were collected from Varangerfjord, Norway (70.36°N, 31.1°E; Fig. 4.1), on 21 March 1992 ($n = 10$), and from the Moray Firth (57.67°N, 3.63°W; Fig. 4.1) and Orkney (59.04°N, 3.12°W; Fig. 4.1), Scotland, in December ($n = 1$), January ($n = 4$), and February ($n = 5$) over the years 1987 and 1989–1992. All specimens were frozen in air-tight plastic bags upon collection. All specimens were collected or salvaged in the course of other investigations and thus do not necessarily represent random samples. However, we believe the specimens nonetheless reflect gross patterns of body composition across the species, sites, and seasons to which we restrict our inferences.

We determined the subspecific identity of Rock Sandpipers based on diagnostic plumage characteristics of the wing and mantle (Gill et al. 2002) and identified the sex of all specimens by gonadal inspection. Rock and Purple Sandpipers are similar in size, with females slightly larger than males (Engelmoer and Roselaar 1998). The *ptilocnemis* subspecies is the largest Rock Sandpiper subspecies (Gill et al. 2002), and the magnitude of size variation in Purple Sandpipers (no subspecies currently recognized, but see Engelmoer and Roselaar 1998) is similar to differences between *ptilocnemis* and *tschuktschorum* Rock Sandpipers (Engelmoer and Roselaar 1998; Gill et al. 2002).

We followed the procedures of Summers et al. (1998) for all body composition analyses. In brief, we dissected each carcass to determine the lean, fat, and water content of major organs and muscle groups. We first plucked the feathers from each bird, separating flight (primaries, secondaries, tertials, and rectrices) and contour (all rest) feathers; feathers were dried and weighed. Next, we removed all the skin and subcutaneous fat from each carcass, and dissected each specimen. Organs and muscle groups were individually weighed immediately after dissection to derive fresh (wet) mass values. The freshly dissected pieces from each bird were dried for ≥24 h at 60°C and reweighed to derive dry mass values, the difference between these two values representing the water mass. Next, we individually wrapped each sample in filter paper and placed it in a Soxhlet apparatus, which extracted each sample's fat by distillation with petroleum ether (distillation fraction 40°–60°C). We considered all the fat to have dissolved when the ether turned clear (typically ~24 h). Samples were again dried for ≥24 h at 60°C and reweighed. The resulting difference between each sample's dry mass and fat-free dry (FFD) mass was the fat mass.

Analysis

We defined Rock Sandpiper samples from Egegik and Punoarat Point from August and September as 'fall' samples, and those collected in Cook Inlet in December and January and the sole specimen from Juneau as 'winter' samples. *Ptilocnemis* and *tschuktschorum* co-occur at sites in western Alaska during fall (Gill et al. 2002), and our long-term banding studies indicate that individuals of both subspecies have similar body masses during fall. The mean body mass of *ptilocnemis* and *tschuktschorum* birds during fall at Punoarat Point was 78.0 ±5.6 SD g (n = 243) and 74.8 ±5.8 SD g (n = 384), respectively. Their combined value was 75.7 ±5.9 SD g. At Egegik, Rock Sandpipers were not identified to subspecific level during banding, but the mean body mass here (74.3 ±6.2 SD g, n = 45) did not differ from that at Punoarat Point (P = 0.17), indicating that patterns of body composition were comparable between the two subspecies across sites during fall. Based on similar reasoning, Summers et al. (1998) assumed that Purple Sandpiper specimens collected during different winter months across different years yielded valid site-specific comparisons.

We compared fat and FFD body components of Rock Sandpipers in fall to winter and of Rock Sandpipers in winter to Purple Sandpipers in winter from Norway and Scotland. To control for differences in body size related to sex, species, and subspecies, we calculated each bird's standard muscle volume (SMV; equation 10, Piersma et al. 1984), a value comprising four skeletal measurements of the keel that yields a volumetric measure of bird size independent of body condition. We included each bird's SMV as a factor using analysis of variance (ANOVA) procedures to control for intrinsic size differences when comparing across groups (e.g., Packard and Boardman 1999). In our comparisons we included nine specific body components (contour feathers, pectoralis muscle, supracoracoideus muscle, leg muscle, stomach [proventriculus + gizzard], intestine, liver, kidney, and skin) and a 10th component called 'rest' which comprised skeleton and associated musculature and integument. We calculated Tukey's HSD values using the multcomp package (Hothorn et al. 2008) in R 3.0.1 (R Development Core Team 2013) to identify group differences. The sole winter Rock Sandpiper specimen from Juneau, Alaska, was not included with Cook Inlet specimens in ANOVA comparisons of winter birds; we discuss the body composition of this specimen more qualitatively (see below).

We conducted principal component analysis (PCA) on lean body components of all specimens (including the winter specimen from Juneau), and plotted these results as a biplot to visualize seasonal and interspecific patterns of body composition. We plotted the scores of each bird for the first two principal components to show the relation of lean body components by species (winter Rock vs. winter Purple Sandpipers) and season (fall vs. winter Rock Sandpipers).

The fresh body masses of eight Rock Sandpipers from fall were not recorded at the time of collection. Because these carcasses were stored frozen for up to five years, we adjusted the freezer-desiccated body masses of these specimens by applying a correction factor of the mean ratio of total body water to fresh body mass derived from Rock Sandpiper specimens with fresh body mass values that were not subjected to long-term freezing. Additionally, original mass values of contour plumage of Purple Sandpipers were unavailable for comparison. We conducted all analyses in R 3.0.1, and differences were considered statistically significant at $\alpha \leq 0.05$; reported values are mean ±SD.

Results

Rock Sandpipers were slightly larger than Purple Sandpipers and females were larger than males in both species (Table 4.1). Measurements were 0.4% (wing length) to 16.4% (SMV) larger for Rock Sandpipers (Table 4.1). Furthermore, the SMV of Rock Sandpipers was significantly greater in winter specimens (*ptilocnemis* birds; 8.13 ±0.53 cm^3) than fall specimens (*tschuktschorum* birds; 7.28 ±0.87 cm^3; $P < 0.01$), again underscoring the importance of correcting comparisons for structural size. All subsequent comparisons used SMV to control for these intrinsic size differences (see Materials and methods).

Table 4.1. Measurements (mean ±SD; n) of Purple (*Calidris maritima*) and Rock Sandpiper (*Calidris ptilocnemis*) specimens used in comparisons of compositional analysis.

	Purple Sandpiper			Rock Sandpiper		
Measure[a]	Females	Males	Combined	Females	Males	Combined
Culmen	31.6 ±2.6; 7	28.9 ±1.0; 12	29.9 ±2.2; 19	33.6 ±1.7; 16	29.2 ±1.3; 18	31.3 ±2.7; 34
Total Head	57.8 ±3.1; 7	54.8 ±1.6; 13	55.9±2.6; 20	61.0 ±2.6; 16	55.7 ±2.3; 18	58.2 ±3.6; 34
Wing[b]	132.9 ±2.9; 7	131.6±2.6; 13	132.1±2.7; 20	134.4 ±4.4; 14	130.6 ±4.4; 13	132.6 ±4.7; 12
SMV[c]	6.9 ±0.6; 7	6.5 ±0.8; 13	6.7 ±0.7; 20	8.1 ±0.6; 16	7.5 ±0.9; 17	7.8 ±0.8; 33

[a] All measures in mm, except SMV (cm^3).

[b] Only specimens with 10th primary intact were included for wing measurements.

[c] SMV = Standard Muscle Volume (Piersma et al. 1984).

Rock Sandpipers exhibited strong seasonal trends in fat content. The fat mass of organs and muscle groups for Rock Sandpipers in fall was essentially zero, and so we report only overall fat mass for this comparison. Overall fat mass was significantly greater for Rock Sandpipers in winter than fall (Table 4.2), and yielded a fat index ([total fat / body mass] × 100) of 1.86% for Rock Sandpipers in fall and 18.15% in winter. Most fat was stored subcutaneously in winter; on average, nearly 70% (13.58 g) of total body fat was contained in the skin component.

Body mass and total body FFD mass were also greater in Rock Sandpipers in winter than in fall, demonstrating an overall increase in lean tissues from fall to winter (Table 4.2). This increase was reflected in nearly all organs and muscle groups; only the FFD masses of the supracoracoideus and leg muscles and intestine did not differ between fall and winter (Table 4.2). Many (8 of 13 specimens) fall Rock Sandpiper specimens were in active body molt, potentially biasing the interpretation of seasonal trends in contour plumage mass. The average mass of contour feathers for molting birds (3.03 ±0.30 g), however, was not significantly different from that of non-molting birds (3.11 ±0.14 g; $P = 0.57$). The mass of Rock Sandpiper contour feathers was significantly greater in winter than fall (Table 4.2).

PCA results indicated that fall and winter Rock Sandpipers differed mainly with respect to principal component 1, which was dominated by negative loadings of all

Table 4.2. Masses (g) of fall ($n = 13$) and winter ($n = 20$) Rock Sandpipers (*Calidris ptilocnemis*) from Alaska. *P*-values derive from Tukey's HSD comparisons after correcting for structural size using Standard Muscle Volume (SMV; see Methods). Values represent uncorrected mean ±SD.

Body Component	Fall	Winter	*P*-value[a]
Body Mass	75.04 ±5.43	108.20 ±9.96	***
Fat mass	1.42 ±0.78	19.68 ±4.27	***
Total FFD	22.91 ±1.56	27.88 ±1.87	***
Contour Feathers	3.06 ±0.25	4.76 ±0.43	***
Pectoralis FFD	4.02 ±0.41	4.70 ±0.42	**
Supracoracoideus FFD	0.64 ±0.10	0.64 ±0.08	
Leg FFD	0.90 ±0.10	0.97 ±0.09	
Stomach FFD	0.99 ±0.24	1.34 ±0.15	***
Intestine FFD	0.90 ±0.15	0.99 ±0.19	
Liver FFD	1.06 ±0.15	1.57 ±0.19	***
Kidney FFD	0.39 ±0.06	0.46 ±0.06	*
Skin FFD	2.34 ±0.27	2.68 ±0.30	*
Rest FFD	6.89 ±0.50	7.84 ±0.69	**

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

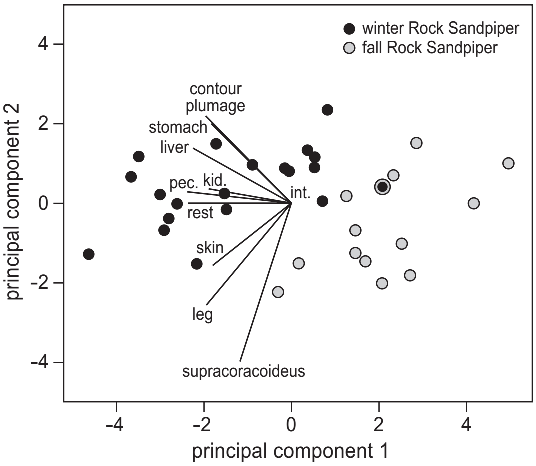

Figure 4.2. Biplot representing principal component analysis of lean body tissues for Rock Sandpipers (*Calidris ptilocnemis*) during fall (Punoarat Point and Egegik, Alaska; open circles) and winter (upper Cook Inlet and Juneau, Alaska; solid circles). 'Kid.' = kidney, 'Pec.' = pectoralis muscle, and 'Int.' = intestine. The vector for intestine is not visible because this variable's principal component scores approach zero; those for stomach and contour plumage nearly overlap. The sole winter bird from Juneau is highlighted by a circle. Vector lengths correspond to each variable's loading in the principal component, and directions display the correlation of the variables to one another (Gabriel 1971; Piersma et al. 1999). Vectors with equal lengths and directions are correlated and bear equal weight in that particular principal component; orthogonal vectors are not related, and vectors oriented in opposite directions are inversely related (Piersma et al. 1999).

variables except intestine (Fig. 4.2). On average, Rock Sandpipers had strongly negative values of principal component 1 in winter, but these values were positive in fall birds. Scores for principal component 2, composed primarily of negative loadings of supracoracoideus, leg, and skin, and positive loadings of contour feathers, liver, and stomach, were positive for Rock Sandpipers during winter and negative during fall, further demonstrating the seasonal reallocation of resources to these specific lean body components (Table 4.2). The lone winter specimen from Juneau had scores that were intermediate between fall birds and the other winter birds (Fig. 4.2). Principal components 1 (variance = 55.1%) and 2 (variance = 13.4%) accounted for 68.5% of the total variation of the PCA model.

Compared to Purple Sandpipers in winter, Rock Sandpipers from upper Cook Inlet exhibited contrasting trends in the allocation of fat. The fat masses of Rock Sandpiper organs and muscle groups during winter were significantly greater (all $P < 0.05$) than those of Purple Sandpipers for all measures except pectoralis muscle and liver (not different from Norway) and kidney (not different from both Norway and Scotland). The overall fat mass of Rock Sandpipers in winter was significantly greater than that of Purple Sandpipers from both sites, which did not differ from one

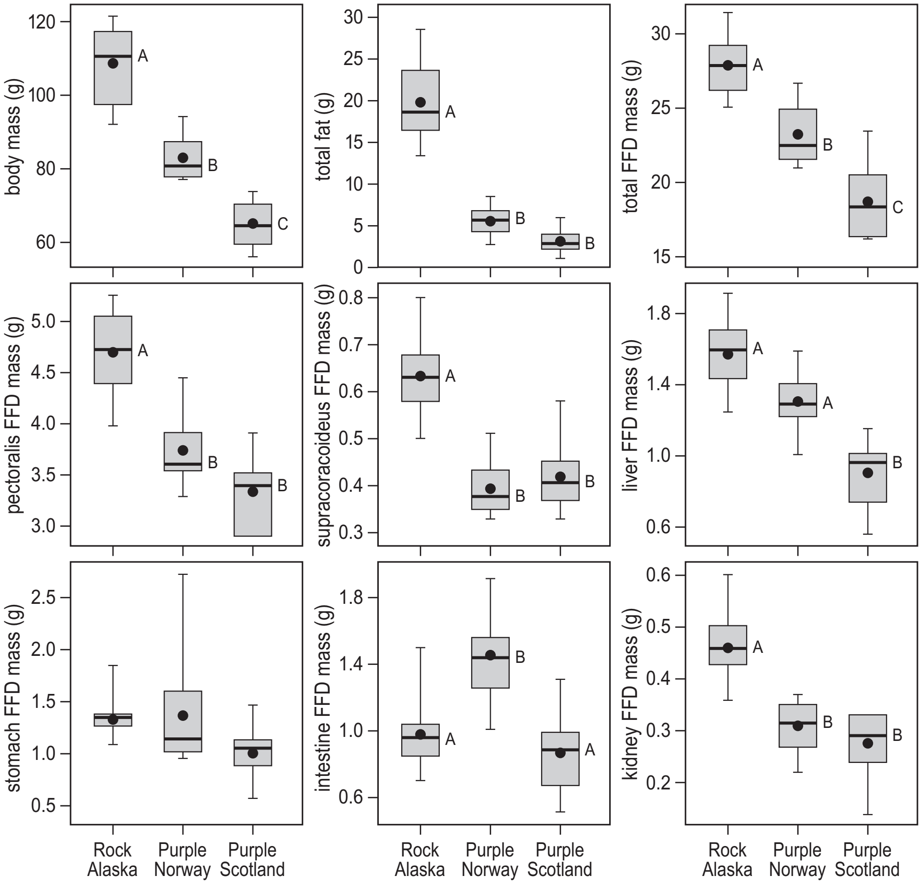

Figure 4.3. Winter fat and fat-free dry (FFD) masses (g) of Rock Sandpipers (*Calidris ptilocnemis*) from Alaska (*n* = 20) and Purple Sandpipers (*Calidris maritima*) from Norway (*n* = 10) and Scotland (*n* = 10). Horizontal line represents median, small circles the mean, box the 25th and 75th percentiles, and whiskers the range of values. Sites with different letters indicate significant differences at $P \leq 0.05$.

another (Fig. 4.3). Expressed as fat index, 18.15% of winter body mass in Rock Sandpipers was composed of fat, compared to 6.44% and 4.40% for Purple Sandpipers from Norway and Scotland, respectively.

Rock Sandpipers in winter also had significantly greater body mass and FFD mass values for total body, pectoralis, supracoracoideus, liver, and kidney components than Purple Sandpipers from Scotland for (Fig. 4.3). Rock Sandpipers were also heavier than Purple Sandpipers from Norway in many of these measures (Fig. 4.3), but Purple Sandpipers from Norway had significantly heavier intestines than Purple Sandpipers from Scotland and Rock Sandpipers (Fig. 4.3). Stomach mass did not differ among the groups (Fig. 4.3).

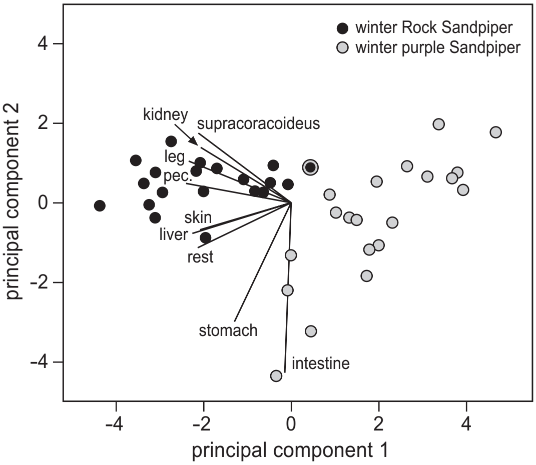

Figure 4.4. Biplot representing principal component analysis of lean body tissues for Rock (upper Cook Inlet and Juneau, Alaska, black circles; *Calidris ptilocnemis*) and Purple (Norway and Scotland, grey circles; *Calidris maritima*) Sandpipers during winter. 'Pec' = pectoralis muscle. The sole winter Rock Sandpiper from Juneau is highlighted by a circle. See Fig. 4.2 for interpretation.

These contrasting trends in fat and lean tissue allocation were also reflected in the principal component analysis. Average scores of principal component 1 were strongly positive for Purple Sandpipers and strongly negative for Rock Sandpipers; principal component 1 (variance = 63.3%) had negative loadings of all variables except intestine, which received almost no weight. The species did not differ strongly in principal component 2, however, with small mean values near zero for both species Principal component 2 (variance = 17.4%) included positive loadings of kidney and supracoracoideus and negative loadings of intestine and stomach components (Fig. 4.4). Scores of the lone Rock Sandpiper specimen from Juneau were intermediate between Rock Sandpipers from Cook Inlet and Purple Sandpipers (Fig. 4.4). Principal components 1 and 2 captured 80.7% of the total variation of the PCA model.

Discussion

Despite their close taxonomic relationship, Rock and Purple Sandpipers exhibit differences in lean and fat body components in winter that are consistent with our predictions regarding the influence of environmental conditions. Due to the constraints of our opportunistically collected samples, determining the causal factors underlying these patterns is problematic. We believe, however, that the starkly different patterns reflect the modulation of phenotypically flexible traits in response to contrasting environmental conditions. For Rock Sandpipers, upper Cook Inlet is more thermally demanding than any other location regularly inhabited by shorebirds during the nonbreeding season (Ruthrauff et al. 2013a, 2013b), and this imposes high energetic costs. Unlike Purple Sandpipers (Summers et al. 1990b; Mittelhauser et al. 2012), *ptilocnemis* birds in upper Cook Inlet forage exclusively on mudflat habitats. On average, these foraging substrates annually diminish by nearly 60% due to the seasonal accretion of shore-fast and sea ice (Ruthrauff et al. 2013*b*), necessitating the accumulation of fat stores in case of daily energy deficits. In contrast, rocky intertidal habitats used by Purple Sandpipers rarely freeze and birds reliably exploit the intertidal epifauna (Strann and Summers 1990; Summers et al. 1990a), eliminating the need for large fat stores.

Differences between Rock and Purple Sandpipers in winter lean tissue composition also likely reflect ambient environmental conditions. The pectoralis and supracoracoideus muscles (together forming the breast muscle complex) and kidneys are heavier in Rock Sandpipers from upper Cook Inlet than in Purple Sandpipers. The breast muscle is the primary thermogenic organ in birds, employed to create heat through shivering thermogenesis (Hohtola 2004; Vézina et al. 2007; Swanson 2010). Given their large fat stores, larger breast muscles also likely counteract increased wing loading and help maintain flight performance (e.g., Dietz et al. 2007). The liver (larger in Rock Sandpipers and Purple Sandpipers from Norway) is also a likely source of thermogenesis in birds by virtue of its great metabolic activity (Vézina et al. 2006), but its primary role concerns digestive and circulatory functions (Battley and Piersma 2005). The kidneys, again larger in Rock Sandpipers, serve excretory and homeostatic functions (Proctor and Lynch 1993).

Interestingly, stomach mass, constituted primarily by the gizzard, did not differ between sites. This suggests that the digestive capacities of Rock and Purple Sandpipers at the three sites are not constrained by their ability to physically crush their hard-shelled prey. Instead, digestive capacities may be limited by organs that did vary across sites, specifically those involved with the chemical break-down and assimilation of nutrients (intestines and liver) and the processing of waste by-products (kidneys). In sum, the high fat loads and comparatively large organs and muscle groups of Rock Sandpipers in upper Cook Inlet during winter reflect the up-regulation of thermogenic and digestive capacities necessary to accommodate the region's high metabolic demands and sporadically inaccessible food resources.

Similar to other northerly wintering shorebirds, Rock Sandpiper body composition is dynamically modulated across seasons. In previous studies, the body mass of northerly wintering shorebirds (including Purple Sandpipers) increased 11–13% as birds completed fall migration and settled at winter nonbreeding sites (Pienkowski et al. 1979; Dugan et al. 1981; Summers et al. 1992; Scott et al. 1994). For Rock Sandpipers, overall fat stores were likewise low during fall (lipid index = 1.86%). By midwinter, however, the body mass of Rock Sandpipers had increased by more than 40%, primarily due to increased lipid stores (nearly 14 times higher in winter than fall; Table 4.2) but also lean components (18% greater in winter than fall; Table 4.2).

High winter fat stores enable two alternative strategies for Rock Sandpipers facing reduced foraging opportunities during severe winter conditions. High levels of stored fat could be used to (1) conduct prolonged fasts, or (2) fuel irruptive movements to more benign regions. Using Ruthrauff et al.'s (2013a) estimated maintenance metabolic rate of 2.6 W for Rock Sandpipers in upper Cook Inlet during December (mean temperature –8.7°C), and assuming a conversion constant of 39.5 kJ g^{-1} fat (Ricklefs 1974), a Rock Sandpiper with average fat stores (19.68 g; Table 4.2) could theoretically endure on lipid stores alone for approximately 85 hours. During not-uncommon periods of cold as low as –25°C (Ruthrauff et al. 2013*b*), such stores would endure for about 65 hours. Alternatively, rocky intertidal habitats less susceptible to freezing exist within 200 km of upper Cook Inlet (Coletti et al. 2010, 2011), and high fat stores could fuel flights to such areas. The proclivity of Rock Sandpipers to conduct fasts is unknown, but Ruthrauff et al. (2013*b*) documented irruptive movements of Rock Sandpipers out of upper Cook Inlet coinciding with periods of extreme cold.

Species or individuals with unpredictable access to food resources tend to have higher body mass (primarily due to increased fat stores [Blem 1990]) than species with predictable food access (Rogers 1987; Witter et al. 1995; Kelly and Weathers 2002; Vézina et al. 2009). Because shorebirds are subject to variable predation danger during the nonbreeding season (Cresswell and Whitfield 1994; Warnock et al. 1997; van den Hout et al. 2008), they must balance the benefit of accumulated energy stores with the increased risk of predation that this entails (Lank and Ydenberg 2003; van den Hout et al. 2010). Increased fat stores improve fasting endurance (Ketterson and King 1977; Blem 1990) but come at the expense of decreased escape performance (Burns and Ydenberg 2002; Dietz et al. 2007). As a corollary, predictions (Houston and McNamara 1993) and empirical evidence (Ydenberg et al. 2002; Piersma et al. 2003; Pomeroy et al. 2008; van den Hout et al. 2010) indicate that shorebirds subject to lower predation danger have higher body mass than conspecifics facing higher predation danger.

The predation danger posed to shorebirds during the nonbreeding season comes primarily from raptors of the order Falconiformes, species which are principally diurnal, visual hunters (Newton 1979; Thiollay 1994; White et al. 1994). Although no published information exists, we have rarely observed raptors (e.g., Northern Goshawks [*Accipiter gentilis* L., 1758], Merlins [*Falco columbarius* L., 1758], and Peregrine Falcons [*F. peregrinus* (Tunstall, 1771)]) during winter in upper Cook Inlet, and only once observed predation (by a Northern Goshawk) during hundreds of hours of observation. In contrast, despite long periods of total darkness during winter in northern Norway, Gyrfalcons (*Falco rusticolus* L., 1758) and Ravens (*Corvus corax* L., 1758) were commonly observed hunting Purple Sandpipers there (RWS pers. obs.), and Payne and Pierce (2002) report that a variety of raptor species prey on Purple Sandpipers during winter in Norway (sites not specified). In Scotland, Purple Sandpipers are also subject to predation danger (Whitfield 1985; Cresswell and Whitfield 1994). Although largely anecdotal, these observations suggest that Rock

Sandpipers in upper Cook Inlet face relatively low predation danger and thus regulate their body mass to augment energy stores at the expense of escape performance while Purple Sandpipers in both Norway and Scotland may modulate fat stores to mitigate predation danger, a trade-off facilitated by their reliable intertidal food resources.

Although such correlative observations are compelling, they fall short of demonstrating causation. We encourage experimental research employing repeated captures and non-lethal techniques to assess body condition (e.g., Dietz et al. 1999; Speakman et al. 2001; Guglielmo et al. 2011) to better determine the mechanistic links between relevant environmental variables and the dynamic somatic response of northerly-wintering shorebirds. Similarly, we also encourage a wider latitudinal range of observation to better quantify within-species patterns at larger spatial scales. For instance, the one winter Rock Sandpiper specimen from Juneau appears to indicate that the body composition pattern characterized by high fat stores and an up-regulation of organ and muscle groups associated with thermogenic and digestive functions is a phenotype restricted to Rock Sandpipers in upper Cook Inlet (Fig. 4.4). The nonbreeding range of the Rock Sandpiper spans more than 25° latitude, and individuals at the southern half of the distribution are *tschuktschorum* individuals (Gill et al. 2002). Similar to Purple Sandpipers, *tschuktschorum* birds are associated primarily with rocky intertidal habitats during the nonbreeding season (Gill et al. 2002). Our sole *tschuktschorum* winter specimen weighed 79.4 g and had a lipid index of 4.1%, values more similar to those of Purple Sandpipers in winter (Fig. 4.3) and Rock Sandpipers in fall (Table 4.2). Despite the comparatively low body mass and lipid stores of the winter *tschuktschorum* specimen, however, this individual's PCA scores revealed an allocation of lean tissues more similar to Rock Sandpipers from Cook Inlet than to Purple Sandpipers (Fig. 4.4). This further demonstrates the nuanced regulation of lean and lipid tissues by these species, illustrating how local environmental (e.g., temperature, prevalence of shore-fast ice) and ecological (e.g., food access, predator abundance) factors determine the expression of phenotypic traits (Piersma and van Gils 2011).

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CHAPTER 5

Identical metabolic rate and thermal conductance in Rock Sandpiper (*Calidris ptilocnemis*) subspecies with contrasting nonbreeeding life histories

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Abstract

Closely related species or subspecies can exhibit metabolic differences that reflect site-specific environmental conditions. Whether such differences represent fixed traits or flexible adjustments to local conditions, however, is difficult to predict across taxa. The nominate race of Rock Sandpiper (*Calidris ptilocnemis*) exhibits the most northerly nonbreeding distribution of any shorebird in the North Pacific, being common during winter in cold, dark locations as far north as upper Cook Inlet, Alaska (61°N). By contrast, the *tschuktschorum* subspecies migrates to sites ranging from about 59°N to more benign locations as far south as ~37°N. These distributional extremes exert contrasting energetic demands, and we measured common metabolic parameters in the two subspecies held under identical laboratory conditions to determine whether differences in these parameters are reflected by their nonbreeding life histories. Basal metabolic rate and thermal conductance did not differ between subspecies, and the subspecies had a similar metabolic response to temperatures below their thermoneutral zone. Relatively low thermal conductance values may, however, reflect intrinsic metabolic adaptations to northerly latitudes. In the absence of differences in basic metabolic rates, the two subspecies' nonbreeding distributions will likely be more strongly influenced by adaptations to regional variation in ecological factors such as prey density, prey quality, and foraging habitat.

Introduction

Life history traits are ultimately determined by an organism's genotype (Stearns 1989), but environmental conditions strongly shape the phenotypic expression of genetic traits (Piersma and van Gils 2011). Comparisons between closely related species, subspecies, or populations with divergent life-history traits can help discern the contributions of genes and environment in determining basic metabolic and physiological variables (Mueller and Diamond 2001, Wikelski et al. 2003). Previous comparisons across a wide array of taxa have investigated a variety of physiological parameters, including metabolic rate (Klaassen 1995, Piersma 1996), immune response (Buehler et al. 2009), total evaporative water loss (Williams et al. 2004, Tieleman 2007), growth rate (Niewiarowski and Roosenburg 1993), digestive function (Mueller and Diamond 2001; van Gils et al. 2005a, b), and thermal conductance (Scholander et al. 1950a, b). Despite numerous studies, however, no predictable patterns have emerged to show how phenotypically flexible traits are modulated across taxa.

As a group, shorebirds in the family Scolopacidae lend themselves to such comparisons because of their diverse life histories (e.g., Pitelka et al. 1974, Piersma 2007) and discrete genetic lineages within species (e.g., Buehler and Baker 2005). Members of this family tend to breed at relatively high latitudes and are highly migratory, most conducting annual migrations totaling 10,000–30,000 km between high-latitude breeding grounds and temperate nonbreeding locations (Piersma et al. 1996b, Battley et al. 2012). Migratory shorebirds exhibit considerable phenotypic flexibility that enables efficient physiological "retooling" to accommodate these migratory behaviors (Piersma and Lindström 1997, Battley and Piersma 2005). For scolopacid shorebirds, a less-common life-history strategy involves staying at or near high-latitude breeding sites throughout the year, but physiological adaptations to this life-history strategy are comparatively little studied. Such a strategy is predicted to also involve great physiological change, including elevated metabolic rates (Weathers 1979, Piersma et al. 1996a), increased lipid stores (White and West 1977, Blem 1990), improved insulative capacities (Dawson and Carey 1976, Carey et al. 1978), and increased digestive and metabolic efficiencies (Dykstra and Karasov 1992, Karasov 1996).

In the North Pacific Basin, the Rock Sandpiper (*Calidris ptilocnemis*) is the shorebird species with the most northerly nonbreeding distribution (Gill et al. 2002). Four subspecies of Rock Sandpiper are recognized on the basis of appearance and morphology (Conover 1944) and genetic analyses (Pruett and Winker 2005), and the subspecies exhibit differential migration patterns. Two subspecies (*C. p. couesi* and *C. p. quarta*) are essentially nonmigratory, moving primarily between upland breeding sites and coastal nonbreeding sites. A third (*C. p. ptilocnemis*) moves relatively short distances (≤1,500 km) between breeding and nonbreeding sites, and the fourth subspecies (*C. p. tschuktschorum*) migrates longer distances (~4,000 km; Gill et al. 2002).

Because of migratory propensity and prevailing environmental conditions, the nonbreeding distributions of *C. p. ptilocnemis* and *C. p. tschuktschorum* represent the life-history extremes for the species. *Calidris p. ptilocnemis* (hereafter *ptilocnemis*) spends the nonbreeding season primarily in upper Cook Inlet, Alaska (61°N, 151°W; Gill et al. 2002), a site with expansive mudflats and abundant food resources. In the winter, the mean daily temperature in this region is <0°C for nearly 5 months from November to March; consequently, the upper intertidal zone in Cook Inlet accretes with thick sea ice, and critical mudflat habitats becomes less accessible as the winter progresses. By contrast, *C. p. tschuktschorum* (hereafter *tschuktschorum*) is distributed along the eastern North Pacific coast from about 59° to 37°N in winter (Gill et al. 2002). The distribution and population structure of *tschuktschorum* across this range are unknown, but in general, *tschuktschorum* individuals less commonly encounter temperatures <0°C, rarely experience ice coverage of preferred rocky intertidal foraging habitats, and exploit longer day lengths than in upper Cook Inlet. Although the subspecies probably co-occur in small numbers at their distributional extremes, their winter distributions are largely non-overlapping.

Latitudinal gradients in environmental conditions at these nonbreeding sites exert contrasting energetic demands. Applying long-term meteorological data, the predicted average maintenance metabolic rate in December for a hypothetical 85-g *ptilocnemis* Rock Sandpiper in upper Cook Inlet is 2.55 W (Table 5.1). Given their wider nonbreeding range, similarly derived values for *tschuktschorum* range from 1.64 to 2.43 W for birds wintering at locations representative of the southern

Table 5.1. Long-term average environmental conditions in December and resulting predicted energetic demands for Rock Sandpipers wintering at distributional extremes. *Calidris ptilocnemis ptilocnemis* winters primarily in upper Cook Inlet, Alaska, and *C. p. tschuktschorum* is widely distributed along the eastern Pacific coast from 59° to 37°N. Metabolic rates refer to the thermostatic costs (i.e., do not include activity costs) and are calculated following equation 5 in Wiersma and Piersma (1994; values for "solitary bird"), using conductance value K_{es} = 0.036 (Calder 1996).

Site[a]	Latitude	Temperature[b]	Wind[c]	Insolation[d]	Daylight[e]	Predicted metabolic rate[f]
UCI	61°N	−5.3, −12.2, −8.7	2.8	6	5:38	2.55
JUN	58°18′N	−0.2, −5.2, −2.7	4.0	10	6:30	2.43
HUM	41°N	12.7, 5.6, 9.1	2.9	70	9:19	1.64

[a] UCI = upper Cook Inlet, Alaska, JUN = Juneau, Alaska, and HUM = Humboldt Bay, California.

[b] High, low, mean (°C; Western Regional Climate Center 2012).

[c] $m\ s^{-1}$ (Western Regional Climate Center 2012).

[d] $W\ m^{-2}$ (National Aeronautics and Space Administration 2012).

[e] Hours:minutes (U.S. Naval Observatory 2012).

[f] Watts (following procedures of Wiersma and Piersma 1994).

(Humboldt Bay, California; 41°N) and northern (Juneau, Alaska; 58°18′N) extents of their nonbreeding range, respectively (Table 5.1). Thus, the nonbreeding distributions and migratory predispositions of these two subspecies represent extremes not only along a life history continuum, but also along an exercise–physiology continuum. Predicted differences in metabolic rates between the two subspecies (4.7–35.7%) and between *tschuktschorum* at the northern and southern extents of their nonbreeding range (32.5%) speak to the inherent expansibility of metabolic rates in shorebirds (Swanson 2010, Piersma 2011), and metabolic expansibility and summit metabolic rates are related to basic physiological measures like basal metabolic rate (Dutenhoffer and Swanson 1996, Rezende et al. 2002). Differences in predicted metabolic rates could thus be reflected by intrinsic differences in Rock Sandpiper physiological parameters.

We tested this on Rock Sandpipers maintained in a common environment, enabling us to assess the degree to which each subspecies' life history is reflected in inherent differences in basic physiological parameters. Previous studies have demonstrated that birds at colder sites or during colder seasons have lower conductance than those at warmer locations or during warmer seasons (Blem 1981, Cooper 2002). When maintained under similar conditions, increased insulative capacity in one population may enable relatively lower metabolic rates and increased cold resistance compared with another population with a lower insulative capacity (West 1972, Vézina et al. 2009). We hypothesized that, given wintering locations that require consistently greater metabolic output and in the absence of metabolic flexibility, *ptilocnemis* would have (1) a higher basal metabolic rate (BMR; the energy consumption of a resting, postabsorptive animal in a normothermic environment; IUPS Thermal Commission 2003), (2) lower metabolic rates at temperatures below their thermoneutral zone, and (3) lower thermal conductance than *tschuktschorum*.

Methods

Experimental animals and maintenance

We included 27 adult Rock Sandpipers in the trials, including 15 *ptilocnemis* (7 females, 8 males) and 12 *tschuktschorum* (6 females, 6 males). The birds were captured on 28 August 2009 at a postbreeding site on the Yukon Delta National Wildlife Refuge, Alaska (61°19′N, 165°47′W). We determined the subspecific identity of birds on the basis of diagnostic plumage characteristics of the wing and mantle (Gill et al. 2002), and sex via standard polymerase chain reaction techniques (Griffiths et al. 1996).

We transported the birds to the NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands, on 21 September 2009. Following a 1-month health quarantine period, the birds were randomly assigned to one of three identical outdoor aviaries on 27 October 2009. The birds were exposed to the local ambient temperature and photoperiod at 51°N, but sheltered from wind and precipitation (for aviary details, see Vézina et al. 2006). The mean (± SE) monthly temperatures during the trial period were 9.6 ± 0.4°C for November 2009, 3.4 ± 0.7°C for December 2009, –0.3 ± 0.4°C for January 2010, 1.2 ± 0.5°C for February 2010, and 5.6 ± 0.6°C for March 2010, as measured at the Royal Netherlands Meteorological Institute station in De Kooij, North Holland (see Acknowledgments), 8 km south of the NIOZ aviaries.

Respirometry

We randomly assigned birds to metabolic trials on the basis of subspecies and sex, selecting one member of each subspecies of each sex per trial. The first respirometry trial was conducted on 23 November 2009, 27 days after the birds were established in outside aviaries. We measured oxygen consumption (V_{O_2}) and calculated metabolic rates using a flow-through respirometry system on ≤4 individuals per trial (for setup details, see Vézina et al. 2006).

Metabolic chambers were held in a dark, climate-controlled thermocabinet, and birds were maintained overnight from 1600 to 0900 hours during all trials. For the BMR trials, birds were held at 18°C, a temperature assumed to be within the species' thermoneutral zone on the basis of comparisons to similar shorebirds (e.g., Ruddy Turnstone [*Arenaria interpres*; Kersten and Piersma 1987], Red Knot [*C. canutus*; Piersma et al. 2004], and Sanderling [*C. alba*; Castro 1987]). We conducted one respirometry trial per bird for BMR calculations. After completing the BMR trials, we observed that metabolic rates were consistent across the latter half of each 17-h trial, and so to augment our ability to measure the metabolic response of Rock Sandpipers to temperature (hereafter "temperature trials"), we conducted subsequent trials at two predictive temperatures per trial. Following this protocol, birds were kept at 18°C for the first 8 h of each temperature trial, and then adjusted to the first predictive temperature for 4 h, followed by a second predictive temperature for another 4 h. After 16 h, the metabolic chambers were once again regulated to 18°C for a 1-h recovery period. We programmed the temperature trials to minimize temperature fluctuations because severe temperature swings induced locomotor activity that disrupted the birds' resting state and increased oxygen consumption. For similar reasons, we paired each trial's two temperatures to minimize temperature fluctuations (i.e., trials at 10°C were paired with measurements at 5°C rather than –20°C). We conducted one respirometry trial per bird for temperature trials in which they were included.

We calculated each bird's metabolic rate over the 10-min period with the lowest V_{O_2} for all BMR and temperature trials. The mean (± SE) respiratory quotient during the BMR trials was 0.715 ± 0.005, a value indicative of fat metabolism in a postabsorptive bird (Bartholomew 1982), and so we used an energy conversion value of 19.8 kJ l^{-1} O_2 (Gessaman and Nagy 1988) and converted this value to watts (1 kJ h^{-1} = 0.277 W). Calculations were performed using Sable Systems ExpeData software (Las Vegas, Nevada). Twenty-seven birds were included in the BMR trials, and 26 birds were included in the temperature trials. Because of conflict with concurrent experiments, not all 26 individuals were measured at all temperatures (for sample sizes, see Fig. 5.1). We measured the metabolic response of 8, 10, and 8 birds at two, three, and six predictive temperatures, respectively. We conducted the BMR trials from 23 to 30 November 2009; trials at 10°C and 5°C from 8 to 11 December 2009; trials at –5°C and –10°C from 13 to 16 December 2009; trials at 14°C and 22°C from 26 to 27 February 2010; and trials at –15°C and –20°C from 5 to 6 March 2010.

Statistical analyses

We fit generalized linear models to assess the effect of relevant biological parameters on the metabolic rate of Rock Sandpipers. We conducted separate analyses for the BMR trials and the temperature trials. For the BMR trials, we modeled the effect of subspecies (*ptilocnemis* or *tschuktschorum*), sex (male or female), and body mass on BMR. We modeled the effect of the aforementioned predictor variables as well as temperature below the lower critical temperature (–20°, –15°, –10°, –5°, 5°, 10°, and 14°C) in temperature trial models and defined these parameters as fixed effects. Because we repeatedly measured many of the same birds at different temperatures in these trials, we used linear mixed-effects models to account for random variation attributable to individual birds and modeled the individual birds as a random effect. To determine the most parsimonious modeling approach, we followed procedures outlined in Zuur et al. (2009) and compared three fully parameterized mixed-effects models that differed only in the correlation structure of the random effect component. This comparison consisted of a model with the random effect modeled as a simple scalar effect, a model fitting the random effect correlated to the level of temperature, and a model defining the random effect as scalar but uncorrelated to the level of temperature. Defining the random variation attributable to individual birds as a simple scalar effect was the most parsimonious approach, and we defined the random effect as such in all temperature models.

Measures of conductance in Red Knots indicated that birds became hypothermic only as low temperatures induced a metabolic response ~5 × BMR (Vézina et al. 2006). Because metabolic outputs in Rock Sandpipers at –20°C only approached ~2.5 × BMR (see below), we assumed that birds were normothermic at all temperatures during temperature trials. There was little individual variation in the body temperature of Rock Sandpipers (mean [± SE] cloacal temperature measured in thermoneutral environment = 42.6 ± 0.13°C; n = 8 individuals). We calculated each bird's thermal conductance at experimental temperatures $t \leq 14$°C using the formula (metabolic rate$_t$ / [temperature$_{\text{body}}$–temperature$_t$]; Piersma et al. 1995). We used the same model set as in the temperature analysis (see below). The results of the two analyses were nearly identical (the same three models in nearly equal proportions accounted for ~80% of the entire model weight in both analyses), and we report only model-averaged parameters and plot model-averaged predictions from the conductance analysis to avoid redundancy.

We followed the multimodel information-theoretic analytical approach outlined in Burnham and Anderson (2002) to examine support for our hypotheses about factors affecting the metabolic rate of Rock Sandpipers. For each analysis, we included different biologically relevant combinations of the explanatory variables. On the basis of results of previous studies, we included body mass in all our BMR models to control for size-related variation in metabolic rates (Packard and Boardman 1999), and temperature in all the mixed-effects models assessing the metabolic response to temperature (Scholander et al. 1950a, Scholander 1955). We compared five models in the BMR analysis and six models in the analyses of metabolic response to temperature and conductance (Table 5.2). We gauged support for each model using Akaike's information criterion adjusted for small sample size (AIC_c) and based model inference on Akaike weights (w_i; Burnham and Anderson 2002). We averaged our model results in proportion to Akaike weights to generate overall parameter and prediction estimates and considered parameters to be biologically meaningful if their model-averaged 95% confidence intervals did not overlap zero. We conducted all analyses in R, version 2.12.2, and fitted generalized linear models for the BMR analysis using the stats package (R Development Core Team 2011), mixed-effects models for the temperature and thermal conductance analyses using the lme4 package (Bates et al. 2011), and averaged model outputs using the AICcmodavg package (Mazerolle 2011). Estimates are presented as means ± SE.

Results

Basal metabolic rate

Body mass of the sexes was similar between subspecies; females (90.2 ± 3.3 g for *ptilocnemis* and 90.5 ± 2.3 g for *tschuktschorum*) weighed ~6% more than males (85.5 ± 2.6 g for *ptilocnemis* and 84.0 ± 3.5 g for *tschuktschorum*).

The model selection process demonstrated limited support for the effect of body mass in predicting Rock Sandpiper BMR, and poor support for the other explanatory variables (Table 5.2). Model ranking indicated that the intercept-only model and a model with just body mass as an explanatory variable were nearly equally supported and together accounted for almost three-quarters of the overall model support (Σw_i = 0.72; Table 5.2). Models that included the effect of subspecies and sex were not well supported (Σw_i = 0.18 and Σw_i = 0.15, respectively; Table 5.2), which indicates that these variables were not useful in predicting BMR. This was corroborated by the 95% confidence intervals of the parameter coefficients overlapping zero for subspecies, sex, and body mass (despite its inclusion in the second-most-supported model; Table 5.3).

We calculated the model-averaged estimates of BMR for each sex of each subspecies using the pertinent mean body mass values reported above, and these values were nearly identical. The estimated BMR for both *ptilocnemis* and *tschuk-*

tschorum females was 0.85 ± 0.02 W, and values for male *ptilocnemis* and *tschuktschorum* were 0.83 ± 0.02 W and 0.84 ± 0.02 W, respectively. These model-averaged predictions closely matched the mean values recorded during the actual trials for each sex of each subspecies (Fig. 5.2).

Table 5.2. Model rankings describing metabolic outputs of Rock Sandpipers. We fitted generalized linear models for the basal metabolic rate (BMR) trials, and linear mixed-effects models for the metabolic response to temperature trials. For BMR models, the number of parameters (*k*) includes +1*k* for an intercept and +1*k* for residual estimate. For temperature models, in addition to +2*k* for intercept and residual term, +1*k* is added to each model representing the random effect attributable to individual birds. We also applied the temperature models to the analysis of thermal conductance; see text for conductance model summaries.

BMR				Temperature			
Model[a]	k	ΔAIC_c[b]	w_i	Model[a]	k	ΔAIC_c[c]	w_i
Intercept	2	0.00	0.37	T	4	0.00	0.33
M	3	0.08	0.35	T + SX + M	6	0.13	0.31
SUB + M	4	1.99	0.14	T + M	5	1.43	0.16
SX + M	4	2.48	0.11	T + SX + SUB + M	7	2.06	0.12
SX + SUB + M	5	4.69	0.04	T + SUB + M	6	3.06	0.07
				Intercept	3	175.51	0.00

[a] M = Mass, T = Temperature, SUB = Subspecies, SX = Sex.
[b] The lowest AIC_c score in the analysis was −53.10.
[c] The lowest AIC_c score in the analysis was −96.59.

Table 5.3. Model-averaged parameter estimates (with 95% confidence intervals in parentheses) for factors predicting the metabolic output (W) and conductance (W °C^{-1}) of Rock Sandpipers. Results are from basal metabolic rate (BMR), metabolic response to temperature below the thermoneutral zone (Temperature), and conductance models presented in Table 5.2.

	BMR (W)	Temperature (W)	Conductance (W °C^{-1})
Parameter	Estimate	Estimate	Estimate
Mass	0.002 (−0.001 to 0.005)	−0.002 (−0.006 to 0.002)	−0.00006 (−0.0002 to 0.00004)
Sex[a]	−0.003 (−0.015 to 0.009)	−0.044 (−0.111 to 0.023)	−0.001 (−0.003 to 0.001)
Subspecies[b]	−0.005 (−0.019 to 0.009)	−0.008 (−0.031 to 0.016)	0.00001 (−0.0004 to 0.0004)
Temperature		−0.030 (−0.033 to −0.028)	0.00015 (0.0001 to 0.0002)
Intercept	0.679 (0.278 to 1.080)	1.729 (1.228 to 2.231)	0.043 (0.029 to 0.056)

[a] Males are the reference level.
[b] *Calidris ptilocnemis ptilocnemis* is the reference level.

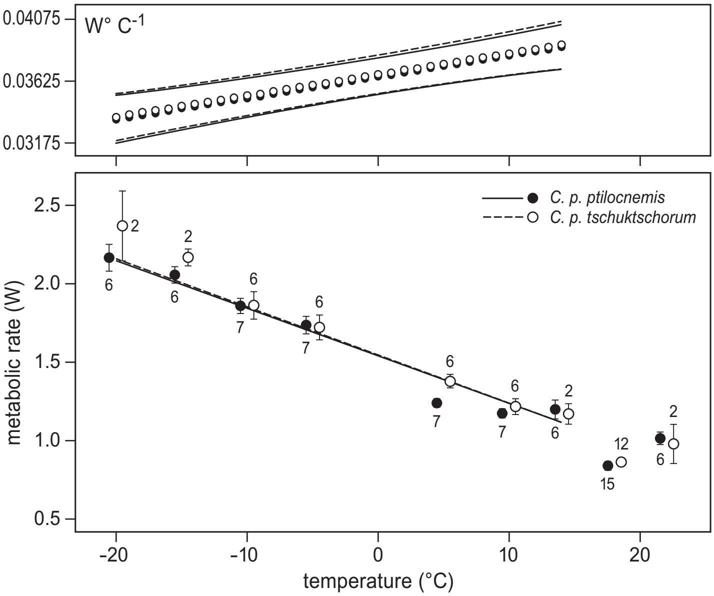

Figure 5.1. Thermal conductance (W° C^{-1}; upper figure) and metabolic rate (W; lower figure) in response to temperature of *Calidris ptilocnemis ptilocnemis* (filled symbols and solid lines) and *C. p. tschuktschorum* (open symbols and dashed lines). For conductance, plot shows model-averaged predictions ± 95% confidence intervals; for metabolic rate, symbols represent measured mean ± SE, lines represent model-averaged predictions, and numbers represent sample size. Values in lower figure are offset from actual predictive temperatures for clarity.

Metabolic response to temperature

As with the BMR trials, females (91.1 ± 3.0 g for *ptilocnemis* and 92.3 ± 1.8 g for *tschuktschorum*) weighed more (~4%) than males (89.2 ± 2.1 g for *ptilocnemis* and 85.2 ± 2.8 g for *tschuktschorum*). The lower critical temperature for both subspecies fell between 14°C and 18°C (Fig. 5.1). We measured the metabolic rate of Rock Sandpipers at one temperature >18°C, and this trial indicated that the upper critical temperature for each subspecies was between 18°C and 22°C (Fig. 5.1). Thus, the exact upper and lower critical temperatures are unknown, but the thermoneutral zone for both subspecies most likely falls between 14°C and 22°C.

The metabolic rate of Rock Sandpipers increased at temperatures below the thermoneutral zone (Fig. 5.1). The model-averaged regression lines for each subspecies climbed with essentially equal slopes and intercepts as temperatures declined (Fig. 5.1). The best-supported model included the effects of temperature alone, and this model accounted for one-third of the total model weight (Table 5.2). As with the BMR analysis, the effects of body mass, sex, and subspecies were minimal: all the model-averaged 95% confidence intervals for these variables overlapped zero (Table 5.3).

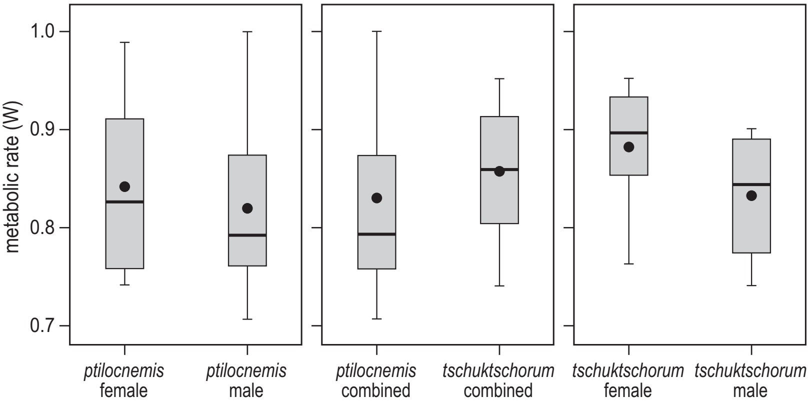

Figure 5.2. Measured basal metabolic rates (W) of Rock Sandpipers by sex and subspecies. Horizontal line represents median, black dot the mean, box the 25th and 75th percentiles, and whiskers the range of values.

The combined model weight for models that included temperature was 1.00, but models that included body mass ($\Sigma w_i = 0.66$), sex ($\Sigma w_i = 0.43$), and subspecies ($\Sigma w_i = 0.19$) were not as well supported, and there was essentially no support for the intercept-only model (Table 5.2). Temperature was also the only predictor variable with 95% confidence intervals that did not overlap zero (Table 5.3). The model-averaged parameter estimate for temperature was –0.03, indicating an increase in metabolic rate of 0.03 W for each 1°C drop in temperature below 14°C.

Thermal conductance

Our analysis of variation in conductance compared the same six models used in the temperature analysis (Table 5.2). As with the temperature trials, the best-supported model contained only temperature, and this model accounted for one-third of the total model weight ($w_i = 0.34$). Models that included temperature, sex, and body mass ($w_i = 0.32$) and temperature and body mass ($w_i = 0.19$) were also well supported, but temperature was the only predictor variable whose 95% confidence interval did not overlap zero (Table 5.3). Model-averaged estimates of conductance decreased slightly with decreasing temperatures in both subspecies (Fig. 5.1). Applying trial-specific mean body masses, the model-averaged estimates of conductance across our range of predictive temperatures were equal for *ptilocnemis* and *tschuktschorum* females (0.039 ± 0.001 W $°C^{-1}$ and 0.034 ± 0.001 W $°C^{-1}$ at 14°C and –20°C, respectively), and differed little from males (0.038 ± 0.001 W $°C^{-1}$ and 0.039 ± 0.001 W $°C^{-1}$ for *ptilocnemis* and *tschuktschorum* males at 14°C; both subspecies 0.033 ± 0.001 W $°C^{-1}$ at –20°C). Minimal thermal conductance occurred at lower rather than higher temperatures below the thermoneutral zone.

Discussion

In contrast to previous studies that documented metabolic differences between closely related study groups (e.g., Niewiarowski and Roosenburg 1993; Klaassen 1995; Mueller and Diamond 2001; Wikelski et al. 2003; Broggi et al. 2004, 2005; Tieleman 2007), we found no evidence of intrinsic differences in basic metabolic parameters between *C. p. ptilocnemis* and *C. p. tschuktschorum* held under identical conditions. There was no variation in BMR or thermal conductance of Rock Sandpipers by sex or subspecies, and the metabolic response of each subspecies to temperature did not differ. Given their more northerly nonbreeding distribution and exposure to colder temperatures, we reasoned that the plumage of *ptilocnemis* would differ from and provide more insulation than the plumage of *tschuktschorum* (e.g., Blem 1981, Piersma et al. 1995), but this was not the case and suggests that the two subspecies derive similar insulation from their plumages.

Although the two subspecies did not differ with respect to these basic metabolic parameters, Rock Sandpipers appear to exhibit unique adaptations to cold environments compared with birds in general. For instance, our measures of BMR did not diverge from expected patterns in shorebirds based on body mass. Substituting the mean body mass of each sex of each subspecies measured during the BMR trials in the shorebird-specific equation derived by Kersten and Piersma (1987) yields BMR estimates for males and females of both subspecies that are within 1–3% of our model-averaged estimates. Our model-averaged estimates of thermal conductance, however, were lower than predicted, and this difference may reflect adaptations to colder environments. Applying trial-specific body masses to equation 8–15 in Calder (1996) yielded estimates of minimal conductance ~10% higher than our model-averaged estimates of thermal conductance at –20°C for both subspecies.

Thermal conductance in both subspecies declined slightly at the lowest environmental temperatures (Fig. 5.1), a phenomenon commonly encountered as animals allow slight drops in their body temperature and/or combine physical and chemical thermoregulation processes at low temperatures (McNab 1980). Additionally, comparisons with other shorebirds show that the model-averaged intercept and slope estimates for temperature are smaller for Rock Sandpipers than for species with more temperate nonbreeding ranges assessed by Kersten and Piersma (1987). Because the intercept term in these models is primarily a function of body mass, the smaller value for Rock Sandpipers is simply a reflection of their smaller mass compared with the larger shorebird species measured by Kersten and Piersma (1987). The model-averaged slope parameter for temperature, however, is 1.5–3.3 times smaller for Rock Sandpipers, indicating that their metabolic rates increase relatively less as temperatures decrease below their thermoneutral zone than for other shorebird species. Thus, thermal conductance values are lower than predicted and the metabolic response to temperature is more moderate in Rock Sandpipers, which may represent intrinsic, genetically fixed adaptations to their year-round existence at thermally demanding high latitude sites. Potential adaptations that may account for these observed deviations from predictions include increased plumage insulation (Dawson and Carey 1976, Swanson 1991), behavioral adaptations (e.g., ptiloerection, Hohtola et al. 1980; shivering thermogenesis, Hohtola 2004), and various nonshivering processes (e.g., chemical thermoregulation; Dawson and O'Connor 1996, Vézina et al. 2011).

Although environmental conditions across their nonbreeding ranges undoubtedly induce different metabolic demands (Table 5.1), the range of demands was not reflected by inherent differences in basic metabolic parameters in the two subspecies. In a similar comparison, the BMR of wild Red Knots of the northerly-wintering *islandica* subspecies was greater than that of tropical-wintering *canutus* (Piersma et al. 1996a), but these measures equalized in captivity when the two subspecies were maintained under identical conditions (Piersma et al. 1996a). Red Knots exhibit a wide range of metabolic response to temperature, and these responses are dictated by acclimatization to prevailing environmental conditions (Vézina et al. 2006, 2007, 2011). The BMR of cold-acclimated Red Knots was 26% higher than warm-acclimated Red Knots (Vézina et al. 2006), and cold-acclimated birds exhibited greater cold tolerance and had higher summit metabolic rates than warm-acclimated birds (Vézina et al. 2006). These results demonstrate the degree to which BMR is phenotypically modulated in migratory shorebirds. Given the predicted differences in metabolic rates of wild Rock Sandpipers (Table 5.1) and the equality of values when held identically in captivity, our results likewise suggest that we measured metabolic outputs of identically acclimatized birds across a range of conditions within the phenotypic breadth of each subspecies.

The thermal environments at the extremes of the two subspecies' nonbreeding ranges appear to be very different (i.e., upper Cook Inlet and Humboldt Bay; Table 5.1), but to a species adapted to the climatic extremes of high-northern latitudes such differences may not be sufficiently strong to induce a detectable metabolic response. Like other high-latitude breeding shorebirds, the two Rock Sandpiper subspecies that we studied must contend with a wide array of environmental conditions throughout their annual cycle (Wiersma and Piersma 1994, Piersma 2002), likely inducing selection for phenotypic flexibility in metabolic output (Kersten and Piersma 1987, Piersma et al. 1995, Piersma 2002). Our initial belief was that strongly contrasting winter conditions would induce fixed metabolic differences between the subspecies, but, as with other shorebird species, it is instead probable that a wide range of cross-seasonal environmental conditions more strongly regulates the metabolic output of Rock Sandpipers (Piersma 1996).

Given the equality of the two subspecies' metabolic capacities, it is likely that ecological factors more strongly determine their nonbreeding distributions. Rock Sandpiper nonbreeding distributions are influenced by myriad biotic and abiotic interactions (e.g., predator abundance, storm severity and duration, food abundance, day length, wind speed, and fasting endurance), and metabolic capacities are undoubtedly just part of the complex process that regulates their distributions. For instance, van Gils et al. (2005b, 2005c) demonstrated that the distribution of Red Knots in the Dutch Wadden Sea is primarily explained by the abundance, quality, and digestibility of their prey and the interaction of these prey characteristics with phenotypically flexible body components like gizzard size. For free-living *ptilocnemis* Rock Sandpipers, acclimatization to low temperatures likely promotes the higher metabolic outputs necessary to occupy upper Cook Inlet during winter. Because of the high energetic demands of wintering at this site (Table 5.1), foraging-related adaptations likely also support their unique nonbreeding distribution. For example, individuals of the *ptilocnemis* subspecies forage exclusively on mudflats in upper Cook Inlet whereas individuals of the *tschuktschorum* subspecies primarily forage on rocky intertidal substrates (Gill et al. 2002), and these habitat preferences are reflected in the two subspecies' winter plumages. The pale gray plumage of *ptilocnemis* provides crypsis on foraging substrates (mudflats) and roosting sites (sea ice and snow-covered shorelines), whereas *tschuktschorum*'s darker plumage blends to its preferred rocky shoreline habitat. Accordingly, their separate distributions may reflect subspecific differences in phenotypically conserved traits like plumage patterns. Given their discrete nonbreeding foraging-habitat preferences (mudflat vs. rocky intertidal), the two subspecies also likely exhibit different foraging ecologies (e.g., search efficiency, prey preferences, prey intake, and processing rates). In the absence of subspecific differences in basic metabolic traits, phenotypically mediated adaptations that allow Rock Sandpipers to safely and predictably satisfy their energetic requirements are instead the likely determinants of subspecific winter distributions.

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CHAPTER 6

Ways to be different: foraging adaptations that facilitate high intake rates in a northerly-wintering shorebird compared to low-latitude conspecifics

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Abstract

At what phenotypic level do closely related subspecies that live in different environments differ with respect to food detection, ingestion, and processing? This question motivated an experimental study on Rock Sandpipers (*Calidris ptilocnemis*), the most northerly wintering shorebird in North America. The species' nonbreeding range spans 20 degrees of latitude, the extremes of which are inhabited by two subspecies: *Calidris p. ptilocnemis* that winters primarily in upper Cook Inlet, Alaska (61°N), and *C. p. tschuktschorum* that overlaps slightly in range with *C. p. ptilocnemis* but whose range extends much farther south (~41°N). In view of the strongly contrasting energetic demands of their distinct nonbreeding distributions, we assessed which aspects of Rock Sandpiper foraging ecology differed between these two subspecies. Three experiments addressed behavioral, physiological, and sensory aspects of the species' foraging ecology, and we used the bivalve *Macoma balthica* for all trials, a prey item commonly consumed by both subspecies. The subspecies were similar in structural size and had equally sized gizzards, but *ptilocnemis* were 10–14% heavier than their same-sex *tschuktschorum* counterparts. *Ptilocnemis* Rock Sandpipers consumed a wider range of prey sizes, had higher rates of energy intake, processed shell waste at higher rates, and handled prey more quickly. Notably, however, the two subspecies did not differ in their abilities to find buried prey. Differences in body mass likely result from hypertrophy of digestive organs (e.g., intestine, liver) related to digestion and nutrient assimilation. These observations fit predictions regarding inherent adaptations in *ptilocnemis* that sustains the consistently higher metabolic demands dictated by their northerly nonbreeding life history. Given the previously established equality of the two subspecies' metabolic capacities, we propose that the high-latitude nonbreeding range of *ptilocnemis* Rock Sandpipers is primarily facilitated by digestive (i.e., physiological) aspects of their foraging ecology rather than behavioral or sensory aspects. These results represent unique evidence of subspecific differences in feeding ecologies that support observed biogeographic patterns.

Introduction

The ways in which animals satisfy their daily energy requirements ultimately influences nearly every aspect of their ecology (Stephens and Krebs 1986, Piersma and van Gils 2011). Given the imperative to remain in energy and nutrient balance, an animal's foraging ecology is subject to strong selection pressure that can reflect an optimization of behavioral, environmental, and physiological stimuli (Perry and Pianka 1997). The differential expression of these stimuli with respect to an animal's life history forms a rich basis for many ecological studies, and has yielded insights into diverse topics like biogeography (Baduini and Hyrenbach 2003, Luck and Daily 2003, Darimont et al. 2004, Costa et al. 2008), interspecific competition (Johnson 2001, Switalski 2003), and intraspecfic niche differentiation (Smith and Skúlason 1996, Bolnick et al. 2003, Svanbäck and Persson 2004, Berumen et al. 2005). More fundamentally, such inquiry has demonstrated the evolutionary significance of seemingly minute differences in foraging adaptations between closely related organisms, describing patterns and traits that help drive speciation (Schluter 1995, Grant 1999).

Due to their relative ease of observation and diversity of foraging strategies, shorebirds (Charadriiformes) are common subjects of foraging studies (Goss-Custard et al. 2006, Colwell 2010). During the nonbreeding season, shorebirds experience relatively high energetic demands (Kersten and Piersma 1987), a natural history trait that also makes shorebirds ideal study subjects of the interplay between an organism's foraging ecology and their energetic requirements (Kvist and Lindström 2003, van Gils et al. 2005b, Yang et al. 2013). Previous studies of intake rates as a function of food abundance in shorebirds during the nonbreeding season have demonstrated that intake rates rapidly increase with prey density, but quickly reach an asymptote beyond which intake rates stabilize. The asymptote defines a constraint to ever-increasing rates of prey intake, constraints which in shorebirds are typically caused by prey handling (Zwarts and Esselink 1989) or digestive (Zwarts and Dirksen 1990, van Gils et al. 2003a) limitations. Such observations conform to the more general patterns first derived by Holling (1959) and elucidated in shorebirds by others (e.g., Piersma et al. 1995; Lourenço et al. 2010). In its simplest form, observations are modeled by the equation:

$$\frac{N}{T} = \frac{aD}{1 + aT_hD}$$

In this model, the number of prey consumed (N) over total time (T) is described as a function of a predator's instantaneous area of discovery (a; $\mathrm{m}^2\ \mathrm{s}^{-1}$; also termed search efficiency; Hassell 1982; van Gils et al. 2005c), prey density (D; m^{-2}), and handling time per prey item (T_h; s).

For molluscivorous shorebirds that must crush their hard-shelled prey in their muscular gizzard, the physical act of crushing and processing prey shell waste is the digestive bottleneck that limits intake rate (Wanink and Zwarts 1985, van Gils et al.

2003a, 2005c). Because molluscivorous shorebirds efficiently exploit small prey even at relatively low densities, their energy intake rates are not typically limited by their ability to find or handle prey but instead by the interaction between the size of their gizzard and the quality (i.e., energy per unit shell mass [kJ g^{-1}]) of the prey itself (Zwarts and Blomert 1992, Yang et al. 2013). The interaction of these factors provides a fruitful experimental context to explore the life-history consequences of these traits within and among species (Dekinga et al. 2001, van Gils et al. 2003b, 2005b, Piersma et al. 2003, Quaintenne et al. 2010). Most previous studies comparing the foraging ecologies of closely-related subjects examined differences in the context of sympatric niche differentiation (Huey and Pianka 1981, Pulliam 1985, Benkman 1993, Labropoulou and Eleftheriou 1997, Kawamori and Matsushima 2012).

Here, we compare two subspecies of the Rock Sandpiper (*Calidris p. ptilocnemis* [hereafter *ptilocnemis*] and *Calidris p. tschuktschorum* [hereafter *tschuktschorum*]), subspecies that are equipped with nearly identical foraging 'tools' (i.e., body size, bill morphology, diets, foraging behaviors), but which endure strongly contrasting environmental conditions across their largely allopatric nonbreeding ranges. We conducted experimental foraging trials on identically-maintained captive individuals of both Rock Sandpiper subspecies to determine if their distinct nonbreeding life histories were reflected by inherent differences in their foraging ecologies. First, we simultaneously offered individual birds different sized unburied *Macoma* to determine size preferences when choice was an option. We predicted that both subspecies would maximize intake rates by selecting the highest quality prey available when given a choice. We next conducted long-term trials where choice was not an option, wherein birds were offered *ad libitum* quantities of unburied *Macoma* of just one size. These trials enabled us to estimate maximum rates of energy and shell waste intake as a function of prey size. Under such conditions, these rates are defined by physiological aspects of digestive capacity. In molluscivorous shorebirds, digestive capacity is both a function of a bird's ability to crush hard-shelled molluscs in their gizzards and their ability to assimilate nutrients and excrete wastes (Battley and Piersma 2005). Because the size of a shorebird's gizzard is directly related to its ability to crush prey (Piersma et al. 1993, van Gils et al. 2005a), these dual processes can be partially disentangled via the non-invasive measurement of gizzard size (e.g., Dietz et al. 1999). Given their consistently higher winter metabolic demands and near complete reliance on *Macoma* as prey in upper Cook Inlet, Alaska, we predicted that *ptilocnemis* would achieve higher rates of energy intake and process shell waste more quickly than *tschuktschorum*. Finally, we conducted trials involving buried *Macoma* of different sizes and densities to determine each subspecies' intrinsic ability to find and handle prey (i.e., functional response), responses measured by estimating the parameters a, T_h, and T_s (search time per prey item [s]). Because *ptilocnemis* exploits primarily mudflat habitats and *tschuktschorum* uses primarily rocky intertidal habitats, we predicted that *ptilocnemis* would more efficiently find prey buried in soft sediments (i.e., they would have a higher instantaneous area of discovery, a [Piersma et al. 1995], and lower T_S), and handle and consume discovered prey more quickly compared to *tschuktschorum* (i.e., they would have a lower T_h). Taken together, differences between the subspecies in these trials would provide measures of the relative importance of behavioral, physiological, and sensory aspects of Rock Sandpiper foraging ecology on the species' biogeography.

The Study System

Rock Sandpipers are the shorebird species with the most northerly nonbreeding distribution in the Pacific Basin, common at locations along the eastern Pacific coast from 61°N (Ruthrauff et al. 2013c) to ~40°N (Gabrielson and Lincoln 1959, Paulson 1993). There are four recognized subspecies of Rock Sandpiper (Conover 1944, American Ornithologists' Union 1957), and the extremes of the species' nonbreeding distribution are occupied by *ptilocnemis* to the north and *tschuktschorum* to the south (Gill et al. 2002). This wide latitudinal range exposes these two subspecies to starkly contrasting environmental conditions, and is reflected by predicted mid-winter maintenance metabolic rates over 30% higher in *ptilocnemis* compared to *tschuktschorum* (see table 1, Ruthrauff et al. 2013a). Despite these predicted differences in site-specific metabolic rates, the basic metabolic capacities of these two subspecies do not differ. Ruthrauff et al. (2013a) determined that the basal metabolic rates, metabolic responses to cold, and thermal conductance values did not differ between the two subspecies maintained under identical laboratory conditions. It was posited that under natural settings the two subspecies acclimated to their respective environmental conditions, a phenotypically flexible response that enables increased metabolic capacities at lower temperatures (Vézina et al. 2011, Ruthrauff et al. 2013a). Because the two subspecies do not differ in their intrinsic energetic capacities, we hypothesized that the consistently higher energetic demands of *ptilocnemis* during winter compared to *tschuktschorum* would be supported by innate differences in foraging ecologies.

Although the winter (October–April) nonbreeding ranges and habitat affinities of *ptilocnemis* and *tschuktschorum* have received little formal study (Gill et al. 2002, Ruthrauff et al. 2013a), observations suggest broad contrasts between the subspecies in these traits. *Ptilocnemis* is distributed primarily on mudflat habitats in upper Cook Inlet, Alaska (61°N, 151°W), during winter (Gill et al. 2002, Ruthrauff et al. 2013c), sites with the coldest winter temperatures regularly experienced by any shorebird species (Ruthrauff et al. 2013b). *Tschuktschorum*, in contrast, is distributed as far south as northern California, primarily on rocky intertidal habitats (~41°N;Paulson 1993; Gill et al. 2002). The two subspecies probably co-occur at the extremes of their distributions, but their winter distributions and habitat affinities are largely distinct. The principal prey items exploited by Rock Sandpipers during the nonbreeding season are hard-shelled molluscs. The small bivalve *Macoma balthica* constitutes the bulk of the *ptilocnemis* diet on the mudflats of upper Cook Inlet (Gill et al. 2002, Ruthrauff et al. 2013c), while *tschuktschorum* consumes invertebrates associated with rocky intertidal habitats (e.g., molluscs [*Mytilus* sp., *Littorina* sp.] and crustaceans [barnacles, isopods]; Gill et al. 2002). The two subspecies co-occur in spring and fall at migratory stopover sites, however, where both consume *Macoma* (DRR and REG pers. obs.), making this familiar food resource an ideal subject of comparative foraging trials between the two subspecies.

Methods

Experimental animals and maintenance

We captured 30 adult Rock Sandpipers on 28 August 2009 at a post-breeding site on the Yukon Delta National Wildlife Refuge, Alaska (61° 19'N, 165° 47'W), and acclimated the birds to captivity prior to transporting them to the Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands, on 21 September 2009. We determined the subspecific identity of birds based on diagnostic plumage characteristics of the wing and mantle (Gill et al. 2002), and sex via standard PCR techniques (Griffiths et al. 1996). Female Rock Sandpipers are larger than males (2–3% greater in wing length and tarsus, ~13% in bill length; appendix 2, Gill et al. 2002), and *ptilocnemis* individuals are slightly larger than *tschuktschorum* individuals (5–8% greater in the same measures; appendix 2, Gill et al. 2002).

In 2010, maximum feeding rate trials were conducted in outdoor aviaries, but the functional response experiments in 2011 were conducted in indoor aviaries maintained at 14°C, conditions under which the birds were also maintained. See Vézina et al. (2006) for aviary details. When not subject to experimental trials, all Rock Sandpipers were fed commercial fish chow (47% protein; manufactured by Skretting, Fontaine-les-Vervins, France). Such soft diets caused the gizzards of a related shorebird, the Red Knot (*C. canutus*), to atrophy (Piersma et al. 1993), and in order to rebuild and maintain the gizzards of Rock Sandpipers we slowly and permanently switched the diet of experimental birds from fish chow to hard-shelled bivalves. Because *Macoma balthica* is the preferred bivalve prey of Rock Sandpipers (Gill et al. 2002), we exclusively used *Macoma* as prey during all experimental trials. We harvested *Macoma* at the Baie de Somme estuary, France (50.2°N 1.6°E), for trials conducted in 2010, and near the mouth of the Kasilof River, Alaska (60.4°N 151.3°W), for trials conducted in 2011. All *Macoma* were maintained at 8°C in large saltwater aquaria at NIOZ. We were unable to reliably collect enough *Macoma* to sustain birds throughout the trial periods, and instead provided *Mytilus edulis* (2010) and a mix of *Cerastoderma edule* and *Mya arenaria* (2011) collected near the island of Texel, The Netherlands. To determine the quality of the *Macoma* prey offered in all trials, we calculated the relationship of shell length to *Macoma* ash-free dry mass (AFDM) and shell mass (i.e., ballast) using standard techniques (Zwarts 1991, van Gils et al. 2005c).

To satisfy underlying model assumptions, we calculated these relationships after log transforming (base 10) values of AFDM and shell ballast (Figure 6.1). We back transformed these estimates to yield outputs in mg. To link intake to metabolizable energy, we converted estimates of shell ballast intake into their energetic equivalent (kJ g^{-1} shell ballast) assuming an energy density of 22 kJ g^{-1} ash-free dry mass *Macoma* flesh (Zwarts and Wanink 1993, van Gils et al. 2005c), and an assimilation efficiency of 0.8 (Yang et al. 2013).

We measured the response of experimental birds to their diet switch by measuring their gizzards using ultrasound techniques outlined by Dietz et al. (1999). We measured the height and width of the gizzards of all birds immediately prior to switching diets and again upon completion of foraging trials. All measurements were collected by AD, and birds were measured using a system that ensured that AD was ignorant of the identity of each bird as they were measured.

Experimental Trials

We randomly assigned individuals to experimental trials from the pool of potential birds based on subspecies and sex, selecting two members of each subspecies of each sex for all experimental trials (eight individuals total). Birds required about three to four weeks to permanently switch diets from fish chow to hard-shelled bivalves, but some individuals had difficulty switching diets and could not maintain healthy body mass. These birds were replaced with new individuals in the experimental trials until we could maintain the body mass of eight Rock Sandpipers on a bivalve diet for all trials. In 2010, we were only able to maintain one *tschuktschorum* female on a bivalve diet, and so we included a third *ptilocnemis* female in these trials. We held four birds per aviary, and provided constant access to fresh and salt water. We removed food from the aviaries at 0800h to ensure that birds were hungry and foraged in a motivated manner during all feeding trials. Trials commenced at 1400h, and trials were conducted simultaneously (two at once; 2010) or consecutively (2011) as dictated by logistic practicalities. Upon completion of each trial, birds were returned to their aviaries and provided food.

We sorted *Macoma* into four size classes for trials in 2010, using a sieve to speed separation of the two smallest size classes, and hand sorting the two larger size classes. This method created slight overlap between adjacent size classes (mean lengths 7.5 ± 0.1 SE mm, 8.8 ± 0.1 SE mm, 11.4 ± 0.1 SE mm and 13.5 ± 0.1 SE mm for size classes 1–4, respectively). We conducted trials from 24–27 March 2010 to determine the prey size preferences of Rock Sandpipers. We presented each bird ten *Macoma* of each size class in four identical petri dishes simultaneously. We randomized the placement of dishes with respect to each other in each trial, and recorded each trial using digital video to assess the order in which *Macoma* were sampled. Upon completion of each trial we counted the number of each size class that was consumed. Trials lasted 15 minutes, and we performed one trial per bird per day across three consecutive days.

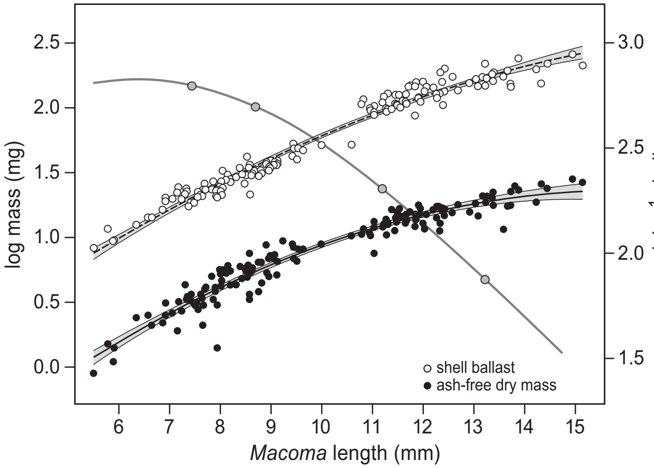

Figure 6.1. Shell ballast (mg; white dots) and ash-free dry mass (mg; black dots) as a function of shell length (mm) for *Macoma balthica*. Response variables are on the base-10 log scale (see Methods). Relationship calculated from *Macoma* used in trials to determine maximum intake rates of *ptilocnemis* and *tschuktschorum* Rock Sandpipers. The solid line (±95% confidence interval) describes the polynomial relationship $log(AFDM) = -1.624 +0.372*(shell\ length) - 0.012*(shell\ length)^2$, and the dotted line (±95% confidence interval) describes $log(shell\ ballast) = -0.684 +0.327*(shell\ length) -0.008*(shell\ length)^2$. Back-transformed estimates of the ratio AFDM:shell ballast were multiplied by metabolizable energy content to represent *Macoma* quality (kJ g^{-1} shell; see Methods), represented on the right-hand axis by the grey line; grey dots mark quality estimates for the four sizes of *Macoma* used in these trials.

Despite conducting initial unrecorded 'training' exercises, these first trials were characterized by an obvious learning period that was reflected by an unwillingness to feed. No *Macoma* were consumed in 14 of 28 prey size selection trials, but such reluctance dropped as birds acclimated to experimental conditions. Thereafter, only 16 of 64 maximum intake trials and 3 of 144 functional response trials yielded no consumptions. One bird, a *ptilocnemis* male, never consumed any *Macoma* in the prey selection or maximum intake trials; this bird was not included as a subject in the functional response trials. Trials where no *Macoma* were consumed were removed from all subsequent analyses.

Using the same group of eight birds from the size choice trials, we conducted trials from 30 March–6 April 2010 to determine the long-term maximum intake rate (mg AFDM *Macoma* s^{-1} and mg *Macoma* shell s^{-1}) of Rock Sandpipers. For these trials, birds were presented a petri dish containing *Macoma* of just one size class. We provided *Macoma* at *ad libitum* quantities (30 to 200 clams, depending on size class) to ensure that a bird could not consume all the prey during a 45-minute trial. We conducted two trials per size class for each bird, and performed one trial per bird per day across eight consecutive days. We recorded each trial using digital video, and abutted a clear plastic barrier against the side of the petri dish facing the video camera to orient the birds such that we could clearly observe all foraging behaviors.

During the maximum intake trials, one *ptilocnemis* male never consumed any *Macoma* in the eight trials in which it was involved. There were eight other trials in which no prey were consumed, one involving size 3 *Macoma* and seven involving size 4 *Macoma*. Five of these eight instances occurred during trials with the two male *tschuktschorum* birds. These two birds never consumed any size 4 *Macoma*. In another trial involving one of these birds, the bird fed reluctantly, consumed only eight size 2 prey items, and spent most of the trial roosting; this trial was also excluded from analysis. Thus, in total we analyzed video from 47 of the 64 maximum intake trials. Exceptions aside, birds fed in a motivated manner during the 45-minute long trials. On no occasion were birds able to consume all the *Macoma* provided during a trial, and the average ±SE number of *Macoma* of size 1, 2, 3, and 4 consumed per trial was 133.5 ±5.9, 78.9 ±4.5, 19.3 ±2.3, and 7.4 ±1.9, respectively.

We conducted trials to determine the functional response of Rock Sandpipers to variation in the density and size of *Macoma* from 9–28 November 2011. We followed the same diet switching protocol as in 2010, but to ease this process we systematically included four birds that participated in 2010 trials to help 'train' four other randomly selected birds. In these trials, *Macoma* were buried in plastic tubs (40 cm wide × 60 cm long × 12 cm deep) filled with sand that we moistened with seawater to approximate natural sandflat conditions. We divided *Macoma* into two non-overlapping size classes (8–10 and 11–13 mm) by hand. We buried all *Macoma* in their natural orientation at 2 cm depth immediately prior to the start of each trial, and randomly distributed the *Macoma* in the tubs based on coordinates across a 1-cm × 1-cm grid. We measured the functional response of Rock Sandpipers to two size classes (see above) of buried prey across three prey densities: 67, 133, and 208 *Macoma* m^{-2} (16, 32, and 50 *Macoma* $tray^{-1}$, respectively). We conducted three trials per bird at each of the six combinations of *Macoma* size and density, and recorded trials using digital video. We placed a small mirror against the back of the tub containing the *Macoma* to ensure that we could clearly observe foraging behaviors regardless of a bird's orientation to the video camera. We observed the trials through a two-way mirror, and trials ended after ten minutes or once five *Macoma* had been consumed, whichever was first. We performed one trial per bird per day across a period of 20 days.

In only 19 of 144 trials did birds consume fewer than 5 *Macoma* in the 10-minute trial period; as with the maximum intake trials, most (n = 14) of these trials involved male *tschuktschorum* subjects. These birds could typically only swallow two or three size 2 prey items before requiring a digestive pause. Every size 1 *Macoma* (8–10 mm) that was brought to the surface of the sand was consumed, but 94 size 2 *Macoma* (11–13 mm) that were brought to the surface of the sand were rejected across 31 trials. *Macoma* were rejected by females and males of both subspecies, and the average length of the rejected *Macoma*s was 12.2 ±0.1 mm.

Video analysis and statistical analyses

Across all trials, video observation conditions were excellent, and before/after counts of *Macoma* corroborated our video observations. We replayed the video of each feeding trial at slow speed and recorded the number and duration of relevant behaviors using JWatcher software (Blumstein and Daniel 2007). In the maximum intake rate trials, we divided the number of *Macoma* consumed over the duration between the consumption of the first and last *Macoma* in each trial. We applied the results of our *Macoma* prey assessments (i.e., mg AFDM and mg shell ballast as functions of shell length) to the mean *Macoma* size for each of the four size classes, and integrated these values to estimate the AFDM (mg) and shell ballast (mg) for each size class. We applied these estimates to calculate the intake rate of *Macoma* flesh (mg AFDM *Macoma* s^{-1}) and shell (mg shell s^{-1}). For the functional response trials, we follow the terminology of Piersma et al. (1995), which derive from Holling's original calculations (1959). We calculated the time each bird spent searching (total time in sand-filled tub – [time loafing + time in digestive pause + time handling discovered prey]) and the handling time for each *Macoma* discovered and brought to the surface of the sand. We sieved each tub following each trial to determine how many *Macoma* were discovered but not consumed and how many were discovered and consumed. We synthesized these data to calculate the average search time per *Macoma* discovered (T_s, in s *Macoma*$^{-1}$) per trial and the handling time per *Macoma* swallowed (T_h, in s *Macoma*$^{-1}$) per trial. We calculated the instantaneous search area a using the formula

$$a = \frac{1}{T_s D}$$

following van Gils et al. (2005c) and Lourenço et al. (2010). Search time, handling time, and instantaneous search area were the response variables in the functional response trials.

We fit generalized linear mixed-effects models to assess the effect of relevant biological parameters on the foraging behaviors of Rock Sandpipers. We followed the multi-model information-theoretic analytical approach outlined in Burnham and Anderson (2002) to examine support for our hypotheses about factors affecting the foraging ecology of Rock Sandpipers. For each analysis, we included biologically relevant combinations of the explanatory variables. For the maximum intake rate trials, these included sex, subspecies, and *Macoma* size. We also included body mass as a covariate in all maximum intake trials to control for potential size-related differences in metabolic rates (e.g., West et al. 2002; McKechnie and Wolf 2004) that might affect intake rates. For the functional response trials we included sex, subspecies, *Macoma* size, and *Macoma* density as explanatory variables. To better fit underlying model assumptions, we transformed search time, handling time, instantaneous search area, and *Macoma* density using base-10 log transformations. We gauged support for each model based on Akaike's Information Criterion adjusted for small sample size (AIC_c) and based model inference on Akaike weights (w_i; Burnham and

Anderson 2002). We averaged our model results in proportion to Akaike weights to generate overall parameter and prediction estimates and considered parameters to be biologically meaningful if their model-averaged 95% confidence intervals did not overlap zero. We conducted all analyses in R version 3.0.1 (R Development Core Team 2013), fit mixed-effects models using the lme4 package (Bates et al. 2013), and averaged model outputs using the AICcmodavg package (Mazerolle 2013). We followed the exclusion approach of Mazerolle (2013) for calculating model-averaged parameter estimates for model sets that included interaction terms. Estimates are presented as mean ± SE.

Results

Size dimorphism between birds included in the experiments followed the sex-specific and subspecific patterns described by Gill et al. (2002). The average length of exposed culmen was 34.2 ±1.1 mm and 29.4 ±0.8 mm for female and male *ptilocnemis*, respectively, and 34.0 ±0.2 mm and 27.3 ±0.6 mm for female and male *tschuktschorum*, respectively. Average body mass at the end of all feeding trials was 82.7 ±0.1 g for *ptilocnemis* females, 75.1 ±0.03 g for *ptilocnemis* males, 74.4 ±0.1 g for *tschuktschorum* females, and 64.8 ±0.1 g for *tschuktschorum* males. The height and width of the gizzards of experimental birds did not differ by sex or subspecies prior to the diet switch (all comparisons $P > 0.49$), but gizzards increased substantially when their diets were switched to hard-shelled prey. The height and width of experimental birds' gizzards increased an average of 35 ±8% and 27 ±6%, respectively, after switching diets (Figure 6.2). The gizzards of females increased more than males ($P < 0.01$ for height, $P < 0.05$ for width), but the gizzard sizes of the subspecies did not differ overall.

Prey quality and size selection

Prey quality was highest in the smallest *Macoma* size class (size 1; 2.80 kJ g^{-1} shell), and only slightly lower in size 2 *Macoma* (2.69 kJ g^{-1} shell). The larger size classes were progressively lower in quality: 2.30 kJ g^{-1} shell for size 3, and 1.87 kJ g^{-1} shell for size 4 (Figure 6.1). In prey size selection trials, birds did not necessarily investigate all four petri dishes prior to their first consumption, but instead discovered and sampled the dishes randomly. Nonetheless, the two smallest size classes of *Macoma* were overwhelmingly consumed in preference to the two larger size classes. Across the 14 trials in which *Macoma* were consumed, only four (2.9%) *Macoma* of the largest size class (size 4) were swallowed; 20 (14.3%) *Macoma* of the second largest size class (size 3) were consumed, and most of the two smallest sizes were consumed (125 [89.3%] and 114 [81.4%] for sizes 1 and 2, respectively). Small within-group sample sizes precluded statistical comparison, and we display summaries of the selection trials in Figure 6.3. In general, *ptilocnemis* consumed more *Macoma* across a wider size range than *tschuktschorum* (Figure 6.3).

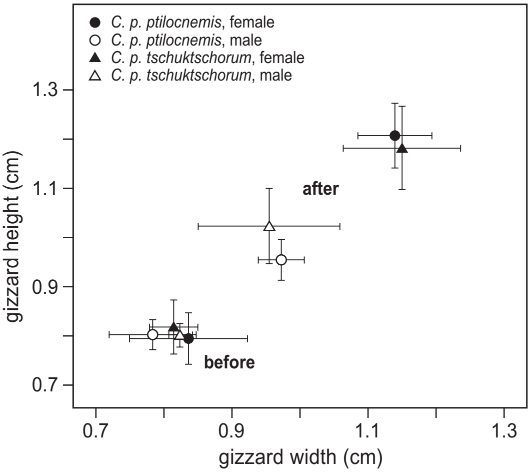

Figure 6.2. Differences in height and width of Rock Sandpiper gizzards when birds were switched from a diet of soft fish chow ('Before') to hard-shelled molluscs ('After'). Measures were made using ultrasonography (see Methods), and values represent mean ± SE. Birds from 2010 (diet of *Mytilus edulis*) and 2011 (diet of *Cerastoderma edule* and *Mya arenaria*) combined. Before (*n* = 14 measures) and after (*n* = 16 measures) measures derive from 12 individual birds, four of which were measured in both years and whose two measures were treated as independent samples.

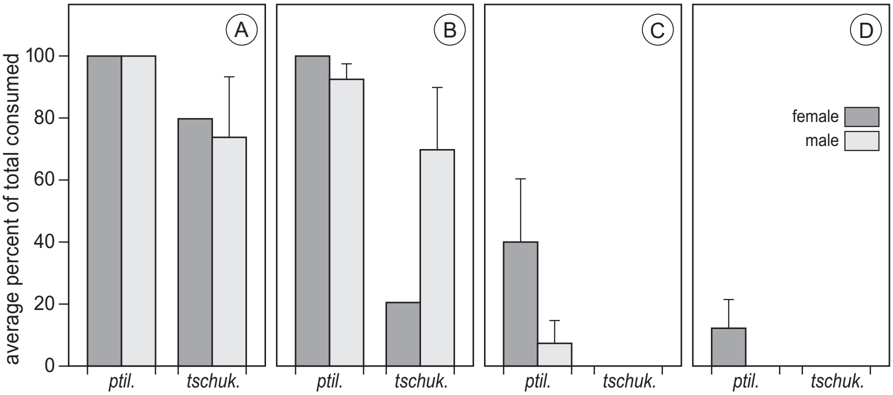

Figure 6.3. Prey size selection by male and female *ptilocnemis* ('*ptil*') and *tschuktschorum* ('*tschuk*') Rock Sandpipers. Birds were simultaneously offered four dishes, each containing 10 *Macoma* of one of four size classes, 1 (smallest; Figure 6.3A)–4 (largest; Figure 6.3D). Bars represent average ± SE proportion consumed of each size class across all trials. Only trials where at least one *Macoma* was consumed are depicted (*n* = 14 trials total, comprising 4 trials each by *ptilocnemis* females and males, 1 trial involving a *tschuktschorum* female, and 5 involving *tschuktschorum* males).

Maximum intake rate of exposed prey

The model selection process demonstrated strong support for the effect of prey size on both AFDM and shell ballast intake rates. The sum of model weights (Σw_i) for models including *Macoma* size was 1.0 for both response variables, but models containing subspecies ($\Sigma w_i = 0.64$ and 0.56 for AFDM and shell ballast, respectively) and sex ($\Sigma w_i = 0.30$ and 0.25 for AFDM and shell ballast, respectively) as covariates received less support. This was further demonstrated by the model-averaged parameter estimates for these variables (Table 6.1); only those for size and subspecies had 95% confidence intervals that did not overlap zero. Model-averaged parameter estimates indicated that the maximum intake rate of both AFDM and shell ballast was higher for the two smaller size classes of *Macoma* than the two larger sizes, and that intake rates for *tschuktschorum* were lower than those for *ptilocnemis* (Table 6.1; Figure 6.4). Maximum rates of ballast intake were achieved for all birds at prey size class 2, but AFDM intake rates were nearly identical for size classes 1 and 2 within each sex/subspecies group (Figure 6.4). The model-averaged point estimates of AFDM and ballast intakes were higher in *ptilocnemis* females than males, which were in turn higher than *tschuktschorum* females; *tschuktschorum* males had the lowest estimated maximum intake rates across all *Macoma* size classes. The 95% confidence intervals on these estimates did not overlap between female *ptilocnemis* and male *tschuktschorum* birds for both AFDM and ballast intake at *Macoma* size classes 1–3, and estimates for all other groups overlapped (Figure 6.4).

Table 6.1. Model-averaged parameter estimates and 95% confidence intervals from linear mixed-effect models used to assess factors influencing maximum intake rates (ash-free dry mass and shell ballast) for *ptilocnemis* and *tschuktschorum* Rock Sandpipers consuming *Macoma balthica*. We included biologically relevant combinations of body mass, *Macoma* size (classes 1 [smallest]–4 [largest]; see Figure 6.1), sex, and subspecies as fixed effects and individual birds as random effects in model sets. Only parameters with confidence limits that do not overlap zero are shown; units for parameters are mg s^{-1}.

	Intake Rate Model Set:	
Parameter	Ash-free Dry Mass	Shell Ballast
Macoma Size 3[a]	-0.059 (-0.074– -0.045)	-0.229 (-0.343– -0.116)
Macoma Size 4[a]	-0.097 (-0.114– -0.079)	-0.324 (-0.464– -0.183)
Subspecies[b]	-0.028 (-0.053– -0.002)	-0.188 (-0.375– -0.001)

[a] *Macoma size* 1 is the reference level.
[b] *Calidris ptilocnemis tschuktschorum* is the reference level.

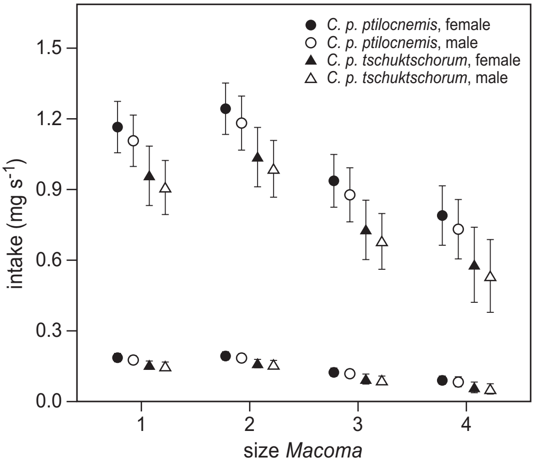

Figure 6.4. Predicted intake rates of shell ballast (upper symbols; values > 0.30 mg s^{-1}) and ash-free dry mass (lower symbols; values < 0.30 mg s^{-1}) for female and male *ptilocnemis* and *tschuktschorum* Rock Sandpipers. Size 1 *Macoma balthica* are the smallest and size 4 the largest (see Methods; Figure 6.1). Values represent model-averaged predictions ± 95% confidence intervals.

Functional response to buried prey

Exploratory plots indicated potential interactions between sex, subspecies, and *Macoma* size with respect to search time (T_S), and so we included models in our analysis of search time to account for these patterns. The model selection process yielded strong support for models including two-way interactions ($\Sigma w_i = 0.99$). Model-averaged parameter estimates indicated a strong interaction between sex and *Macoma* size, with males requiring more time to find larger prey (Table 6.2). Similarly, search time decreased as prey density increased, *tschuktschorum* required more search time to discover *Macoma* than *ptilocnemis*, and birds required more time to find size 2 *Macoma* than size 1 (Table 6.2). For small *Macoma*, model-averaged predictions of search time for females and males of both subspecies were similar and decreased as prey densities increased (Figure 6.5, upper half). For large *Macoma*, however, males of both subspecies (but especially *tschuktschorum*) required more time than females to find prey (Figure 6.5, lower half).

Due to confounding factors relating to the interaction between sex and prey size (see above), we modeled the effects of prey density, subspecies, and sex on a only for small (size 1) *Macoma*. There was little support for any of the predictor variables in our model set: the confidence intervals of the model-averaged parameter estimates overlapped zero for all predictor variables, and the intercept-only model was most highly supported in our modeling process ($w_i = 0.34$). The first key assumption of Holling's model is that a is constant across densities (Holling 1959), and our results

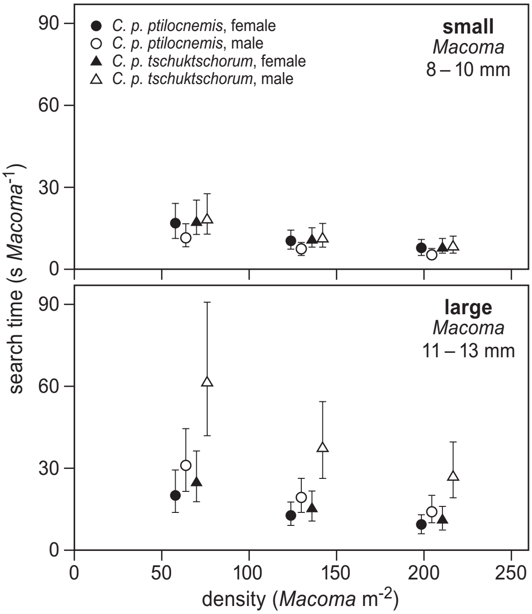

Figure 6.5. Predicted search time (s *Macoma*$^{-1}$) for female and male *ptilocnemis* and *tschuktschorum* Rock Sandpipers to find buried small (upper half) and large (lower half) *Macoma balthica*. Values represent model-averaged predictions ± 95% confidence intervals, and result from base-10 back-transformations of model output. Predictions estimated at densities of 67, 133, and 208 *Macoma* m^{-2}, and values are offset from each other for clarity.

support this assumption: the model-averaged predictions of *a* within each subspecies and sex group varied by less than 3% across the range of densities in our trials. Furthermore, these estimates were essentially equal across groups. At densities of 133 *Macoma* cm^{-2}, the back-transformed model-averaged predictions of *a* (cm^2 s^{-1}) were 7.79 (5.51–11.01 [lower and upper 95% confidence interval]) for *ptilocnemis* females, 8.13 (5.73–11.55) for *ptilocnemis* males, 7.02 (5.02–9.80) for *tschuktschorum* females, and 7.19 (5.05–10.22) for *tschuktschorum* males.

Upon bringing a prey item to the surface of the sand, larger prey required more handling time for Rock Sandpipers than smaller prey. Within a size class, handling time did not vary by prey density (Figure 6.6), satisfying the second key assumption of Holling's model (Holling 1959). The model selection process yielded strong support for an effect of *Macoma* size ($\Sigma w_i = 1$) on handling time and limited support for differences between the two subspecies ($\Sigma w_i = 0.5$). Along with estimates of the intercept, these were the only variables in the handling time analysis with model-averaged estimates and 95% confidence intervals that did not overlap zero. Parameter estimates indicated that larger *Macoma* required more handling time before swallowing than small *Macoma*, and that *tschuktschorum* handled *Macoma*

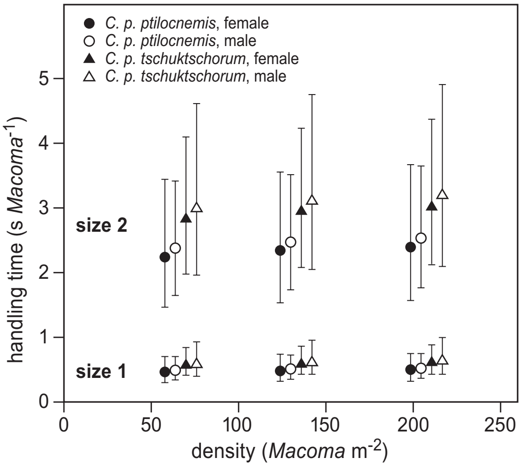

Figure 6.6. Predicted handling time (s *Macoma*$^{-1}$) for female and male *ptilocnemis* and *tschuktschorum* Rock Sandpipers before swallowing small (Size 1) and large (Size 2) *Macoma balthica*. Values represent model-averaged predictions ± 95% confidence intervals, and result from base-10 back-transformations of model output. Predictions estimated at densities of 67, 133, and 208 *Macoma* m^{-2}, and values are offset from each other for clarity.

Table 6.2. Model-averaged parameter estimates and 95% confidence intervals from linear mixed-effect models used to assess factors influencing the functional response of *ptilocnemis* and *tschuktschorum* Rock Sandpipers to buried *Macoma balthica*. We included biologically relevant combinations of *Macoma* density, *Macoma* size (classes 1 [small] and 2 [large]), sex, and subspecies as fixed effects and individual birds as random effects in model sets; search time (s *Macoma*$^{-1}$), handling time (s *Macoma*$^{-1}$), and instantaneous search area (cm^2 s^{-1}) were the response variables. All parameters in the analysis of the instantaneous search area overlapped zero except the intercept (0.848; 0.34–1.356). Search time models included interaction terms, but handling time and instantaneous search area models did not. Only parameters with confidence limits that do not overlap zero are shown; units for response variables are on the base-10 log scale (see Methods).

	Functional Response Model Set:	
Parameter	Search Time	Handling Time
Log10(*Macoma* Density)	-0.715 (-0.953- -0.476)	—
Macoma Size[a]	0.301 (0.201–0.401)	0.698 (0.650–0.746)
Subspecies[b]	0.162 (0.021–0.302)	0.206 (0.034–0.377)
Sex X Macoma Size[c]	0.355 (0.141–0.570)	Not applicable
Intercept	2.517 (1.994–3.04)	-0.454 (-0.121- -0.787)

[a] *Macoma* size 2 is the reference level.
[b] *Calidris ptilocnemis tschuktschorum* is the reference level.
[c] (Male X Size 2 *Macoma*) is the reference level.

longer than *ptilocnemis* (Table 6.2). These patterns were evident in plots of model-averaged prediction estimates; despite overlap in estimated 95% confidence intervals, the point estimates for handling time per swallowed prey item were lower for *ptilocnemis* than for *tschuktschorum*, and these estimates did not vary by prey density (Figure 6.6). Prey handling times averaged about five times longer (2.2–3.2 s) for large *Macoma* compared to small *Macoma* (.4–.6 s), and the 95% confidence intervals did not overlap between the two size classes (Figure 6.6).

Discussion

Compared to other closely related shorebirds, *ptilocnemis* and *tschuktschorum* Rock Sandpipers are unusual in that they possess nonbreeding habitat affinities (mudflat vs. rocky intertidal) that should seemingly favor disparate foraging modes (remote sense via probing vs. visual). Despite the differences in foraging habitat preferences, we found no parallel differences in the ability of the two subspecies to remotely sense buried prey. We detected no differences between the two subspecies in their instantaneous area of discovery, *a*, the functional response parameter that describes an organism's effective search area per unit time. We did, however, observe clear differences in other aspects of the foraging ecologies of *ptilocnemis* and *tschuktschorum* Rock Sandpipers. Results from experimental trials indicated that *ptilocnemis* had higher AFDM intake rates and shell processing capacities than *tschuktschorum* (Table 6.1, Figure 6.4), were more effective at handling prey (T_h; Table 6.2, Figure 6.6), and could consume larger prey than *tschuktschorum* (Figure 6.3). And although the instantaneous area of discovery did not differ between the subspecies, we noted apparent differences between the subspecies in the time necessary to find buried *Macoma* (T_s; Table 6.2, Figure 6.5). Taken together, differences between the subspecies reflect the importance of high sustained rates of energy intake for *ptilocnemis*.

The lack of difference in instantaneous search area between the subspecies, however, is more difficult to interpret. Such similarity may represent a relatively low importance of habitat-specific foraging adaptations (i.e., remote sense vs. visual cues) in Rock Sandpipers; with prey densities in upper Cook Inlet exceeding 400 *Macoma* m^{-2} (Ruthrauff et al. 2013c), detecting prey via remote sense may not be subject to strong selection pressure. Alternatively, given the reliance of *tschuktschorum* on probe-feeding during migratory staging periods in spring and fall, the similar subspecific values for instantaneous search area may instead reflect the shared importance of this trait between the subspecies. Affirming these interpretations requires additional study.

While differences in prey size preferences likely relate to physical limitations of smaller birds compared to larger birds (e.g., smaller gape and esophagus), other differences between the two subspecies do not obviously correlate with structural size. Maximum intake rates are primarily determined by the physical capacity of a bird's digestive 'machinery', and reflect physiological aspects of their foraging ecology (McWilliams and Karasov 2001, Battley and Piersma 2005). Alternatively, prey handling potentially represents a mix of behavioral (e.g., learned aspects related to orientation and mandibulation of prey items) and structural (e.g., intrinsic aspects of prey handling related to bill length or size of gape) adaptations. While within-sex differences between *ptilocnemis* and *tschuktschorum* in bill length and gizzard size (see Results) were small, differences in body mass between the trial subjects, however, were more pronounced. *Ptilocnemis* females and males were ~ 10–14% heavier than their same-sex *tschuktschorum* counterparts (see Results). Such differences suggest that physiological processes unrelated to structural size influence aspects of Rock Sandpiper foraging ecologies, especially maximum intake rates. As indicated by ultrasound measurements (Figure 6.2), gizzards may have reached an upper (and equal) size limit in both subspecies, and differences in body mass may reflect subspecific differences in other digestive organs that facilitate higher intake rates in *ptilocnemis* (e.g., Diamond 2002, Battley and Piersma 2005). For example, in a comparison of nonbreeding populations of the closely-related Purple Sandpiper (*C. maritima*) from Norway and Scotland, Summers et al. (1998) detected no difference in stomach mass (primarily composed of gizzard) between individuals from the two locations, but birds from Norway had significantly heavier livers and heavier and longer intestines than birds from Scotland. These differences were interpreted as a flexible phenotypic response to the higher rates of food intake needed to satisfy the higher energetic demands of wintering in Norway (Summers et al. 1998). We did not sacrifice the birds at the end of the trials to compare the morphologies of relevant digestive organs, but given the similarity between the subspecies in sex-specific structural and gizzard sizes, it is our belief that differences in body mass between the trial birds represents a hypertrophy of digestive organs that facilitate higher intake rates in *ptilocnemis*. Such phenotypic changes in gut morphology and function are well documented in many species in response to a variety of environmental and life-history stimuli (Dykstra and Karasov 1992, Starck 1999, Clissold et al. 2013, Price et al. 2013). However, given the identical holding conditions of our experimental setup, differences between the subspecies noted herein instead appear to reflect intrinsic adaptations rather than phenotypic responses.

In the functional response trials, it was counterintuitive that larger prey items with a greater cross-sectional area should seemingly have been more difficult for substrate-probing shorebirds to find. Upon closer examination of trial videos, it was evident that longer search times simply resulted from underlying differences in prey size preferences. During trials involving large (size 2) buried *Macoma*, it was clear when buried prey items were discovered: birds would widen the gape of their bill, cease probing, and reposition their head and feet to more easily extract the *Macoma* from the sand. Just as shorebirds do in the wild, these birds would then often assess the size of the *Macoma* while the prey still sat below the surface of the sand, reject it in place, and resume their search for additional (smaller) prey items. Because birds did not bring such large prey items to the surface of the sand where they were visible to us, we could not be certain that they had in fact encountered a prey item. Hence, such behaviors inflated the amount of time that these birds searched before apparently 'finding' a prey item (i.e., raised the item to the surface).

It was our perception that smaller Rock Sandpipers (especially *tschuktschorum* males) more often rejected large buried *Macoma* in the functional response trials, a result that was reflected by a perceived increase in search time (Table 6.2, Figure 6.5) and by the positive interaction between sex and *Macoma* size (i.e., males and large *Macoma*s; Table 6.2). These findings were meaningful in the context of prey size thresholds, but obscure unbiased assessment of instantaneous search area. To avoid such biases, we parsed the dataset to focus only on trials with small *Macoma*, which were never rejected by any birds during the trials, to assess factors influencing a. Contrary to our prediction, we found no evidence of a difference between the subspecies in their intrinsic search efficiencies. Thus, although the two subspecies have different intake rates, evidence suggests that this derives from differences in digestive capacities and not sensory differences related to their ability to find buried prey.

Because AFDM and shell ballast are allometric, non-linear functions of shell length (Figure 6.1), the ratio of AFDM to ballast decreases as *Macoma* size increases. As such, it is instructive to view prey intake both as a function of its profitability (energy intake as a function of searching and handling time) and its quality (energy intake as a function of shell ballast; both definitions *sensu* van Gils et al. 2005c). For instance, model results indicate that a female *ptilocnemis* Rock Sandpiper requires about 3.5 s more time to find, handle, and swallow large *Macoma* compared to small *Macoma*. Although more costly with respect to foraging time, on a per-*Macoma* basis such a strategy yields higher short-term rates of energy intake (1.03 mg AFDM s^{-1} for size 2 compared to 0.83 mg AFDM s^{-1} for size 1). For digestively constrained foragers like Rock Sandpipers, however, rates of energy intake are better predicted over longer durations as a function of prey quality (van Gils et al. 2005c, Quaintenne et al. 2010), a relationship that maximizes the ratio of energy to shell ballast. In the aforementioned example, short-term rates of ballast intake are nearly 30% higher (8.34 mg shell ballast s^{-1} compared to 5.80 mg shell ballast s^{-1}) for the same bird consuming size 2 *Macoma* compared to size 1 *Macoma*. Thus, long-term prey selection on the basis of energy per unit shell ballast maximizes energy intake with respect to ballast intake, effectively prolonging the duration over which consumers can forage before requiring a digestive pause.

In this context, Rock Sandpipers of both subspecies exhibited a clear preference for smaller sized *Macoma* across all experimental trials, an indication that birds selected prey based on quality over profitability. The highest AFDM intake rates for all birds in the maximum intake rate trials occurred at the two smallest prey size classes (Figure 6.4), but the highest ballast intake rates occurred at the second size class alone (Figure 6.4). If energy intake rates are equal between two size classes, birds ought to prefer the size that is easier to crush and process; as a function of ballast intake, smaller *Macoma* are the easiest to crush (Piersma et al. 1993) and provide the highest ratio of energy to shell waste (Figure 6.1). In the size selection trials, the smallest sized *Macoma* were consumed in preference to the larger sizes (Figure 6.3), supporting our prediction that prey size preferences would reflect prey quality. These preferences were evident for males and females of both subspecies (Figure 6.3).

The differences between the subspecies in intake rates, handling efficiencies, and prey size choices have obvious consequences for birds attempting to satisfy high energetic demands in cold nonbreeding environments. Such experimental observations obviously require validation in a natural setting. *Macoma* densities in upper Cook Inlet, Alaska, are among the highest reported in Alaska (Ruthrauff et al. 2013c), and far exceed the densities at which we conducted our experiments. Furthermore, *Macoma* ≤ 8 mm long constitute a high proportion of the standing *Macoma* biomass in upper Cook Inlet (table 2, Ruthrauff et al. 2013c). Because molluscivorous shorebirds reach digestive bottlenecks at relatively low prey densities (van Gils et al. 2005c, Goss-Custard et al. 2006), we predict that *ptilocnemis* Rock Sandpipers in upper Cook Inlet feed on *Macoma* of high quality (i.e., relatively small) such that net energy intake is maximized as a function of shell waste. Given the lack of inherent differences in metabolic rates between *ptilocnemis* and *tschuktschorum* (Ruthrauff et al. 2013a), we posit that intrinsic physiological differences of the digestive system related to assimilation and excretion, but not the physical crushing of food, likely play the largest role in facilitating the high-latitude nonbreeding distribution of *ptilocnemis* Rock Sandpipers. Such adaptations represent unique evidence among shorebirds of intrinsic foraging-related adaptations to divergent physiological stimuli between conspecifics.

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CHAPTER 7

Out in the cold: environmental and ecophysiological constraints on the winter distribution of rock sandpipers *Calidris p. ptilocnemis* at the northern extent of its range

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Abstract

Study of organisms at the extents of their biogeographic range can provide insights into underlying processes that determine observed distribution patterns. Rock Sandpipers (*Calidris p. ptilocnemis*) have the most northerly nonbreeding distribution of any shorebird in the Pacific Basin (upper Cook Inlet, Alaska [61°N, 151°W]), a location that is also the coldest nonbreeding site regularly used by shorebirds during winter. We integrated physiological, metabolic, behavioral, and environmental aspects of the nonbreeding ecology of *ptilocnemis* at the northern extent of their range to determine the relative importance of these factors in facilitating their unique nonbreeding ecology. Not surprisingly, estimated daily energetic demands were greatest (373 kJ) during the coldest periods of winter (January). These estimates are up to 7.2 times greater than *ptilocnemis* basal metabolic rates, a scope of increase that approaches the maximum sustained rates of energetic output by migrating shorebirds, and far exceeds them in duration. We assessed the quality of their primary prey, the bivalve *Macoma balthica*, across a range of shell sizes to determine the daily foraging duration required by *ptilocnemis* to satisfy such energetic demands. Based on size-specific estimates of *Macoma* quality, *ptilocnemis* requires 15.4–21.4 h d^{-1} of foraging time in upper Cook Inlet in January. This range exceeds the maximum daily duration of mudflat availability in this region (~18 h). Furthermore, areal extent of mudflat annually decreases in extent due to the accumulation of shorefast ice. *Ptilocnemis* likely maximizes access to foraging sites by following the exposure of ice-free mudflats across the upper Cook Inlet region, and selects smaller, higher quality *Macoma* to minimize foraging times. Ultimately, this unusual nonbreeding ecology hinges upon the high quality of their *Macoma* prey resources. Compared to other sites across their range, *Macoma balthica* from upper Cook Inlet have relatively light shells, potentially a result of the region’s depauperate invertebrate predator community. In the future, potential thermogenic benefits to *ptilocnemis* of a warming upper Cook Inlet climate may be offset by impacts to *Macoma balthica* survival and quality.

Introduction

Animal distributional patterns reflect a multitude of physical, social, and biological interactions (MacArthur 1984, Brown 1995, Gaston 2003), but at the most fundamental level an animal's distribution is determined simply by the species' ability to survive in a given environment. This characteristic reflects an organism's adaptive, ecophysiological response to its environment (Root 1988, Spicer and Gaston 1999), and study of organisms at the limits of their geographic ranges can elucidate factors shaping these limits (Gaston 2009, Sexton et al. 2009). At high northern latitudes during winter, environmental conditions are often characterized by low temperatures and low availability of food resources. From a physiological perspective, range limits in these environments are thus often influenced by an animal's ability to satisfy high cold-induced energetic demands in the face of low resource abundance.

Shorebirds (Charadriiformes, suborders Charadrii and Scolopaci) are a globally distributed, highly diverse avian taxa (Piersma et al. 1996) that constitute a conspicuous part of wildlife communities along marine and freshwater shorelines. Most shorebird species use their highly sensitive bills to peck or probe in soft substrates for prey resources, a mode of foraging that predisposes them to regions of the globe that ensure access to ice-free habitats (Piersma 1996, Piersma et al. 1996). Additionally, because shorebirds have relatively high metabolic rates (Kersten and Piersma 1987), they risk starvation when subjected to extended periods without access to food (Marcström and Mascher 1979, Davidson and Evans 1982, Camphuysen et al. 1996). These life history traits effectively serve to constrain the nonbreeding distribution of most shorebirds to shorelines in temperate and tropical regions (Piersma 1996, Colwell 2010).

Despite their nonbreeding affinity for shoreline habitats, most shorebird species breed at inland sites, often at high northern latitudes, and conduct long annual migrations between breeding and nonbreeding sites (Piersma et al. 1996, van de Kam et al. 2004). Shorebirds are renowned for conducting long-distance migrations (Piersma and Davidson 1992, Battley et al. 2000, Gill et al. 2009), a natural history characteristic that has evolved to exploit ephemerally abundant resources at breeding sites during spring and summer. As the breeding season wanes and conditions at these sites deteriorate, such migratory behavior also avoids the risk of starvation that shorebirds would otherwise face by remaining at high northern latitudes during winter. The life history of shorebirds breeding at high northern latitudes, then, is generally characterized by long migrations between breeding sites with ephemerally abundant food resources and nonbreeding sites at temperate or tropical locations with predictable food resources (Piersma et al. 1996, Colwell 2010).

A few species of shorebird serve as exceptions to these trends, however, and spend the nonbreeding season at high latitude sites that experience cold, dark winters (Cramp and Simmons 1983, Summers et al. 1990). One such shorebird is the Rock Sandpiper (*Calidris ptilocnemis*). Rock Sandpipers are common residents of the

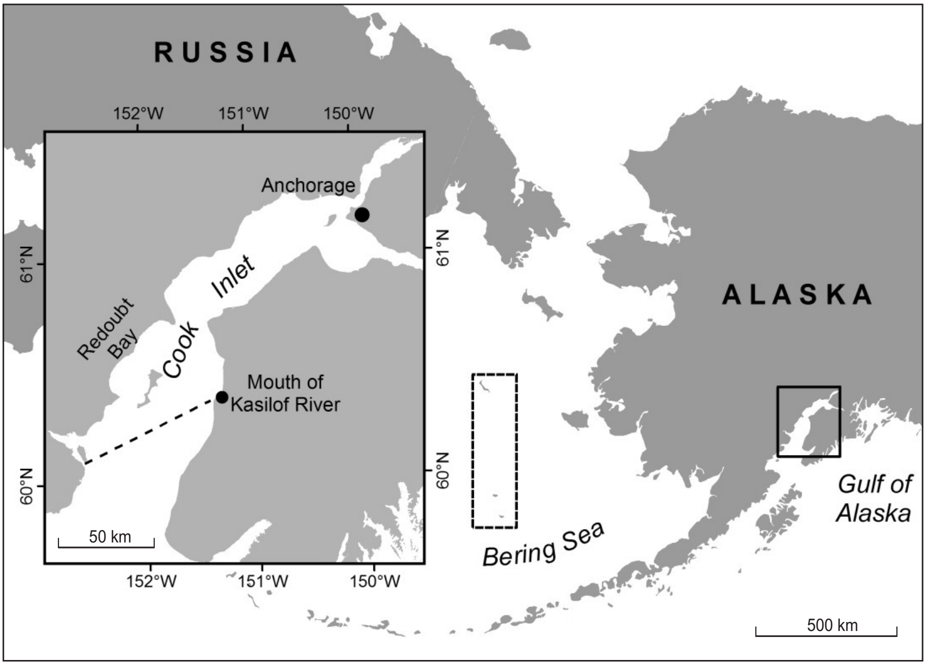

Figure 7.1. Primary North Pacific distribution of Rock Sandpiper *Calidris p. ptilocnemis*. *Ptilocnemis* breeds on small islands in the central Bering Sea (box with dashed border), and is distributed primarily in upper Cook Inlet, Alaska, during the nonbreeding season (box, enlarged in inset to left). Inset: dashed line delineates upper and lower Cook Inlet, and place names refer to upper Cook Inlet locations mentioned in the text.

North Pacific Basin (Gill et al. 2002), and are not unusual in size, appearance, or habits compared to other shorebirds breeding at high latitude sites. Rock Sandpipers are unique, however, for the range of environmental conditions they experience across their nonbreeding distribution. Rock Sandpipers comprise four subspecies (Conover 1944, Pruett and Winker 2005) that exhibit differential migration patterns, a trait that exposes each subspecies to distinct environmental conditions. At one extreme, most *C. p. tschuktschorum* individuals migrate relatively long distances between comparatively benign nonbreeding sites along the Pacific Northwest coast of North America and breeding sites in western Alaska and the Chukotskiy Peninsula, Russia (Gill et al. 2002, Lappo et al. 2012). At the other extreme, *C. p. quarta* and *C. p. couesi* are essentially non-migratory subspecies that spend the annual cycle at sites in the Commander Islands (*C. p. quarta*) and the Aleutian Archipelago and Alaska Peninsula (*C. p. couesi*; Gill et al. 2002, Lappo et al. 2012). Unique among North American shorebirds, the primary nonbreeding location of the fourth subspecies, *C. p. ptilocnemis* (hereafter *ptilocnemis*), is further north (1–4° latitude) than its breeding grounds (Figure 7.1). *Ptilocnemis* conducts an east-west migration between their central Bering Sea breeding grounds (Gill et al. 2002, Ruthrauff et al. 2012) and their primary wintering range in upper Cook Inlet, Alaska (Gill and Tibbitts 1999, Ruthrauff et al. 2013c).

The northern extent of the *ptilocnemis* nonbreeding range represents the most northerly winter distribution of any shorebird in the Pacific Basin (Ruthrauff et al. 2013c). Gill and Tibbitts (1999) first formally documented the high-latitude nonbreeding distribution of *ptilocnemis* in Cook Inlet, Alaska (61°N, 151°W; Figure 7.1), and subsequent work by Ruthrauff et al. (2013c) further documented that environmental conditions at this site were the coldest experienced by any nonbreeding shorebird in the world. The average daily high temperature in this region is ≤0°C for nearly 140 consecutive days between early November and mid-March (Ruthrauff et al. 2013c), and such cold induces high metabolic demands in birds (Vézina et al. 2006, Swanson 2010, Ruthrauff et al. 2013a). For *ptilocnemis* in Cook Inlet, these energetic demands are satisfied primarily by the consumption of the bivalve *Macoma balthica* (Gill and Tibbitts 1999, Gill et al. 2002). *Macoma* occur in high densities in Cook Inlet (Ruthrauff et al. 2013c), but are only accessible to *ptilocnemis* during periods of low tide. Cook Inlet experiences tidal fluctuations of over 10 m (Oey et al. 2007) across mudflats that extend up to 7 km at low tide; when coupled with the region's cold temperatures, *ptilocnemis* foraging habitats are subject to both direct freezing as well as coverage by sea and shore-fast ice (Ruthrauff et al. 2013c). Thus, *ptilocnemis* must satisfy their high daily energetic requirements by exploiting a feeding window initiated by the exposure of the mudflats on falling tides, hastened by the freezing of exposed mudflats, and terminated by coverage with sea or shore-fast ice and, finally, a flooding tide.

We have recently identified numerous physiological (Ruthrauff et al. 2013b, Ruthrauff et al. in prep.), metabolic (Ruthrauff et al. 2013a), behavioral (Ruthrauff and Eskelin 2009, Ruthrauff et al. in prep.), and environmental (Ruthrauff et al. 2013c) factors that together support this unique nonbreeding life history. Herein we integrate these various components across a range of climatological scenarios to model the constraints that *ptilocnemis* faces in upper Cook Inlet, Alaska, during winter. We demonstrate how stochastic periods of deep cold create energetic bottlenecks that necessitate the abandonment of Cook Inlet by *ptilocnemis*. We also document unique qualities of *ptilocnemis*' preferred prey in Cook Inlet, *Macoma balthica*. *Macoma* are an important prey resource for molluscivorous shorebirds throughout the northern hemisphere (Goss-Custard et al. 1977, Zwarts and Blomert 1992), but we demonstrate that *Macoma* in Cook Inlet are prey of exceptional quality compared to *Macoma* stocks from locations in Europe. Finally, we examine this unique winter ecology in the context of climate change. Because warmer temperatures will relax metabolic burdens on *ptilocnemis*, climate change potentially offers energetic benefits to these birds. We hypothesize, however, that increasing winter temperatures may actually prove detrimental to these cold-hardy birds due to bottom-up processes that may decrease the quality of their bivalve prey and offset potential thermogenic benefits.

Methods

Our assessments are projected across the months during which *ptilocnemis* is present in upper Cook Inlet (October–April; Ruthrauff et al. 2013c). We integrated summaries of long-term climatological and environmental conditions in upper Cook Inlet along with interrelated ecological components that reflect ecophysiolocial characteristics of *ptilocnemis* or their primary prey, *Macoma balthica*. These components include presence/absence estimates of *ptilocnemis* in upper Cook Inlet during winter, intake rates and size preferences of *ptilocnemis* feeding on *Macoma*, lipid stores and sizes of relevant organ groups of *ptilocnemis* during winter, and size-related estimates of *Macoma* quality.

Climatological and Environmental Summaries

Climatological summaries follow procedures outlined by Ruthrauff et al. (2013c) to derive values for long-term (1952–2013) average and extreme temperatures and average winds in upper Cook Inlet (National Climatic Data Center 2014). For these summaries, we used datasets for Anchorage, Alaska, a city located along the shores of upper Cook Inlet (Figure 7.1) and the site with the region's most extensive historical climatological information. Ruthrauff et al. (2013c) determined that temperatures at this location were representative of those at the nearby (within 100 km) locations primarily used by *ptilocnemis* birds. We calculated monthly average estimates of solar insolation in upper Cook Inlet using National Aeronautics and Space Administration (2014) datasets, and estimated the average monthly and historical extremes of shore-fast ice extent using National Ice Center datasets (2014) from the period October 2006–April 2014 following procedures described by Ruthrauff et al. (2013c).

To estimate the amount of time that mudflats were exposed and potentially available for foraging to *ptilocnemis* each day, we analyzed archived images from the Federal Aviation Administration (2014) taken overlooking the northern portion of Redoubt Bay (Figure 7.1), one of the primary sites used by *ptilocnemis* in upper Cook Inlet (Ruthrauff et al. 2013c). Images were taken at 10-minute intervals, and we observed diurnal images only on days during which the mudflats were clearly visible throughout the entire day. The time period over which we analyzed images did not contain shore-fast ice, and as such these summaries yield estimates of maximum potential mudflat exposure.

Ptilocnemis Occurrence in Upper Cook Inlet

The winter abundance and distribution of *ptilocnemis* in upper Cook Inlet was summarized from 99 aerial surveys across 16 winter seasons by Ruthrauff et al. (2013c). Ruthrauff et al. observed large numbers of *ptilocnemis* displaced from preferred sites in northern Cook Inlet to less-commonly used southern sites on two occasions, and these displacement events coincided with periods of unusually low temperatures that deviated by as much as 20°C from long-term averages (Ruthrauff et al. 2013c). Based on the distribution patterns of *ptilocnemis* during (southward displacements and decreasing survey totals) and immediately following (northward movements and increasing survey totals) the periods of deep cold, Ruthrauff et al. (2013c) assumed that the aberrantly low temperatures created unsustainable energetic demands that precipitated the movement to less thermally-demanding sites outside the survey area. For the purposes of this model, we considered the environmental conditions during these two cold periods as threshold values in our energetic model.

Ptilocnemis Intake Rates

We applied estimates of long-term maximum prey intake rates in *ptilocnemis* to determine the amount of foraging time required to satisfy energetic demands under the various environmental scenarios. In molluscivorous shorebirds like Rock Sandpipers, energy intake rates are constrained by the act of crushing and processing shell waste (Piersma et al. 1993, van Gils et al. 2005b), and so we modeled intake rates with respect to shell intake (mg s^{-1} shell). Van Gils et al. Van Gils et al. (2013) determined that intake rates of *Macoma* in the molluscivorous shorebird Red Knot (*C. canutus*) were accurately described as a function of fresh gizzard mass (g) by the equation Intake = 0.05 × (*Gizzard Mass*)^2. We thus calculated intake rates based on this relationship using the average winter gizzard mass value for *ptilocnemis* (5.32 g) reported by Ruthrauff et al. (2013b).

Ptilocnemis Body Composition

We applied information from Ruthrauff et al. (2013b) on the winter mass of organ groups related to digestive capacity to estimate rates of energy intake (see above). We specifically focused on the winter mass of *ptilocnemis* stomachs (primarily composed of the gizzard, the organ responsible for physically crushing prey; Piersma et al. 1993, 1999) as a method to calibrate intake rates, and qualitatively considered the masses of the intestine (the site of enzymatic digestion and absorption; Dykstra and Karasov 1992, Battley and Piersma 2005) and the liver (the site of nutrient metabolism and bile production; Proctor and Lynch 1993, Battley and Piersma 2005) for further insights into *ptilocnemis* digestive capacities.

Macoma Quality and Ptilocnemis Diet Reconstruction

To determine the quality of *Macoma balthica* as prey, we calculated the relationships of both the ash-free dry mass (AFDM) of *Macoma* flesh and *Macoma* shell mass (i.e., ballast) to *Macoma* shell length using standard techniques (Zwarts 1991, van Gils et al. 2005b). For molluscivores like Rock Sandpipers, quality is determined by the ratio of AFDM to shell ballast, and this value varies as a function of *Macoma* shell length. We derived these relationships from 109 *Macoma* (lengths 6.5–15.4 mm) collected at the mouth of the Kasilof River (Figure 7.1) in upper Cook Inlet on September 27 and

28, 2011. To satisfy model assumptions of linear regression, we calculated these relationships after log transforming (base 10) values of AFDM and shell ballast, and back-transformed these estimates to yield outputs in mg. For comparative purposes, we similarly determined the quality of 158 *Macoma balthica* (lengths 5.5–15.2 mm) collected from the Baie de Somme estuary, France (50.2°N, 1.6°E), on 9 and 10 March, 2010.

We estimated *ptilocnemis* prey size preferences using diet reconstruction techniques (Dekinga and Piersma 1993). Because the hinges of *Macoma* shells are relatively durable, they are preserved in the gizzards of molluscivorous shorebirds. We first estimated the relationship between *Macoma* shell length and the height of each hinge (i.e., 'hinge plus top' height, Dekinga and Piersma 1993) by fitting a two-parameter power law function using the aforementioned 109 *Macoma* specimens from upper Cook Inlet. We next removed hinges from the gut contents of eight *ptilocnemis* specimens (two females, six males) collected in upper Cook Inlet on 15 January 1997 (n = 4 specimens) and 14 March 1998 (n = 4 specimens). We measured all hinges and shell lengths using a 10× dissecting scope equipped with digital measuring software (Leica Application Suite; Leica Microsystems, Wetzlar, Germany). The *ptilocnemis* specimens were collected approximately 100 km north from where we collected the *Macoma* specimens, and we assumed that the relationship between *Macoma* hinge height and *Macoma* shell length was similar between these sites. We applied the relationship relating *Macoma* length to hinge height to the hinges recovered from the *ptilocnemis* specimens to estimate the lengths of the consumed *Macoma*.

Model Parameterization

We integrated these biotic and physiological measures into model 5 of Wiersma and Piersma (1994) to estimate the metabolic rate of *ptilocnemis* across the range of environmental scenarios described above. This model estimates maintenance metabolic rates (Watts), defined as basal metabolic rate (the energy consumption of a resting, postabsorptive animal in a normothermic environment; IUPS Thermal Commission 2003) plus any extra energetic demands associated with thermoregulation at environmental temperatures below the thermoneutral zone (Wiersma and Piersma 1994). The model integrates energetic costs associated with environmental conditions (e.g., wind, temperature, solar insolation), as well as microhabitat and thermal conductance (Wiersma and Piersma 1994). Ranges of values for the first three variables are described above (see Climatological and Environmental Summaries). Microhabitat-specific model parameters derive from values in table 1 of Wiersma and Piersma (1994). In general, observations of *ptilocnemis* in upper Cook Inlet primarily constitute closely huddled roosting birds or loose groups of birds foraging on mudflats. Such observations correspond to Wiersma and Piersma's 'Dense group' (i.e., roosting) and 'Mudflat and bare salt marsh' (i.e., birds foraging in loose groups) microhabitats, and we applied the appropriate microhabitat conductance parameters for each scenario(see table 1, Wiersma and Piersma 1994). We used a value of 42.6°C

(Ruthrauff et al. 2013a) for the body temperature of *ptilocnemis*, and used equation 8-15 from Calder (1996) to estimate thermal conductance of *ptilocnemis* as a function of body mass. We applied the average body mass value of *ptilocnemis* in upper Cook Inlet during winter (108.2 g) for this calculation (Ruthrauff et al. 2013b).

To more accurately reflect the daily activity budget of *ptilocnemis*, we allocated 12 hours of time to both roosting and foraging behaviors. To further incorporate additional energetic demands associated with foraging behaviors (e.g., food processing [Piersma et al. 2003] and locomotion activities [Bruinzeel and Piersma 1998]), we applied results from doubly-labeled water experiments on Red Knots (Piersma et al. 2003) to estimate the proportion of the daily energy budget comprised by other activities associated with foraging behaviors. Piersma et al. (2003) determined that 32.3% and 18.0% of the energy budget of foraging Red Knots was constituted by food processing and foraging-related locomotion, respectively, and we augmented the maintenance metabolic rates estimated for foraging birds accordingly. We summed these behavior-specific totals for each day to estimate the daily energetic demands of *ptilocnemis*. We converted estimated metabolic rates into daily energetic equivalents (1 Watt = 3.601 kJ h^{-1}).

To determine feeding durations, we considered these daily energetic demand estimates as energy deficits requiring fulfillment via the consumption of *Macoma*. We estimated the duration of time necessary to satisfy these deficits based on long-term maximum rates of *Macoma* intake (mg s^{-1} shell ballast; see above). To link intake to metabolizable energy, we converted estimates of shell ballast intake into their energetic equivalent (kJ g^{-1} shell ballast) assuming an energy density of 22 kJ g^{-1} ash-free dry mass *Macoma* flesh (Zwarts and Wanink 1993, van Gils et al. 2005b), and an assimilation efficiency of 0.8 (Yang et al. 2013). Because the ratio of AFDM of *Macoma* flesh to *Macoma* shell ballast varies by shell length, we integrated these estimates across a range of representative shell lengths determined by our diet reconstruction results. We conducted all analyses in R version 3.0.1 (R Development Core Team 2013).

Results

Climatological and Environmental Setting

The average daily temperature (the mean of each day's average high and low temperature) and extreme temperatures during winter in upper Cook Inlet, Alaska are plotted in Figure 7.2. Average monthly temperatures (the mean of the average daily temperatures) are ≤0°C for the months November–March (Table 7.1), and January is the month with the coldest average daily temperature (-9.4°C). The average wind speed varies little over the winter period (~3 m s^{-1}), but the amount of incident solar radiation varies by a factor of about 25 between the months of December (6.25 Watts m^{-2}) and April (165.42 Watts m^{-2}).

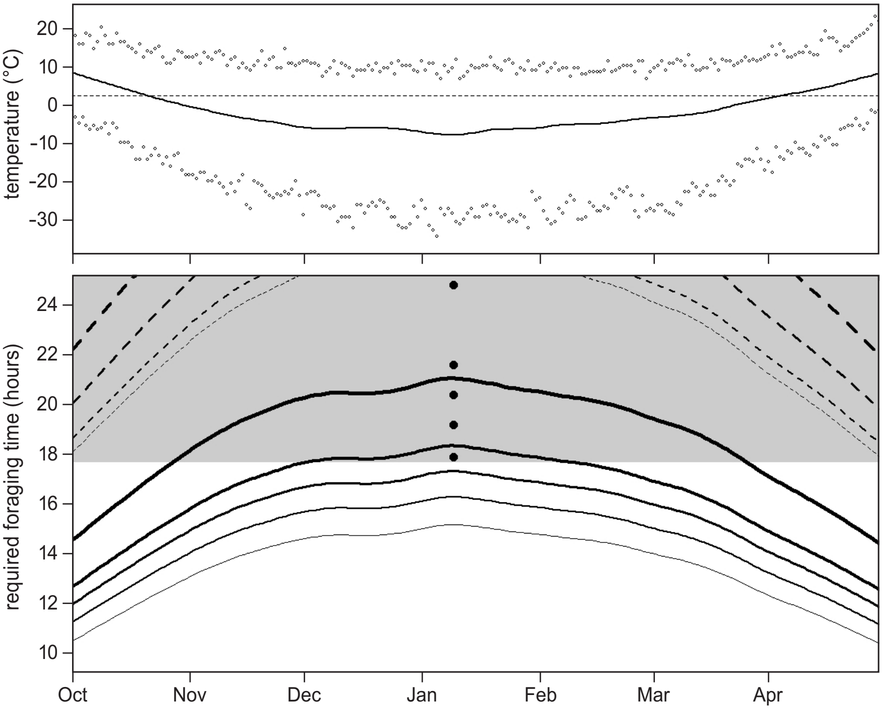

Figure 7.2. Upper figure: long-term daily average (solid line) and extreme temperatures (small circles) during winter in Anchorage, Alaska (upper Cook Inlet); dashed line delineates 0°C. Lower figure: predicted minimum foraging durations necessary to satisfy estimated daily metabolic demands of Rock Sandpipers (*Calidris p. ptilocnemis*) during winter in upper Cook Inlet. Estimates integrate average temperatures, wind speeds, and rates of solar insolation. The increasing weights of the lines represent estimated foraging durations for *ptilocnemis* feeding on 6.46 mm, 8.33 mm, 9.94 mm, 11.42 mm, and 14.96 mm *Macoma*, respectively (see Results for rationale behind size classes). Solid lines represent estimates for birds feeding on *Macoma* from upper Cook Inlet, and dashed lines represent estimates for birds feeding on lower quality *Macoma* (Baie de Somme, France; see Figure 7.3). Shaded region includes foraging durations that exceed the average daily maximum duration of mudflat exposure at Redoubt Bay, Alaska, one of the primary wintering sites used by v in upper Cook Inlet. Filled circles represent point estimates of foraging durations for *ptilocnemis* feeding on Cook Inlet *Macoma* of the 5 size classes under aberrantly cold climatic conditions believed to have displaced *ptilocnemis* within the region (see Methods: *ptilocnemis* Occurrence in Upper Cook Inlet for details). These estimates are plotted at January 9, the day with the longest estimated foraging durations under average conditions, for comparison, and increase with *Macoma* size.

The extent of mudflat habitat in the regions of upper Cook Inlet used by *ptilocnemis* is about 610 km^2 (Ruthrauff et al. 2013c). We analyzed archived images documenting mudflat exposure at Redoubt Bay over periods of both high and low tides, and the average diurnal period of these observations was 11.3 ±0.2 SE h. Of this period, 8.3 ±0.3 SE h constituted periods when mudflats were at least minimally exposed. We extrapolated these values across a 24-h period, and estimate that the average daily duration of mudflat exposure at Redoubt Bay is 17.7 ±0.5 SE h. Because we classified the mudflats as exposed in images when any mudflat remained uncovered by water, this total serves as a maximum value that potentially decreases with accretion of shore-fast ice. The accumulation of shore-fast ice in upper Cook Inlet tracks monthly temperatures in winter. Shore-fast ice is typically present in upper Cook Inlet from November–March (Poole and Hufford 1982, Ruthrauff et al. 2013c), and averages ≥200 km^2 in extent from December–March. The maximum areal extent of shore-fast ice (301.2 ±49.6 SE km^2) occurs in January, a time coinciding with the winter season's coldest temperatures.

Macoma Quality and Ptilocnemis Diet Reconstruction

The relationships describing AFDM (mg) and shell ballast (mg) as a function of shell length for *Macoma balthica* from upper Cook Inlet, Alaska, are log(AFDM) = -0.772 + 0.222(shell length) – 0.004(shell length)^2 and log(shell ballast) = -0.318 + 0.238(shell length) – 0.004(shell length)^2, respectively (Figure 7.3). Similar assessments of *Macoma balthica* collected in Baie de Somme, France, are described by the relationships log(AFDM) = -1.624 + 0.372(shell length) – 0.012(shell length)^2 and log(shell ballast) = -0.684 + 0.327(shell length) – 0.008(shell length)^2. The 95% confidence intervals on these estimated relationships are largely non-overlapping between sites; only the confidence intervals for shell mass overlap at small-sized *Macoma* (Figure 7.3).

Table 7.1. Long-term average climatic conditions from October–April, upper Cook Inlet, Alaska, and concomitant maintenance metabolic rates and daily energetic demands for *ptilocnemis* Rock Sandpipers. Historical climate information summarized for Anchorage, Alaska. Metabolic rate estimates are derived for two habitat-specific scenarios representing roosting and foraging behaviors. Hourly metabolic rates were extrapolated across 12 hours for each behavior and converted to kJ equivalents to yield daily energetic demands; see Methods for full model parameterization.

Month	Climate Variable			Estimated Metabolic Rate (Watts)		Estimated Daily Energetic Demand (kJ)
	Mean Temp. (°C)	Wind (m s^{-1})	Insolation (Watts m^{-2})	'Roosting'	'Foraging'	
October	1.5	3.00	57.50	1.98	4.80	293.53
November	-5.6	2.91	20.00	2.34	5.66	346.48
December	-8.6	2.82	6.25	2.48	6.00	367.15
January	-9.4	2.86	12.92	2.52	6.10	373.31
February	-7.1	3.08	40.83	2.42	5.88	359.55
March	-3.9	3.13	97.08	2.23	5.43	332.09
April	2.3	3.26	165.42	1.90	4.62	282.85

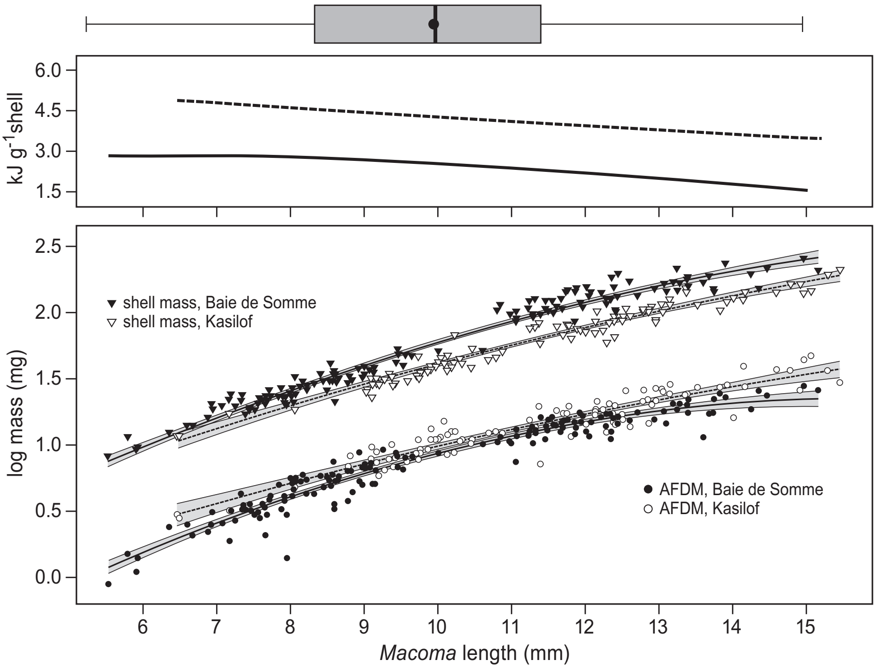

Figure 7.3. Characteristics of the bivalve *Macoma balthica*, primary prey of Rock Sandpipers (*Calidris p. ptilocnemis*) in upper Cook Inlet, Alaska, during winter. Boxplot (top) is based on diet reconstruction techniques and represents the size distribution of *Macoma* consumed by *ptilocnemis* in upper Cook Inlet during winter .Thick vertical line represents the median, circle the mean, box the 25th and 75th percentiles, and whiskers the range of values. The middle figure depicts estimates of *Macoma* quality (kJ g^{-1} dry shell mass) as a function of shell length for *Macoma* from Kasilof, Alaska (dashed line), and Baie de Somme, France (solid line). Values reflect metabolizable energy estimated by applying an energy density of 22 kJ g^{-1} ash-free dry mass (AFDM) *Macoma* flesh and an assimilation efficiency of 0.8 (see Methods) The lower figure demonstrates the relationship between *Macoma* shell length (mm) and AFDM (circles) and shell mass (triangles) for *Macoma* from upper Cook Inlet, Alaska, and Baie de Somme, France. AFDM and shell mass values are on log10 scale, and shading between lines represent 95% confidence intervals.

AFDM estimates are slightly higher for same-sized *Macoma* from upper Cook Inlet compared to Baie de Somme, while the estimates for shell mass are lower at upper Cook Inlet compared to Baie de Somme.

The ratio of AFDM to shell mass, and thus quality, is highest in small *Macoma* at both sites, and the ratio decreases with increasing shell size (Figure 7.3). Estimates of quality range from 3.47–4.86 kJ g^{-1} shell for *Macoma* from upper Cook Inlet and 1.54–2.81 kJ g^{-1} shell for *Macoma* from Baie de Somme (Figure 7.3). Quality varied less by size for *Macoma* from upper Cook Inlet (28.6% difference between maximum and minimum values) compared to Baie de Somme (45.2%). The relationship of shell length (SL) to hinge + top height (HTH) for *Macoma* from upper Cook Inlet is described by the equation SL = 14.094(HTH)$^{.754}$. We recovered 347 hinges from the eight *ptilocnemis* specimens (range 12–78 hinges per specimen), and applied this formula to estimate *Macoma* lengths. Based on this relationship, the mean length of *Macoma* consumed by the eight *ptilocnemis* specimens was 9.94 ±0.11 SE mm (range 5.23–14.96 mm; Figure 7.3).

Seasonal Energetic Demands

Estimated seasonal maintenance metabolic rates (Watts) and concomitant daily energetic demands (kJ) are presented in Table 7.1. Average estimated metabolic rates are greatest for *ptilocnemis* during January (2.52 [‘roosting' scenario]–6.10 [‘foraging' scenario] Watts; Table 7.1) and lowest in April (1.90 [‘roosting' scenario]–4.62 [‘foraging' scenario] Watts; Table 7.1). Daily energetic demands follow the same seasonal patterns as metabolic rates (Table 7.1), and vary by approximately 24% across the winter season (Table 7.1).

Ruthrauff et al. (2013c) conducted two surveys under unusually cold conditions during which they detected relatively few birds present in upper Cook Inlet, and only at less-preferred southern sites. The average temperature for the week preceding these two surveys was 10.6°C colder than normal, and the average minimum temperature during these periods was -27.5°C. Metabolic rate estimates during these cold periods ranged from 3.00 (‘roosting' scenarios)–7.27 (‘foraging' scenarios) Watts. In contrast, *ptilocnemis* was distributed at preferred, more northerly sites during surveys conducted immediately prior to and following these ‘cold period' observations (Ruthrauff et al. 2013c). The daily averages during these periods were just 0.5°C below long-term averages and minimum temperatures averaged -16.0°C. Estimated metabolic rates during these periods were ~18% lower (2.46 [‘roosting' scenarios] –5.97 [‘foraging' scenarios] Watts) during these ‘normal' periods preceding and following the ‘cold' observations. The estimated daily energetic demand for *ptilocnemis* during these periods of unusual cold was 443.95 kJ, a value about 16% higher than the maximum estimated value during average conditions (January; Table 7.1).

Estimated Intake Rates and Minimum Required Foraging Durations

Following the technique of van Gils et al. (2003), we estimated that the intake rate of *ptilocnemis* during winter in upper Cook Inlet was 1.42 mg shell s^{-1} (see Methods). We applied this value to determine the daily minimum foraging duration required by *ptilocnemis* to satisfy their daily energetic demands. We estimated daily minimum foraging durations for five sizes of *Macoma*: 6.5 mm (size of smallest *Macoma* in samples used to calculate quality estimates, Figure 7.2), 8.3 mm and 11.4 mm (interquartile values based on diet reconstruction, Figure 7.3), 9.9 mm (mean value based on diet reconstruction, Figure 7.3), and 15.0 mm (upper limit based on diet reconstruction, Figure 7.3). Estimated daily minimum foraging durations increase as average winter temperatures decrease (Figure 7.2), and are shortest for birds feeding on the highest quality *Macoma* (6.5 mm) and longest for birds consuming the lowest quality *Macoma* (15.0 mm). Within a *Macoma* size class, estimates vary by ~33.1% between the lowest and highest estimates across the season (Figure 7.2). Across all sizes of *Macoma*, the day with the shortest estimated foraging time is 30 April, while the day with the longest estimated foraging time is 9 January (Figure 7.2).

For insights into scenarios when *ptilocnemis* was potentially unable to meet their energetic demands over the course of a day, we estimated the minimum working day for *ptilocnemis* during the two aforementioned periods of extreme cold when birds were displaced from northern sites to more southerly sites (see above). Estimated minimum daily foraging durations ranged from 17.9–24.8 h across the different sizes of *Macoma* (Figure 7.2). These estimates are 13.6% higher than the maximum estimated value under average conditions (9 January; Figure 7.2). To assess realistic impacts of prey quality, we calculated the minimum required foraging duration for *ptilocnemis* hypothetically feeding on lower quality *Macoma* (i.e., *Macoma* from Baie de Somme, France). These estimates were ≥40% higher than those for birds feeding on same-sized *Macoma* from upper Cook Inlet (Figure 7.2), and ranged from 17.8 h (6.5 mm *Macoma* on 30 April) to 48.4 h (15.0 mm *Macoma* on 9 January).

Discussion

Estimating the Cost of Wintering in upper Cook Inlet, Alaska

Shorebird species are renowned for their ability to sustain high levels of metabolic output (Kersten and Piersma 1987, Piersma 2011), feats that are heretofore recognized primarily for shorebirds during migrations spanning periods <10 days (e.g., Pennycuick and Battley 2003, Gill et al. 2005). Such observations yield estimated maximum sustained outputs 8–10 times above basal metabolic rates (Piersma 2011). *Ptilocnemis* Rock Sandpipers represent a unique addition to these observations, due both to the duration of their metabolic output and the season. We estimate that *ptilocnemis* must feed for ≥12 h d^{-1} during the majority of winter in upper Cook Inlet, regardless of which size *Macoma* they consume (Figure 7.2), and that the estimated metabolic rates during these foraging periods exceed basal metabolic rate (.85 Watt; Ruthrauff et al. 2013a) by a factor of 5.4–7.2 (April and January, respectively; Table 7.1). Thus, although the levels of metabolic output are lower than the those of shorebirds during active migration, they are nonetheless very high in an absolute sense (Hammond and Diamond 1997, Piersma 2011), and unprecedented in duration for a shorebird species.

Ruthrauff et al. (2013c) counted an average of 8,191 *ptilocnemis* Rock Sandpipers during 99 aerial survey of upper Cook Inlet during winter, a sum constituting nearly 50% of the subspecies' estimated population size (Ruthrauff et al. 2012). It is thus evident that *ptilocnemis* are predictable and abundant inhabitants of upper Cook Inlet during typical winter conditions. Stochastic periods of low temperatures offer insight into climatic thresholds beyond which *ptilocnemis* cannot apparently occupy upper Cook Inlet. Such cold not only increases thermogenic costs, but also increases the amount of shore-fast ice and decreases the amount of time that exposed mudflats remain unfrozen. Thus, not only do metabolic costs increase under such conditions, but the availability of mudflat foraging habitats decrease as well. The estimated minimum required foraging times during Ruthrauff et al.'s (2013c) two 'cold period' observations were 13.6% higher than the maximum values estimated under average conditions (January 9, the coldest day of the year in upper Cook Inlet; Figure 7.2), and these estimates exceed the maximum duration of mudflat exposure under ice-free conditions (Figure 7.2). Thus, even during periods of 'normal' cold, *ptilocnemis* foraging durations routinely approach threshold values described during stochastic periods.

To assess the plausibility of our estimates, we compared metabolic rate estimates derived using Wiersma and Piersma's (1994) model to laboratory-derived measures of *ptilocnemis* at temperatures ranging from 5°– -20°C (Ruthrauff et al. 2013a). On average, estimates derived following Wiersma and Piersma's method were just 1.9% higher than those directly measured via respirometry. Our derivation of *Macoma* shell intake rates based on fresh gizzard mass derives from work on Red Knots (van Gils et al. 2003) and yields an estimate (1.42 mg shell s^{-1}) that is in accordance with laboratory-derived estimates (1.21 mg shell s^{-1}; Ruthrauff et al. in prep.). The estimate implemented herein is nearly 15% higher than those derived under experimental settings, but the latter value was derived from *ptilocnemis* birds maintained in aviaries at 14°C. Birds experience their lowest metabolic demands under normothermic conditions (Scholander et al. 1950, Swanson 2010), and it is likely that the gizzard sizes of these birds were not maximized. In contrast, the *ptilocnemis* specimens from which we derived our estimates were collected in the middle of winter. Ruthrauff et al. (2013b) documented a significant increase in gizzard mass from fall to winter in wild Rock Sandpipers, a phenotypically flexible increase that they attributed to the increased foraging demands experienced by birds in winter.

Beyond scrutinizing the underlying model assumptions, are these estimates of minimum foraging durations reasonable within an ecological context? The value for the maximum duration of mudflat exposure at Redoubt Bay (17.7 h d^{-1}) exceeds the estimated foraging durations for *ptilocnemis* feeding on all but the two largest *Macoma* size classes (Figure 7.2). Our estimate of mudflat exposure duration was similar to those estimated at other nearby sites (e.g., figure 2 in Ezer and Liu 2010), and it is probable that patterns of sediment input (Bartsch-Winkler and Ovenshine 1984) and currents (Johnson 2008) interact with tides (Oey et al. 2007) to create similar mudflat geomorphologies, and hence inundation patterns, across this relatively small region. Nonetheless, upper Cook Inlet's mudflats are annually reduced by an average of 50% due shore-fast ice, placing a premium on *ptilocnemis* foraging habitats in midwinter. However, Ruthrauff et al. (2013c) describe how shore-fast ice is not uniformly distributed in the region due to current patterns, and so certain *Macoma*-rich intertidal regions are reliably free of shore-fast ice under all but the coldest conditions.

Thus, we are confident of the accuracy of underlying model parameters, and we believe that the model results are realistic in an ecological context. Anecdotal evidence suggests, however, that our estimates are potentially high. *Ptilocnemis* possesses certain physiological traits (e.g., dense plumage, high lipid stores; Ruthrauff et al. 2013b) that potentially lower metabolic costs. Applying Piersma's (1996) shorebird-specific model relating body mass and plumage, the plumage mass of *ptilocnemis* during winter (table 2, Ruthrauff et al. 2013b) is 33.1% greater than estimates based on body mass alone. Furthermore, average lipid stores in *ptilocnemis* are among the highest reported for shorebirds during winter, constituting 18.2% of winter body mass (Ruthrauff et al. 2013b). Although likely of importance primarily as energy stores (Blem 1990), high lipid stores undoubtedly offer insulative gain as well. These two factors likely lower conductance values for *ptilocnemis* in their natural settings, but the estimate of conductance that we applied in this exercise is calculated based on body mass alone (Calder 1996). Wiersma and Piersma's (1994) model is sensitive to such adjustments; in our example, a 10% reduction in the conductance parameter results in 7.4% lower foraging durations, a reduction of at least .8 h d^{-1} across all *Macoma* size classes.

While Wiersma and Piersma's model (1994) accurately estimates metabolic rates from which we derived foraging durations, *ptilocnemis* birds undoubtedly make behavioral adjustments that facilitate foraging access as well. In a similar tidally-structured feeding environment, van Gils et al. (2005a) describe how Red Knots in the Dutch Wadden Sea forage for nearly 17 h d^{-1} by moving east from their roost with the rising tide. Due to the difficulty of accessing remote locations in Cook Inlet during winter, such observations are lacking for *ptilocnemis*. Given the relatively small size of the upper Cook Inlet region (~50 km × ~170 km), however, it is likely that *ptilocnemis* moves between sites on rising and falling tides, day and night, to maximize their exposure to ice-free mudflat foraging habitats.

Impact of Macoma Quality on Ptilocnemis Winter Ecology

An unanticipated result from this study was the important role of prey quality in enabling *ptilocnemis*' unique nonbreeding ecology. Given Ruthrauff et al.'s (2013c) observations of *ptilocnemis* abandonment of upper Cook Inlet during stochastic periods of cold, it is likely that *ptilocnemis* regularly feeds at maximum rates with little buffer to accommodate increased energetic demands. As a corollary, when faced with invariant metabolic demands but lower quality prey, the only way to decrease foraging durations is via commensurate increases in intake rates. Such an adjustment is unlikely for *ptilocnemis* in upper Cook Inlet. In order for foraging durations of *ptilocnemis* feeding on low-quality prey (i.e., *Macoma* from Baie de Somme) to match those of *ptilocnemis* feeding on high-quality prey (i.e., *Macoma* from Kasilof), maximum intake rates would need to increase by ≥70%, requiring an increase in gizzard mass of ≥32%. Although shorebirds demonstrate an impressive ability to regulate the size of their gizzard in response to energetic demands (Landys-Ciannelli et al. 2003, Battley and Piersma 2005, van Gils et al. 2005a), such an adjustment is unlikely for *ptilocnemis*. Given that *ptilocnemis* is apparently already operating near the limit of its energetic thresholds in upper Cook Inlet, it is likely that its gizzard is at or approaching a physiological maximum.

Our estimates of quality for *Macoma* from Baie de Somme are similar to other published estimates from the Atlantic Basin (e.g., van Gils et al. 2005a, 2005b, Quaintenne et al. 2010), and we believe that these estimates are lower than those for *Macoma* from upper Cook Inlet due to site-specific differences in the presence of invertebrate predators (e.g., decapods [crabs, shrimp], gastropods [snails]). We propose that *Macoma* from upper Cook Inlet possess relatively light shells due to a relaxed selection pressure on this attribute compared to other sites with a more diverse benthic predator community. Although foraging shorebirds undoubtedly exert selection pressure for stronger shells on their bivalve prey, Rock Sandpipers crush in their gizzard any *Macoma* that they are able to swallow (Ruthrauff et al. in prep.). It is believed that bivalves instead attempt to avoid shorebird predation principally by adjusting their burying depth (Zwarts and Blomert 1992, Zwarts et al. 1992, Zwarts and Wanink 1993, Edelaar et al. 2003). Heavier shells, especially in small-sized *Macoma* that would otherwise be easily consumed by shorebirds, likely play a relatively greater role in reducing predation by invertebrates (e.g., Beukema et al. 1998, van der Veer et al. 1998, Hiddink et al. 2002). Such bivalve predators are prevalent and abundant at lower latitude sites throughout the range of *Macoma* balthica (e.g., Commito 1982, Beukema et al. 1998, Hiddink et al. 2002, Seitz et al. 2003).

Implications of a Warming Climate

Given that *ptilocnemis* appear to function at or near their metabolic limits for months at a time during winter in upper Cook Inlet, projected warming of high-latitude regions due to climate change (0.3°–4.8°C over the next century; IPCC 2013) has positive implications for the species. Warming temperatures will relax thermogenic costs, which will in turn decrease daily energetic demands and foraging durations. Thus, warming winter temperatures would appear to relax certain physiological constraints and enable *ptilocnemis* to more easily exploit foraging opportunities between falling and rising tides.

Such warming comes with costs, however, that could negatively impact the quality of *Macoma*. *Macoma balthica* is a cold-adapted species, and studies have already noted fitness impacts on the species due to warming conditions (Philippart et al. 2003, Beukema et al. 2009). Thus, a warmer Cook Inlet environment will potentially reduce *Macoma* reproduction and recruitment, leading to declines in density. In addition, warming conditions will potentially permit the range expansion (McCarty 2001, Walther et al. 2002, Parmesan and Yohe 2003), or invasive introduction (Strayer 1999, Compton et al. 2010, Falk-Petersen et al. 2011), of *Macoma* predators that would alter their quality as *ptilocnemis* prey. Such predators are apparently very uncommon or altogether absent from upper Cook Inlet's mudflats (Lees et al., 2001; DRR and REG pers. obs.). It has been proposed that glacier-derived sediments (Bartsch-Winkler and Ovenshine 1984) in western Cook Inlet decrease local primary productivity; in conjunction with dominant current patterns, this may impede the immigration and survival of planktonic larvae in the region (Foster et al. 2010). The scouring action of tidally-driven sea ice and exposure to cold winter temperatures likely further decreases the suitability of upper Cook Inlet's mudflats to such invertebrate predators. Future impacts of climate warming on these physical processes in upper Cook Inlet are unknown, but as noted above, the occurrence of such predators may account for site-specific differences in *Macoma* quality related to shell mass. Given our estimates for *ptilocnemis* birds feeding on low quality prey (Figure 2), any thermogenic benefits due to projected warming would potentially be counteracted by deterioration in *Macoma* quality.

In this context, it is notable that Cook Inlet is a relatively recent geographic feature (~14,000 YBP; Karlstrom 1964, Schmoll et al. 1972) formed by retreating glaciers during Holocene warming (Schmoll et al. 1999). Thus, the winter occupancy of upper Cook Inlet by *ptilocnemis* is a tangibly recent phenomenon; that *ptilocnemis* uses this site to the exclusion of other shorebird species is curious. Given the abundance of high quality prey, why do no other shorebird species occur in upper Cook Inlet during winter? Assuming that *ptilocnemis* maximizes fitness by employing a northerly-wintering life history (e.g., Stearns 1992), quantifying the interaction between the aforementioned environmental (e.g., temperature, wind, ice), physiological (e.g., intake rates, insulative adjustments), and behavioral (e.g., irruptive movements, small-scale site selection) factors under natural field conditions is necessary to understand the adaptive significance and continued persistence of this unusual nonbreeding life history.

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Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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CHAPTER 8

General discussion

Daniel R. Ruthrauff

An animal's distribution reflects a multitude of meaningful interactions between the species in question and its environment. That is, animals occur where they do because they are adapted to be there. So when closely-related individuals of the same species have different distributions, it begs the question of whether the differences are simply random and hold little adaptive significance, or they are adaptive life-history traits that reflect the influence of genetic, epigenetic, ontogenetic, or learned (or some combination thereof) factors.

As a group, shorebirds (Charadriiformes, suborders Charadrii and Scolopaci) present ample opportunity to explore such ideas due to their distinct phylogenies and varied life histories. Many shorebird species are migratory, and such migrations expose shorebirds to a variety of different habitats and environmental conditions across their annual cycle. For example, the Bar-tailed Godwit *Limosa lapponica baueri* moves between Arctic tundra, Southern-hemisphere estuaries, and temperate mudflats over the course of annual migrations totaling about 30,000 km. This peripatetic life history has evolved to take advantage of seasonally abundant resources at geographically disparate locations, and shorebirds must master these distinct environments to survive. As such, migratory shorebirds exhibit a diversity of life-history strategies to accommodate these varied influences.

From a physiological perspective, these migrations define the known limits of long-term metabolic exertion. Sustained metabolic output requires extensive physiological adjustment, and shorebirds are renowned for their abilities to adaptively regulate lean and lipid components of organs and muscle groups. Such physiological flexibility entails rapid and reversible adjustments of relevant body components. Indeed, the body composition of a breeding shorebird is distinctly different from that of a migrating shorebird, which in turn differs from that of a nonbreeding shorebird. For example, shorebirds exhibit extensive hypertrophy and atrophy of muscle and organ groups over the course their migrations. Prior to migration, the gizzard increases and the gut elongates to accommodate increased foraging demands; the liver enlarges to facilitate increased rates of energy assimilation; the heart and flight muscles enlarge to improve flight performance. Shorebirds feed insatiably in the weeks prior to migration in order to accumulate the fat loads necessary to fuel these flights. As departure approaches, digestive organs begin to atrophy—unwanted baggage for a long migration. And once aloft, shorebirds slowly burn their lipid stores, and flight muscles and heart atrophy. Upon arrival at their destinations, shorebirds have often burned as much as half of their body mass en route. Shorebirds are thus paragons of phenotypic flexibility, able to adaptively regulate rapid changes in body composition across their annual cycle.

Migratory behavior is common in shorebird species breeding at high northern latitudes, and is a response to the rapid deterioration of site conditions at these locations with the onset of autumn. Shorebirds, as their name suggests, are typically associated with shores and wetlands during the nonbreeding season. Most species use their long, sensitive bills to probe for buried prey in soft substrates, or to pick prey from rocky substrates. As such, shorebirds require access to unfrozen foraging substrates, a life-history trait that mostly restricts their distributions to temperate and tropical regions. In temperate regions periodically susceptible to freezing temperatures, shorebird species exhibit pronounced seasonal trends in fat stores. Most species slowly accumulate fat stores as fall turns to winter, and peak fat loads constituting ≤15% of total body mass coincide with the season's coldest periods. Given this midwinter peak in fat stores, these tissues are believed to serve primarily as energy supplies that help birds compensate for cold-induced energy deficits.

Though the subject of relatively little scientific attention, a few hardy shorebird species forgo long migrations and instead spend the nonbreeding season at high northern latitudes. The Purple Sandpiper (*Calidris maritima*) has the most northerly nonbreeding distribution of any shorebird and is the most well studied of these species. Purple Sandpipers occur along rocky coastlines throughout the North Atlantic during winter, common even as far north as 70° latitude in the northeast Atlantic. Compared to other high-latitude regions in the world, the northeast Atlantic is predictably mild due to the moderating influence of the Gulf Current. Purple Sandpipers typically carry relatively low fat stores (~6%) at these far northern sites, an indication of the reliable availability of their intertidal food resources. Nonetheless, shorebirds adaptively regulate lean tissues at these high-latitude sites in ways that meaningfully reflect environmental conditions. For instance, compared to conspecifics wintering at milder sites in Scotland, Purple Sandpipers in northern Norway have similar fat stores but relatively heavier livers and longer and heavier intestines. These differences reflect an up-regulation of tissues associated with digestive processes at colder, more northerly sites with higher energetic demands. Thus, just as shorebirds exhibit marked phenotypic flexibility with respect to migratory demands, shorebirds wintering at high-latitude sites likewise adaptively regulate body tissues in response to their surroundings.

Such variation in the life history of nonbreeding shorebirds at high northern latitudes forms the basis of this dissertation. In the Pacific Basin, Rock Sandpipers (*C. ptilocnemis*) are the sister taxon of Purple Sandpipers and are the shorebird with the most-northerly nonbreeding distribution in this region. Rock Sandpipers breed at coastal sites throughout the Bering Sea region, primarily in North America but also in small numbers in Russia (Chukotskiy Peninsula and the Commander Islands). Four subspecies of Rock Sandpiper are recognized based on patterns of morphology and appearance; the nominate subspecies, *C. p. ptilocnemis* (hereafter *ptilocnemis*) is the primary subject of this dissertation. *Ptilocnemis* breeds on small islands in the Bering Sea totaling just ~510 km^2, an area of similar size to the subspecies' primary nonbreeding range, the mudflats of upper Cook Inlet, Alaska (610 km^2; 61° N, 151° W). The 'discovery' of these birds in upper Cook Inlet during winter was a relatively recent phenomenon; given the region's low winter temperatures, short day lengths, and extensive coverage by sea and shore-fast ice, upper Cook Inlet was considered an unlikely site to host shorebirds. Nonetheless, sporadic observation in the 1970s and

1980s led to dedicated survey efforts by Bob Gill, Jr., of the US Geological Survey beginning in 1997. Winter conditions in the region seemed inhospitable to wading birds, and this raised obvious questions about just how *ptilocnemis* managed this unusual feat. I initiated this dissertation to explore the behavioral, environmental, and physiological aspects of this unique winter ecology.

We conducted winter aerial surveys of sites along the shores of upper Cook Inlet, a region delineated by sites north of Tuxedni Bay in western Cook Inlet and the Kasilof River in eastern Cook Inlet. This region is characterized by large, glacier-fed rivers draining into broad embayments interspersed with eroding bluffs. Extensive mudflats border the bays, uncovered twice per day by Cook Inlet's ~10 m tides. We conducted 99 surveys over 16 consecutive winter seasons, and counted an average of about 8,200 Rock Sandpipers on each survey. The population estimate for *ptilocnemis* is about 20,000 birds; that nearly half the population is regularly counted in the region underscores the importance of upper Cook Inlet to these birds during winter. During surveys, Rock Sandpipers were detected only on or adjacent to mudflat habitats. Conveniently for our sake, the nonbreeding plumage of *ptilocnemis* is distinct from the other three Rock Sandpiper subspecies, and periodic ground-based observations confirmed that essentially only *ptilocnemis* occurs in upper Cook Inlet during winter. These birds exhibit unique behaviors in upper Cook Inlet. On high tides, *ptilocnemis* regularly roosts on sea ice, while on falling tides *ptilocnemis* forages on benthic invertebrates scoured from the mud by retreating blocks of sea ice. During a few notable observation periods coinciding with temperatures as low as –23°C, I also observed numerous *ptilocnemis* with extensive icing on both their plumage and tarsi. Individuals did not apparently suffer ill-effects from this icing, observations which only increased our curiosity about these cold-hardy birds.

Thus, *ptilocnemis* annually occur in high numbers in upper Cook Inlet each winter, and this occurrence defines the most-northerly nonbreeding distribution of any shorebird in the Pacific Basin. Moreover, to the best of our knowledge upper Cook Inlet is also the coldest site to regularly host nonbreeding wading birds. The daily average temperature in the region is below freezing for nearly 140 consecutive days during winter, and average daily low temperatures approach –15°C in January, the region's coldest month. Such cold creates high metabolic demands in *ptilocnemis*, and field observations and analysis of stomach contents indicate that the bivalve *Macoma balthica* constitutes nearly the entirety of the *ptilocnemis* diet in winter. *Macoma* occur at high densities at sites across upper Cook Inlet (~300–3,000 *Macoma* m^{-2}), but *ptilocnemis* can only exploit these prey when tides expose upper Cook Inlet's mudflats. The window of exploitation is not solely a function of tide, as shore-fast ice annually accretes along the shores of upper Cook Inlet. In January, an average of about 300 km^2 of mudflat is rendered inaccessible due to shore-fast ice. Simultaneously, low temperatures slowly freeze the upper layers of Cook Inlet's mudflats. Thus, *ptilocnemis* must satisfy their high daily metabolic demands in winter by accessing ever-diminishing mudflats.

Clearly, Cook Inlet poses many environmental hurdles to *ptilocnemis* during winter. In addition to behavioral responses noted above, *ptilocnemis* extensively alters lean and lipid body components in response to winter conditions in upper Cook Inlet. A mid-winter sample of *ptilocnemis* from upper Cook Inlet revealed patterns of resource allocation focused on digestive and thermogenic processes. *Ptilocnemis* increases the size of its gizzard, liver, and kidney from fall to winter to facilitate the rapid intake and assimilation of *Macoma*. *Ptilocnemis* also increases the size of its pectoralis muscle, mass of its body plumage, and overall fat stores. The first two body components are clearly associated with heat production; in birds, rapid contraction of the breast muscles (i.e., shivering) is the primary avenue of heat production, while heavier, more extensive plumage offers obvious insulative benefits. Increased fat stores are likely of primary benefit as energy buffers during periods of high energy demand, but these stores may also provide insulation. Curiously, many of the changes in lean and lipid body components exhibited by *ptilocnemis* in winter mimic those of shorebird species prior to departure on long-distance migrations; although the contexts differ, the focus on sustained metabolic outputs are similar.

Such extensive physiological 're-tooling' in *ptilocnemis* begs the question of whether these birds exhibit intrinsic adaptations to their cold nonbreeding environment. Winters in upper Cook Inlet create high energetic demands in *ptilocnemis*. Given the many unique aspects of *ptilocnemis*' nonbreeding ecology, we reasoned that there were two likely scenarios by which such energetic demands could be satisfied. One would be via unique metabolic adaptations (as evidenced by measures of basal metabolic rate or metabolic response to temperature, for example), the other via unique ecophysiological adaptations (as measured by energy intake rates, prey size preferences, or prey-finding abilities, for example). We chose an experimental approach to address these questions, not only to avoid the numerous logistical difficulties associated with studying these birds in their cold, remote natural setting, but also because such an approach provided the opportunity to compare Rock Sandpiper subspecies with different life histories. For this comparison we chose individuals of the subspecies *C. p. tschuktschorum* (hereafter *tschuktschorum*). *Tschuktschorum* breeds at coastal sites in western Alaska and on the Chukotskiy Peninsula, Russia. Relative to the other Rock Sandpiper subspecies, *tschuktschorum* exhibits a more typical migratory life history, and thus serves as an intriguing contrast to *ptilocnemis*. *Tschuktschorum* moves up to 4,000 km between their breeding sites and nonbreeding sites along the northwest Pacific coast of North America (~37°–59° N). Thus, *ptilocnemis* is exposed to more severe environmental conditions than *tschuktschorum* during winter, and we assessed whether such long-term exposure had manifested itself in intrinsic differences between the subspecies.

To assess potential metabolic differences, we compared the basal metabolic rate and metabolic response to temperature of *ptilocnemis* and *tschuktschorum* using a flow-through respirometry system. We maintained the birds under identical conditions in outdoor aviaries exposed to ambient temperatures (–0.3°–9.6°C) during these trials. There was little evidence of differences in basic metabolic measures between the two subspecies. The basal metabolic rates (the metabolic rate of a resting, postabsorptive organism at normothermic temperatures) of the two subspecies did not differ; moreover, these rates simply followed previously established shorebird-specific patterns based on body mass alone. The two subspecies also had similar metabolic responses across a range of temperatures (–20°–14°C) below their thermoneutral zone. Metabolic rates increased similarly as temperatures declined, but the rate of this increase was relatively more moderate in these two subspecies than in other shorebird species with more southerly nonbreeding distributions. Nonetheless, wintering in upper Cook Inlet's cold environment did not confer any unique, intrinsic metabolic abilities on *ptilocnemis* compared to *tschuktschorum*. Other studies have demonstrated the positive effect of long-term acclimatization in elevating metabolic outputs, a phenotypically flexible response to variable environmental conditions. It is probable that *ptilocnemis* and *tschuktschorum* likewise exhibit such differences in their natural settings.

Given an apparent lack of difference in the basic metabolic machinery between the two subspecies when held under identical experimental conditions, we next assessed evidence for intrinsic differences in their foraging abilities. Given the high survival cost associated with satisfying energetic demands, *ptilocnemis* birds facing consistently high metabolic requirements in Cook Inlet may have evolved unique behavioral, physiological, or sensory aspects to their foraging ecology. We again compared *ptilocnemis* and *tschuktschorum* in our experiments, and used *Macoma balthica* as prey in all trials. *Macoma* are a prey item exploited by *tschuktschorum* primarily during migratory periods, but are of special importance to *ptilocnemis* throughout the winter in Cook Inlet. We conducted a series of trials to compare size preferences, maximum rates of long-term energy and shell intake, and the functional response of both subspecies to buried prey. Because Rock Sandpipers swallow *Macoma* whole and crush the shells in their muscular gizzards, these trials required an extensive 'training' period whereby we switched the diets of the trial birds from soft, easy to digest pellets (fish chow) to *Macoma*. We monitored the progress of this diet switch by measuring the birds' gizzards using ultrasonography; once the birds had increased the size of their gizzards such that they could easily subsist on hard-shelled prey alone, we initiated the experimental trials. We used digital video to record each trial, and played these videos in slow-motion to accurately record the relevant behaviors of the birds.

We detected numerous subtle but meaningful differences in the foraging ecologies of the two subspecies. *Ptilocnemis* consumed a wider range of prey sizes, had higher maximum rates of energy intake, processed shell waste at higher rates, and handled prey more quickly than *tschuktschorum*. Female Rock Sandpipers are slightly larger than males, but within-sex comparisons between the subspecies indicated that the two subspecies were similar in their structural size. Yet despite being maintained under identical experimental conditions, *ptilocnemis* birds were heavier than same-sex *tschuktschorum* individuals, a difference that we attributed to intrinsic physiological differences of the digestive system. These differences in body mass likely reflected an up-regulation of digestive organs (e.g., increased intestine and liver sizes) in *ptilocnemis* that promote higher prey intake rates.

Notably, however, the two subspecies did not differ in their abilities to detect buried prey. During the nonbreeding season, *ptilocnemis* primarily forages by probing for buried prey on Cook Inlet's mudflats while *tschuktschorum* visually gleans epibenthic organisms from rocky intertidal habitats. We predicted that these differences would be reflected by an innate ability of *ptilocnemis* to more easily find buried prey. The apparent lack of difference may indicate that Cook Inlet's high *Macoma* densities do not require a heightened sense of prey detection; alternatively, it may demonstrate that probe feeding is actually a highly-conserved trait in shorebirds, even for shorebirds like *tschuktschorum* Rock Sandpipers that probe-feed relatively infrequently. In sum, these foraging-related differences indicated the relative importance of physiological aspects rather than behavioral or sensory aspects in maintaining high intake rates for *ptilocnemis* compared to *tschuktschorum*.

Ultimately, to understand how *ptilocnemis* Rock Sandpipers are able to successfully pass the winter in upper Cook Inlet requires an integration of numerous puzzle pieces. Like most good puzzles, it is unclear how the pieces fit, or even whether we have all the pieces. But slowly a picture has formed. We synthesized relevant behavioral, environmental, metabolic, and physiological factors of *ptilocnemis* and their primary prey, *Macoma balthica*, to determine the relative importance of these various factors in promoting the winter occurrence of *ptilocnemis* in upper Cook Inlet. Our results suggest that *ptilocnemis* consistently approaches metabolic thresholds ultimately regulated by the required foraging time necessary to satisfy cold-induced metabolic demands. We estimated metabolic rates based on long-term climatological information, and these estimates were greatest in January, the region's coldest month. These rates were over 7 times higher than the basal metabolic rate of *ptilocnemis*, a scope of metabolic increase approaching that of shorebirds during active migration. It seems that for *ptilocnemis*, spending the winter in upper Cook Inlet more and more approximates the metabolic and physiological adjustments observed in other shorebird species with respect to long-duration migrations. Such migrations occur over a relatively brief period, however, while *ptilocnemis* exhibits greatly elevated metabolic rates for months at a time.

For molluscivore shorebirds like *ptilocnemis* Rock Sandpipers, benthic prey typically occur at high enough densities that rates of energy intake are not limited by a bird's ability to actually find the buried prey. Instead, digestive bottlenecks occur due to limitations associated with crushing and processing the shell itself. Because small *Macoma* have a higher ratio of flesh mass to shell mass than large *Macoma*, small *Macoma* yield more energy per gram of shell waste. In the context of digestively constrained foragers like *ptilocnemis*, small *Macoma* are thus higher quality prey than large *Macoma*. Accordingly, the estimated duration of foraging time for *ptilocnemis* in upper Cook Inlet varies based on *Macoma* size. For instance, on the coldest day of the year in upper Cook Inlet (January 9), estimated required foraging durations range from 15.4 (6.5 mm *Macoma*)–21.4 (15 mm *Macoma*) h d^{-1}. This range overlaps our estimate of the average daily maximum duration of mudflat exposure (17.7 h), a rigid time deadline for these birds. Moreover, the duration of mudflat exposure further declines as shore-fast ice accumulates along the upper margins of the mudflats, effectively reducing the availability of foraging habitat. Thus, *ptilocnemis* probably minimizes foraging durations by selecting relatively small, high quality prey, and maximizes exposure to mudflats by following rising and falling tides across sites in upper Cook Inlet.

This work details the many behavioral and physiological adjustments that *ptilocnemis* Rock Sandpipers exhibit that enable their winter occupancy of upper Cook Inlet, Alaska. Much of the work completed over the course of this dissertation was, by necessity, observational or experimental, and the next challenge comes in translating these results to a field setting. Given the relatively small size of upper Cook Inlet, the study system would seemingly lend itself to detailed tracking of *ptilocnemis* movements via remote telemetry. In conjunction with research employing repeated captures and nonlethal techniques to assess body condition, one could meaningfully document the mechanistic links between environment, behavior, and physiology in this unique study system. Unfortunately, given the prevalence of icing on both plumage and limbs of *ptilocnemis* in upper Cook Inlet, the attachment of such tracking units may well alter behaviors (e.g., tagged birds would depart upper Cook Inlet in search of warmer sites less prone to freezing), and potentially cause death due to ice accumulation. Moreover, the capture of birds that often roost on sea ice and move between vast, knee-deep mudflats has so far proven intractable. Thus, we await technological advances to enable such pursuits.

An unanticipated result from this study, however, concerns the important role that *Macoma balthica* plays in facilitating *ptilocnemis* occupancy of upper Cook Inlet. Compared to other sites, *Macoma* from upper Cook Inlet are superfood for *ptilocnemis* by virtue both of their relatively light shells and high flesh content. Bivalves are relatively easy (but not cheap!) to monitor, and repeated baseline collections in upper Cook Inlet would greatly facilitate the interpretation of *ptilocnemis* distribution patterns. Such information is especially valuable in light of future climate scenarios. For instance, projected climate warming would seem to offer thermogenic benefits for *ptilocnemis* by decreasing metabolic stress and, hence, foraging durations. However, warming may prove detrimental to *Macoma* in ways that might override benefits to *ptilocnemis*. In other regions, invertebrates (e.g., crabs, shrimp, snails) constitute an important component of the *Macoma* predator community. Such predators, however, are uncommon in Cook Inlet. It is believed that the region's high turbidity and prevailing current patterns serve to limit primary productivity, while low winter temperatures further impede colonization of mudflat habitats by *Macoma* predators. A warmer Cook Inlet may prove more inviting to these invertebrate predators, and because *Macoma* reduce invertebrate predation by augmenting shell mass, such introductions could precipitate rapid selection for heavier shells in *Macoma*. This would come at the expense of *ptilocnemis*; our work suggests that even small decreases in *Macoma* quality would push *ptilocnemis* beyond foraging thresholds dictated by tidal exposure. Thus, monitoring the quality and distribution of *Macoma* in upper Cook Inlet can provide crucial insights into current and future *ptilocnemis* distribution patterns.

Whatever a warming climate augurs for *ptilocnemis* and *Macoma* in Alaska, it is noteworthy that Cook Inlet has existed as a geographic feature for only about 14,000 years. Geologists estimate that this was when Holocene glaciers retreated from the region, allowing for salt water inundation and subsequent colonization by benthic bivalves. Hence, the use of upper Cook Inlet by both *ptilocnemis* and *Macoma* is a relatively recent, and undoubtedly rapidly evolving, phenomenon. Beringia, the North Pacific region in which Rock Sandpipers have evolved, is a region that has experienced great environmental and physical change in the Pleistocene and Holocene epochs, change characterized by dynamic climate patterns, multiple periods of glacial advance and retreat, and persistent regions of glacial refugia. The range of both phenotypically flexible and intrinsic responses that *ptilocnemis* currently exhibits with respect to environmental conditions in upper Cook Inlet undoubtedly reflect these historical inputs, and such traits bode well for the continued persistence of this unique nonbreeding ecology.

Nederlandse samenvatting

De verspreiding van een diersoort is de weerspiegeling van een verscheidenheid van aanpassingen aan potentiële leefomgevingen. Soorten komen dus alleen voor in gebieden waaraan zij zich hebben kunnen aanpassen. Wanneer ondersoorten verschillende verspreidingsgebieden hebben, rijst de vraag of dat een toevalligheid is; een verschil van weinig adaptieve betekenis, of dat het kenmerkende aanpassingen in de levensloop (*life-history traits*) van de ondersoort zijn die de invloed van genetische, epigenetische, ontogenetische, aangeleerde factoren (of een combinatie hiervan) representeren.

Steltlopers (orde Charadriiformes, subordes Charadrii en Scolopaci) zijn dankzij de duidelijke fylogenetische stamboom en variaties in levensstijl een ideale soortgroep om dergelijke aanpassingen bij te onderzoeken. Veel steltlopersoorten zijn trekvogels, die jaarlijks geconfronteerd worden met een verscheidenheid aan gebieden en omgevingsfactoren. De Rosse Grutto *Limosa lapponica baueri*, bijvoorbeeld, trekt vanuit de Arctische toendra naar riviermondingen op het Zuidelijk Halfrond en passeert daarbij waddengebieden in gematigde streken. Deze vogels overbruggen daarbij jaarlijks een afstand ongeveer 30.000 km. Deze peripatatische levensloop is ontstaan om optimaal te kunnen profiteren van seizoensgebonden pieken in voedselaanbod in ver uiteengelegen gebieden. Migrerende steltlopers moeten elk van deze gebieden grondig leren kennen en zich op hun rondreis steeds opnieuw aan andere omstandigheden leren aanpassen om te kunnen overleven. Vanuit een fysiologisch perspectief, laten dergelijke migraties zien welke enorme krachtsinspanningen er geleverd kunnen worden. Lange afstandstrek is topsport en een langdurige inspanning, zoals die tijdens deze trek geleverd moet worden, vereist ingrijpende fysiologische aanpassingen. Steltlopers staan bekend om hun vermogen om het vetgehalte en de functionaliteit van organen en spiergroepen naar behoefte te kunnen aanpassen. Deze fysiologische flexibiliteit impliceert snelle en omkeerbare aanpassingen van relevante organen. Inderdaad verschilt de lichaamssamenstelling van een broedende steltloper enorm van die van een migrerend dier, die op zijn beurt weer erg verschilt van een overwinterend exemplaar. Tijdens de trek ondergaan steltlopers verschillende fasen van hypertrofie en atrofie van spieren en orgaangroepen. Alvorens te vertrekken neemt de maaggrootte toe en het darmkanaal verlengt zich om aan de plotseling vergrote voedselbehoefte te kunnen voldoen. De lever wordt groter, zodat energie sneller kan worden omgezet, maar ook de omvang van het hart en de vlieg spieren nemen toe om de vliegprestaties te verbeteren. Om voldoende vetreserves op te slaan, noodzakelijke brandstof tijdens de trek, zijn steltlopers in de weken voorafgaande aan hun vertrek ogenschijnlijk onverzadigbaar. Wanneer het vertrek aanstaande is, slinken de verteringsorganen, want zij vormen ongewenste bagage tijdens de lange vlucht. Tijdens de reis verbranden steltlopers langzaam hun vetreserves, terwijl hun hart- en vliegspieren slinken. Als de steltlopers arriveren hebben ze ongeveer de helft van hun totale lichaamsgewicht verbrand. Steltlopers zijn dus toonbeelden van fenotypische flexibiliteit, dankzij hun adaptieve vermogen om jaarlijks snelle en ingrijpende fysiologische veranderingen in te reguleren.

Veel steltlopers broeden in het hoge noorden en migreren zuidwaarts wanneer de omstandigheden verslechteren en de herfst zijn intrede doet. Steltlopers, zoals de Engelse naam *shorebirds* suggereert, worden buiten het broedseizoen vooral gezien langs de kust en in waddengebieden. De meeste soorten gebruiken hun lange, gevoelige snavels om in zacht sediment naar begraven prooidieren te zoeken. Andere soorten pikken prooidieren van een rotsachtige ondergrond. Steltlopers hebben vanwege deze binding met zachte sedimenten en daarin begraven levende prooidieren over het algemeen problemen met vorst en ijs. Een consequentie daarvan is dat hun verspreiding grotendeels beperkt blijft tot gematigde en tropische gebieden. In gematigde streken, waar korte perioden van vorst kunnen voorkomen, laten steltlopers uitgesproken seizoensgebonden trends in de opbouw en afbraak van vetreserves zien. De meeste soorten bouwen in de herfst langzaam een vetvoorraad op en bereiken een piek in vetreserves (≤15% van het totale lichaamsgewicht) gedurende de koudste periode van de winter. Het aanleggen van vetreserves in de winter is vermoedelijk vooral bedoeld als energievoorraad, waarmee de vogels perioden van extreme kou en de daarmee samenhangende voedselschaarste kunnen overleven.

Er bestaat echter ook een groep taaie, relatief minder bekende steltlopersoorten die afziet van een lange zuidwaartse migratie. In plaats daarvan overwinteren deze soorten in het hoge noorden. De Paarse Strandloper *Caldris maritima* heeft het meest noordelijke overwintergebied en dit is van alle steltlopers de best bestudeerde soort. Paarse Strandlopers komen voor langs rotsachtige kusten in het Noord-Atlantische gebied en zijn 's winters zelfs talrijk tot op 70° noorderbreedte. In vergelijking met andere noordelijke gebieden in de wereld is het klimaat hier onder de invloed van de Golfstroom relatief mild. Paarse Strandlopers hebben opvallend weinig vetreserves (~6%), wat een indicatie mag zijn dat hun voedselvoorraden langs de kust in dit gebied steeds beschikbaar blijven. Steltlopers reguleren hun vetvrije massa in deze noordelijke gebieden adaptief, om zo optimaal in te spelen op de heersende omgevingsfactoren. In vergelijking met soortgenoten die in mildere streken, zoals in Schotland overwinteren, hebben Paarse Strandlopers in Noord-Noorwegen misschien wel overeenkomstige vetreserves, maar relatief zware levers en een uitgebreider maag-darmkanaal. Deze fysiologische verschillen zijn een afspiegeling van de verschillen in voedselbehoefte die bestaan tussen overwinteraars in koude, noordelijke overwinteringsgebieden en die in een gematigder klimaat.

Zoals migrerende steltlopers opvallende fenotypische flexibiliteit laten zien om in verschillende gebieden te kunnen overleven, zo vertonen steltlopers die overwinteren in het hoge noorden fenotypische aanpassingen die tegemoetkomen aan een meer extreme omgeving. De variatie in levensloopstrategieën van overwinterende steltlopers in noordelijke streken vormt het onderwerp van dit proefschrift. In de Stille Oceaan is de Beringstrandloper *C. ptilocnemis*, een nauw aan de Paarse Strandloper verwante soort, de steltloper met het meest noordelijk gelegen overwinteringsgebied.

Beringstrandlopers broeden in kustgebieden rond de Beringzee, voornamelijk in Noord-Amerika maar ook in kleine aantallen in Rusland (Tsjoektsjenschiereiland en de Komandorskieilanden). Er worden vier ondersoorten onderscheiden op basis van morfologische en uiterlijke kenmerken. De nominaat, *Calidris p. ptilocnemis* (hierna: *ptilocnemis*) broedt op kleine eilanden in de Beringzee, een gebied met een oppervlakte van slechts ~510 km^2., Het belangrijkste overwinteringgebied van deze ondersoort is niet veel groter (610 km^2): de wadplaten in het noorden van Cook Inlet, Alaska (61°N, 151°W). De 'ontdekking' van deze vogels in dit gebied is van betrekkelijk recente datum. Door de lage wintertemperaturen in deze regio, de geringe daglengte en de uitgebreide bedekking door zee- en landijs werd het noorden van Cook Inlet als ongeschikt terrein voor steltlopers beschouwd. Toch vormden sporadische observaties van strandlopers in de 70er en 80er jaren van vorige eeuw de aanleiding dat Bob Gill Jr. van de US Geological Survey hier vanaf 1997 met gericht veldonderzoek is begonnen. Omdat de strenge winterse omstandigheden het gebied ongeschikt leken te maken voor waadvogels, rees de vraag hoe *ptilocnemis* het dan voor elkaar kreeg om hier toch de winter door te brengen. Ik ben deze promotie begonnen om de ecologie van het gedrag, de omgeving en fysiologische aspecten van dit unieke winterse systeem te kunnen bestuderen.

In de winter zijn veldobservaties gedaan langs de kust in het noorden van Cook Inlet, een gebied gesitueerd tussen Tuxedni Bay in het westen en de Kasilof rivier in het oosten. Cook Inlet wordt gekenmerkt door grote, gletsjergestuurde rivieren die uitlopen in brede baaien met geërodeerde, steile rivierbeddingen. De uitgestrekte wadplaten vallen twee keer per dag droog en het getijverschil rond Cook Inlet bedraagt ~10 m. We hebben 99 surveys uitgevoerd in 16 opeenvolgende winters, waarbij gemiddeld 8200 Beringstrandlopers werden geteld. De populatie *ptilocnemis* wordt geschat op zo'n 20.000 vogels. Dat bijna de helft van die populatie regelmatig in dit gebied werd vastgesteld, onderstreept het belang van het noorden van Cook Inlet als overwinteringsgebied voor deze ondersoort. Tijdens onze surveys werden Beringstrandlopers alleen op of nabij het wad waargenomen. Het onderscheiden van *ptilocnemis* was eenvoudig, aangezien het winterkleed verschilt van dat van de andere drie ondersoorten. Veldobservaties bevestigden dat 's winters alleen *ptilocnemis* voorkomt in het barre studiegebied.

Tijdens hoogwater verzamelt *ptilocnemis* zich op hoogwatervluchtplaatsen die op zeeijs zijn gesitueerd. Tijdens afgaand tij foerageren de vogels op kleine ongewervelden die vooral langs met het water meegesleurde blokken zee ijs worden gevonden. Bij extreme koude, bij temperaturen van –23°C, zag ik soms strandlopers met dikke klonten ijs op hun veren en poten. De dieren leken er geen nadelige gevolgen van te ondervinden, iets dat onze nieuwsgierigheid naar deze koubestendige vogels alleen nog maar verder aanwakkerde.

Ptilocnemis overwintert elk jaar in grote aantallen in het noorden van Cook Inlet, waarmee dit als het meest noordelijk gelegen overwinteringsgebied voor steltlopers in de gehele Stille Oceaan gezien mag worden. Het is bovendien voor zover bekend het koudste gebied dat regelmatig overwinterende wadvogels herbergt. Het vriest hier gemiddeld 140 dagen aan een stuk en in januari, de koudste maand van het jaar, bedraagt de gemiddelde minimum temperatuur ongeveer -15°C. Zulke extreme condities zorgen voor hoge metabole kosten. Zowel veldobservaties als analyses van de maaginhoud lieten zien dat het voedsel van *ptilocnemis* bijna uitsluitend uit Nonnetjes *Macoma balthica* bestaat. Nonnetjes komen op veel plaatsen in grote dichtheden voor in het noorden van Cook Inlet (~300-3000 m^{-2}). De strandlopers hebben echter alleen toegang tot deze prooidieren wanneer de wadplaten droogvallen. De beschikbaarheid hangt bovendien af van de jaarlijkse aangroei van landijs: in januari is gemiddeld zo'n 300 km^2 ontoegankelijk geworden door de vorming van landijs langs de kust. Tegelijkertijd zorgen de aanhoudend lage temperaturen ervoor, dat de bovenste lagen van de wadplaten bij Cook Inlet geleidelijk aan bevriezen. Als gevolg daarvan moeten de strandlopers in de loop van een winter in een steeds kleiner wordend foerageergebied aan hun voedselbehoefte voldoen

Het is duidelijk dat de strandlopers in dit gebied met barre omstandigheden te maken krijgen. Afgezien van de al genoemde bijzonderheden in het foerageergedrag, ondergaan de vogels fenotypische veranderingen om de winterse condities succesvol het hoofd te kunnen bieden. De fysiologische aanpassingen bleken vooral te maken te hebben met de spijsvertering en met thermogene processen. Zo vergroten de strandlopers in het begin van de winter maag, lever en nieren, om een snelle en efficiënte verwerking van schelpdieren mogelijk te maken. Tegelijkertijd vergroot de borstspier, verdikt het verenkleed en worden vetreserves opgeslagen. Deze eerste twee aanpassingen zijn geassocieerd met warmteproductie. Bij vogels is het snel aanspannen van de borstspieren (d.w.z. rillen) de beste manier om warmte te produceren. Het zwaardere en dikkere verenkleed zorgt vervolgens voor een betere isolatie. De toegenomen vetopslag is in de eerste plaats vermoedelijk een energieopslag, om perioden van schaarste of extreme kou wanneer veel energie vereist is door te kunnen komen, maar ook de vetreserves hebben een isolerende werking. Merkwaardig genoeg zijn veel van deze fenotypische aanpassingen aan winterse omstandigheden in *ptilocnemis* vergelijkbaar met aanpassingen die steltlopers ondergaan ter voorbereiding op lange afstandsmigraties. Hoewel de omstandigheden verschillen, is de nadruk op een duurzame energiehuishouding vergelijkbaar.

Deze uitgebreide 'her-uitrusting' door *ptilocnemis* in de winterkwartieren roept de vraag op, of deze vogels beschikken over intrinsieke aanpassingen aan een koude leefomgeving. De winters in het noorden van Cook Inlet stellen hoge energetische eisen aan deze vogels. Vanwege de unieke ecologische aanpassingen van deze ondersoort aan zijn extreme overwinteringsgebieden, namen wij aan dat er twee mogelijke oplossingen zijn om aan deze energiebehoefte te voldoen. *Ptilocnemis* zou aan de energiebehoefte kunnen voldoen door aanpassingen in de energiehuishouding (wat zou kunnen blijken uit metingen van het basaalmetabolisme, of uit de metabolische gevolgen van temperatuursveranderingen), of door middel van ecofysiologische aanpassingen (wat bijvoorbeeld gemeten kan worden aan de hand van opnamesnelheden, een voorkeur wat betreft prooigrootte, of bijzondere vaardigheden bij het vinden van ingegraven prooidieren). Omdat er praktische en logistieke problemen zijn bij het bestuderen van deze vogels in hun koude, ver afgelegen, natuurlijke omgeving, hebben we gekozen voor een experimentele aanpak om deze vragen te kunnen beantwoorden. Deze experimentele benadering stelde ons bovendien in staat om Beringstrandlopers van verschillende ondersoorten, met verschillende levensstijlen, met elkaar te vergelijken.

Voor deze vergelijking hebben we exemplaren van de ondersoort *C. p. tschuktschorum* (hierna *tschuktschorum*) en *C. p. ptilocnemis* gebruikt. *Tschuktschorum* broed langs de kust van West-Alaska en op Tsjoektsjenschiereiland (Rusland). In vergelijking met de andere ondersoorten van de Beringstrandloper is *tschuktschorum* een uitgesproken trekvogel. Deze eigenschap zou interessante vergelijkingen met *ptilocnemis* op moeten leveren. *tschuktschorum* legt afstanden van zo'n 4000 km af, tussen de broedgebieden en het overwinteringgebied in de Stille Oceaan aan de noordwest kust van Noord Amerika (~37°–59° N). *Ptilocnemis* wordt in zijn hoognoordelijke overwinteringsgebieden blootgesteld aan veel extremere winterse omstandigheden dan de wegtrekkende ondersoort *tschuktschorum*. Wij wilden onderzoeken of die blootstelling aan extreme condities intrinsieke verschillen tussen de beide ondersoorten aan het licht zou kunnen brengen.

Om de mogelijke verschillen in energiehuishouding tussen *ptilocnemis* en *tschuktschorum* te onderzoeken, vergeleken we het basaalmetabolisme en de invloed van temperatuur op de stofwisseling met behulp van een respirometer. Tijdens deze tests werden alle vogels bloot gesteld aan vergelijkbare omgevingstemperaturen (-0.3°–9.6°C) in identieke buitenvolières. Het basaalmetabolisme van de beide ondersoorten bleek niet te verschillen. Feitelijk kwamen de gemeten waarden zelfs overeen met eerder gevonden patronen in steltlopers die alleen gebaseerd waren op het lichaamsgewicht. De twee ondersoorten vertoonden een vergelijkbare stofwisselingssnelheid onder koude omstandigheden (-20°–14°C; onder hun thermoneutrale temperatuur). De stofwisseling nam toe wanneer de temperatuur daalde, maar de mate waarin was voor beide ondersoorten relatief laag in vergelijking met steltlopersoorten met een meer zuidelijk gelegen overwinteringsgebied. Het overwinteren in de koude omgeving in het noorden van Cook Inlet zorgt dus niet voor unieke, intrinsieke verschillen in stofwisseling voor *ptilocnemis* ten opzichte van *tschuktschorum*. Andere studies vonden positieve effecten van langdurige aanpassing aan verhoogde stofwisseling, zoals een verhoogde fenotypische flexibiliteit naar aanleiding van veranderende omgevingsfactoren. Verwacht wordt dat *ptilocnemis* en *tschuktschorum* vergelijkbare verschillen vertonen in hun natuurlijke omgeving.

Omdat we geen verschil vond in het basaalmetabolisme van beide ondersoorten onder gelijke experimentele condities, hebben we ons gericht op intrinsieke verschillen in hun foerageervaardigheden. De barre omstandigheden op Cook Inlet kunnen tot unieke aanpassingen hebben geleid in gedrag, fysiologie en het waarnemingsvermogen van *ptilocnemis* tijdens het foerageren, om zo aan de hoge energiebehoefte te kunnen voldoen. We hebben opnieuw *ptilocnemis* en *tschuktschorum* vergeleken en gebruikt daarbij Nonnetjes als prooi in alle experimenten. Nonnetjes worden door *tschuktschorum* alleen tijdens de trekperiode gegeten, terwijl *ptilocnemis* in de winter in Cook Inlet volledig afhankelijk is van dit prooidier. We hebben een serie experimenten uitgevoerd waarin we de voorkeur voor de grootte van de prooi, de maximale opnamesnelheden op lange termijn (in schelpen en energie) en de functionele respons van beide ondersoorten op ingegraven prooien hebben gemeten. Omdat Beringstrandlopers schelpen in zijn geheel inslikken en de schelpen kraken met een krachtige spiermaag, was er voorafgaand aan de experimenten een uitgebreide training nodig. Voorafgaand aan de experimenten leefden de vogels op een dieet van eenvoudig verteerbare, zachte korrels (visvoer), waardoor de maag niet goed meer op het kraken van harde schelpen was voorbereid. De vogels moesten dus eerst weer wennen aan het eten van schelpdieren. De aanpassingen van het verteringssysteem tijdens de overgang van zachte naar harde prooien werd bijgehouden door het meten van de maaggrootte van de vogels behulp van echografie. Wanneer de maaggrootte dusdanig was toegenomen dat de vogel gemakkelijk zou kunnen overleven op een dieet van uitsluiten schelpdieren konden de experimenten beginnen. De vogels zijn tijdens deze experimenten gefilmd, waardoor alle relevante gedragingen van de dieren achteraf, in slow-motion, geanalyseerd konden worden.

We ontdekten verscheidene subtiele, maar belangrijke verschillen in de foerageerecologie van beide ondersoorten. *Ptilocnemis* had een bredere prooikeuze (schelpformaat), een hogere maximale energie inname, produceerde schelpafval sneller en verteerde de prooien sneller dan *tschuktschorum*. Vrouwelijke Beringstrandlopers zijn iets groter dan mannetjes, maar wijfjes en mannetjes van de beide ondersoorten hebben dezelfde structurele grootte. Ondanks een gelijke behandeling tijdens de experimenten waren vogels (gecorrigeerd voor sexe) van de ondersoort *ptilocnemis* gemiddeld zwaarder dan *tschuktschorum* . Dit verschil weten wij aan de intrinsieke fysiologische verschillen van het verteringstelsel. De verschillen in lichaamsgewicht zijn waarschijnlijk het resultaat van de stimulatie van organen die verantwoordelijk zijn voor de snellere vertering (bijv. vergrootte darm en lever) bij *ptilocnemis*.

Opvallend genoeg verschilden de twee ondersoorten niet in hun vaardigheid om begraven prooisoorten op te sporen. Buiten het broed seizoen foerageert *ptilocnemis* voornamelijk op begraven prooien in de wadplaten van Cook Inlet terwijl *tschuktschorum* foerageert op zichtbare organismen die ze al pikkend verzamelen in rotsachtige getijdegebieden. We voorspelden dat eventuele verschillen in foerageertechniek het resultaat zou zijn van een aangeboren vaardigheid van *ptilocnemis*, die het opsporen van ingegraven prooien eenvoudiger zou maken. De afwezigheid van een verschil in zoekefficiëntie zou een indicatie kunnen zijn dat de hoge dichtheden aan Nonnetjes op Cook Inlet een bijzondere vaardigheid bij het zoeken van ingegraven prooien overbodig maken. Aan de andere kant zou het ook een aanwijzing kunnen zijn dat het foerageren op tast (noodzakelijk voor het opsporen van ingegraven schelpdieren) een geconserveerde eigenschap is in steltlopers, zelfs voor een ondersoort zoals de *tschuktschorum*, die deze manier van foerageren normaliter weinig gebruikt. De hogere snelheid in voedselinname en -verwerking door *ptiloc-*

nemis in vergelijking met *tschuktschorum* lijkt het resultaat van fysiologische verschillen tussen de beide ondersoorten.

Om te begrijpen hoe het mogelijk is dat Beringstrandlopers van de ondersoort *ptilocnemis* succesvol de winter doorkomen in het noorden van Cook Inlet moeten nog heel wat puzzelstukjes op hun plaats vallen. Zoals bij de meeste goede puzzels is het niet gemakkelijk te zien hoe de stukjes in elkaar passen, zelfs wanneer we alle puzzelstukjes bezitten. Toch beginnen we langzaam aan een idee te krijgen hoe het allemaal functioneert. We beschikken over de relevante informatie wat betreft het gedrag, de omgeving, de stofwisseling en de fysiologische kenmerken van *ptilocnemis* en zijn belangrijkste prooidier, het Nonnetje, om vast te kunnen stellen wat de rol van deze factoren is bij het overwinteren van *ptilocnemis* in het noorden. Onze resultaten suggereren dat *ptilocnemis* voortdurend tegen energetische grenzen aanloopt, omdat lange, aaneengesloten foerageerperiodes nodig zijn om aan de hoge energiebehoefte in een koude omgeving te kunnen voldoen. We schatten de stofwisselingsnelheid aan de hand van langjarige, klimatologische informatie. Hieruit leidden we af dat de snelste stofwisseling plaatsvindt in januari, de koudste maand in de regio. Deze toename in stofwisselingssnelheid was zeven keer hoger dan het basaalmetabolisme van *ptilocnemis*, vergelijkbaar met dat van steltlopers tijdens de trek. Het lijkt erop dat *ptilocnemis*, om de winter door te brengen in het noorden van Cook Inlet, vergelijkbare metabole en fysiologische veranderingen ondergaat, zoals die worden waargenomen bij migrerende steltlopers. Actieve migratie vindt echter plaats tijdens een relatief korte periode, terwijl *ptilocnemis* maanden lang een verhoogde stofwisseling moet onderhouden.

Benthische organismen komen over het algemeen in zulke hoge dichtheden voor, dat de voedselopname voor molluscivore steltlopers zoals *ptilocnemis* niet beperkt wordt door de tijd die nodig is om de begraven prooien te vinden. De beperkende factor is de spijsvertering, omdat de maag tijd nodig heeft voor het kraken en verwerken van de schelp. Omdat kleine Nonnetjes een gunstiger vlees/schelp-ratio hebben dan grote exemplaren, leveren zij meer energie per gram schelpafval op. Voor foeragerende vogels zoals *ptilocnemis* die in hun voedselinname beperkt worden door hun verteringsnelheid, vormen kleine Nonnetjes een kwalitatief hoogwaardigere voedselbron dan grote. Inderdaad hangt de foerageertijd voor *ptilocnemis* in het noorden van Cook Inlet af van de grootte van de beschikbare Nonnetjes. Onder de meest barre omstandigheden in het noorden van Cook Inlet (januari), varieert de benodigde foerageertijd, afhankelijk van de geconsumeerde schelpgrootte, van 15.4 (uitgaande van Nonnetjes van 6.5 mm) tot 21.4 u d^{-1} (15 mm). Omdat de gemiddelde duur van het droogvallen van de wadplaten 17.7u bedraagt, kunnen de vogels zich feitelijk geen prooidieren van lage kwaliteit permitteren. Wanneer het landijs zich sterk ontwikkelt, neemt de beschikbare tijd om aan voedsel te komen nog eens verder af. *Ptilocnemis* minimaliseert zijn foerageertijd daarom door te selecteren op kleine, kwalitatief hoogwaardige prooien en door het gebruik van de wadplaten te optimaliseren door het opkomende en afvallende tij te volgen.

Dit werk beschrijft de vele gedrags- en fysiologische aanpassingen die het *ptilocnemis* Beringstrandlopers mogelijk maken hun winter door te brengen in hoge noorden van Alaska. Veel van het werk dat werd uitgevoerd tijdens dit promotieonderzoek was, noodzakelijkerwijs, gebaseerd op observaties of experimenten. De volgende uitdaging ligt in het vertalen van deze resultaten naar het veld. Gegeven het relatief kleine oppervlakte van het studiegebied lijkt het onderzochte systeem zich goed te lenen voor een gedetailleerd onderzoek naar de verplaatsingen van strandlopers met behulp van telemetrie. Wanneer dit tegelijk wordt uitgevoerd met onderzoek waarbij gebruikt gemaakt wordt van het (terug-)vangen van individuen en niet-invasieve technieken om orgaangroottes en vetreserves te meten, zou men belangrijke mechanistische verbanden tussen de omgeving, het gedrag en de fysiologie van dit unieke systeem kunnen vastleggen. Jammer genoeg maakt het regelmatige bevriezen van poten en veren van *ptilocnemis* het bevestigen van zenders problematisch. Het gedrag van de vogels zou kunnen veranderen, de vogels zouden het gebied kunnen verlaten, of ze kunnen voortijdig kunnen sterven wanneer het ijs zich aan de zender hecht. Daarbij heeft ervaring ons geleerd dat vogels die zich verplaatsen tussen uitgestrekte, zachte moddervlaktes en hoogwatervluchtplaatsen op het zeeijs erg moeilijk te vangen zijn. Daarom wachten we op technologische verbeteringen die het ons mogelijk zullen maken onze doelen na te streven.

Een onverwacht resultaat van deze studie is de ontdekking dat Macoma balthica een primaire rol speelt in het faciliteren van *ptilocnemis* in het noorden van Cook Inlet. In vergelijking met andere locaties zijn Nonnetjes in het noorden van Cook Inlet, door de relatief dunne schelp en grote hoeveelheid vlees, bijzonder goed voedsel voor *ptilocnemis*. Schelpen zijn relatief gemakkelijk te inventariseren (maar niet goedkoop!) en het herhaaldelijk verzamelen in het noorden van Cook Inlet zou de interpretatie van de verspreidingspatronen van *ptilocnemis* mogelijk maken. Deze informatie is vooral kostbaar in het licht van toekomstige klimaatveranderingen. De voorspelde opwarming van het klimaat zou bijvoorbeeld thermogene voordelen voor *ptilocnemis* kunnen betekenen, waardoor de stofwisselingsnelheid verlaagd kan worden en waardoor de benodigde foerageertijd kan verminderen. Opwarming zou aan de andere kant ook nadelig uit kunnen pakken voor Nonnetjes, zodanig dat de mogelijke voordelen voor *ptilocnemis* helemaal teniet worden gedaan. In andere, meer gematigde gebieden spelen ongewervelden (zoals krabben, garnalen en slakken) een belangrijke rol als predator van Nonnetjes. Dit soort predatoren zijn nu zeldzaam in Cook Inlet.

Er wordt gezegd het troebele water en de heersende stromingrichtingen de primaire productiviteit van het gebied beperken, terwijl de lage winter temperaturen voorkomen dat wadplaten gekolonialiseerd worden door de voornaamste predatoren van Nonnetjes. Wanneer Cook Inlet opwarmt zou dit de introductie van ongewervelde predatoren kunnen faciliteren. Omdat ongewervelden vooral kleine 'Nonnetjes met dunne schelpen consumeren, zouden deze predatoren kunnen veroorzaken dat er een snelle selectie voor zwaardere schelpen in Nonnetjes ontstaat.

Dit zou ten koste van *ptilocnemis* gaan en ons werk wijst erop, dat zelfs een kleine afname van de kwaliteit van Nonnetjes in dit gebied het voor *ptilocnemis* onmogelijk zou maken om hier te kunnen overwinteren. Het systematisch inventariseren van de kwaliteit en de verspreiding van Nonnetjes in het noorden van Cook Inlet zou dus belangrijke inzichten kunnen verschaffen over actuele en toekomstige verspreidingspatronen van *ptilocnemis*.

Wat voor effect het opwarmen van het klimaat ook heeft op *ptilocnemis* en zijn prooidieren in Alaska, het is van belang om te noemen dat foerageergebieden van Cook Inlet geologisch van recente datum zijn. Geologen schatten dat de Holocene gletsjers zich ongeveer 14.000 jaar geleden terugtrokken uit de regio, waardoor zout water de kans kreeg om over het vrijgekomen land te stromen. Deze nieuwe getijzone werd vervolgens gekolonialiseerd door bentische tweekleppigen. Het gebruik van Cook Inlet door Beringstrandlopers is dus een betrekkelijk nieuw fenomeen en zal ongetwijfeld aan voortdurende veranderingen onderhevig zijn.

Beringia, het noordelijke gebied in de Stille Oceaan waar Beringstrandlopers zijn geëvolueerd, is een gebied dat enorme veranderingen heeft ondergaan tijdens het Pleistoceen en Holoceen. Als gevolg van een dynamisch klimaat waren er opeenvolgende periodes van toe- en afname van de hoeveelheid landijs. Andere gebieden bleven min of meer permanent bedekt met ijs. Deze historische klimaatschommelingen hebben ongetwijfeld een rol gespeeld in de mate waarin *ptilocnemis* nu beschikt over zijn fenotypische flexibiliteit en intrinsieke reacties op de extreme omgevingsfactoren van het noorden van Cook Inlet. Deze eigenschappen vormen een goede basis voor het verdere voortbestaan van deze unieke overwinteringsecologie.

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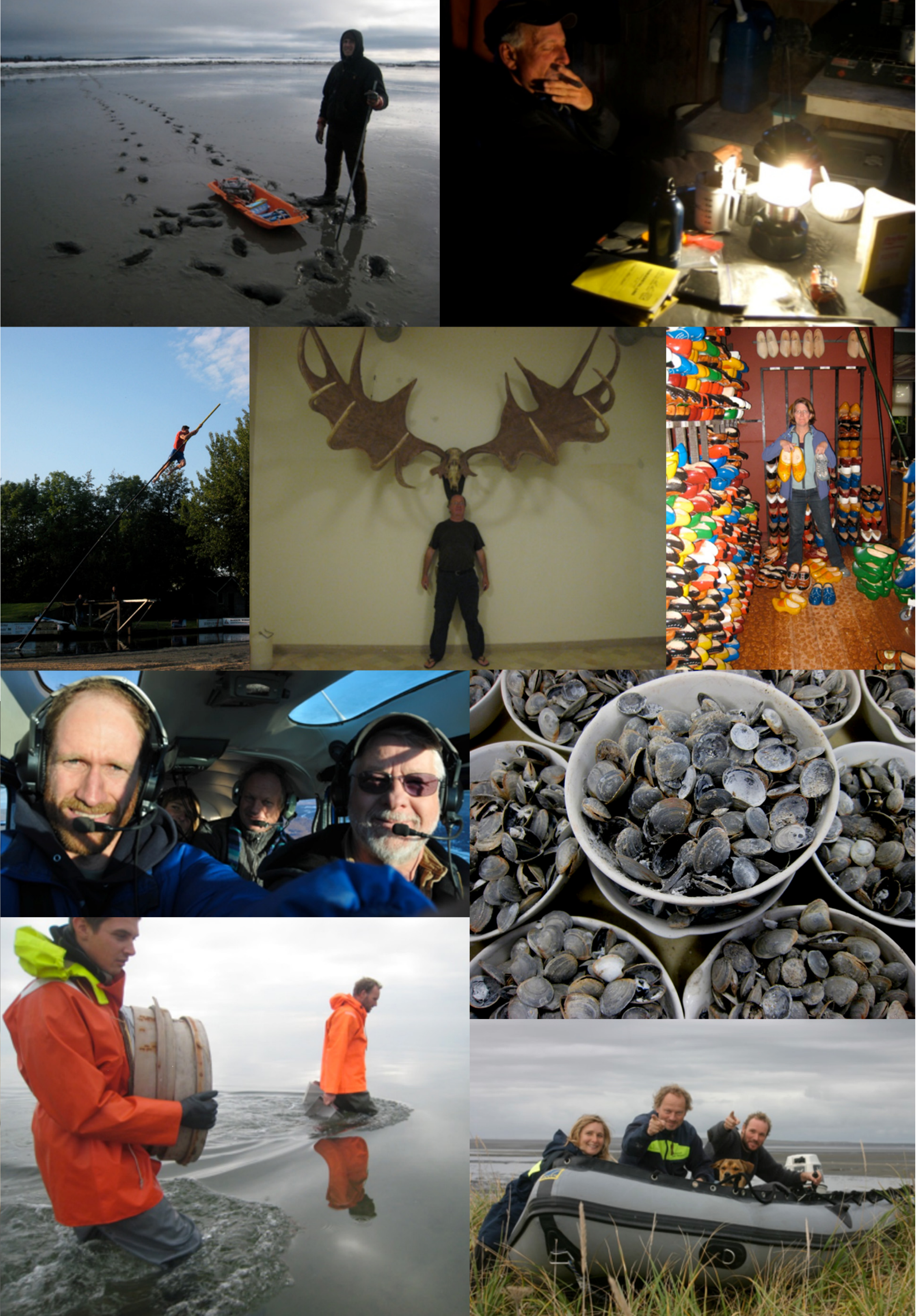

"One flock of about 20 birds was found at Cold Bay…they were found as usual huddled closely together on a slippery, spray-washed rock, apparently oblivious of everything, and showing no particular interest in life." Wilfred Osgood, 1904, Biological reconnaissance of the base of the Alaska Peninsula, North American Fauna

Wilfred Osgood's observations always remind me that when faced with the opportunity to conduct PhD research, I chose to investigate the nonbreeding ecology of a species that does not chase the sun. Had I cleverly chosen Bristle-thighed Curlews for my focal species, I might be summarizing observations of birds roosting in coconut palms on atolls in the South Pacific. But Rock Sandpipers, as Osgood suggests, are hardy and practical birds, flying only as far as suits them each winter. And this life history, though full of ice, wind, and long winter nights, is fascinating for its apparently illogical nature. So I have no regrets about my choice, a choice only made possible by the help, support, encouragement, and hard work of many collaborators.

A list of acknowledgements can be nearly endless if one honestly considers the many influences and interactions that led one to the present moment. And so it is for me, with a long backwards gaze. I cannot acknowledge those who helped on this thesis without also sincerely thanking those who led me to the opportunity. For this, I first thank my family for their long support. Their enthusiasm about my travels and work (and seeming lack of concern about my poverty, non-existent health insurance, and protracted adolescence) bolstered my confidence as I became more and more certain in my pursuits. I thank them for their love and encouragement that allowed me the comfort to explore, knowing that I had a home to return to when things got tight. Thank you all for supporting me.

Over the course of my career I have also been fortunate to interact with numerous individuals who slowly but surely spurred my interest in shorebirds. For my introduction both to shorebirds and Alaska, I thank Lee Tibbitts. I arrived in Alaska in 1996 to volunteer on her project studying the breeding and foraging ecology of boreal-nesting shorebirds. I was fresh off the island of Hawaii, having spent a wonderful winter trapping and banding forest passerines. I freely admit that I was not very enthusiastic to leave Hawaii for Alaska in order to study Greater and Lesser yellowlegs, two shorebird species renowned for their grating loquacity, but Lee introduced me to the splendor of shorebirds and became a fast friend and continued mentor. It all started here, swatting mosquitoes in the bogs around Anchorage, and somehow it stuck. Lee's curiosity, enthusiasm, and dogged tenacity have helped to overcome many shorebird obstacles. Thank you, Lee; it's been a great run so far.

As the summer of 1996 wound down and Lee's volunteer opportunity ended, I was lucky enough to land a job within the same office working for Colleen Handel. Between Lee and Colleen, I was now firmly and happily stuck in the shorebird world. Although I spent two years working with Colleen on a study of forest passerines, she encouraged my nascent shorebird pursuits. Colleen's interests are varied and deep, but shorebirds are a constant theme. So when I began to inquire about graduate school opportunities, she introduced me to her close friend Brian McCaffery. Colleen put in a good word for me, and Brian took me on to pursue a Master's degree on the Yukon Delta National Wildlife Refuge studying the reproductive ecology of Western Sandpipers. If boreal shorebirds were the bait, tundra-breeding shorebirds set the hook. I was in heaven. And it wasn't just the birds; Brian's mad-scientist passion, observational acuity, discipline, and pun-strewn humor helped me to see the birds differently, and better at that. Memories from those three summers inspire me still. Thank you, Brian, for your continued friendship, and for always pushing me further by setting your fine examples.

Footloose and jobless upon completion of my Master's degree in 2002, Lee angled to get me back to Anchorage for the summer to help on some projects that she and Bob Gill were pursuing. When I first worked with Lee in 1996, she was into her first decade of working with Bob Gill on the endless list of under-studied shorebirds in Alaska. At that time Bob was, to me, a slightly imposing, businesslike boss that I only rarely saw as he came and went on his rambles with energetic Russians to study Surfbirds and Wandering Tattlers. Now in 2002, I was actually working closely with Bob, and the previously stiff employer-employee relationship quickly faded. Marooned on St. George Island that spring with Lee, Bob, and Maksim Dementyev, it was a wonderful shorebird boot camp. And if I didn't know Bob well previously, I certainly did by the end of this summer. With trips to Cook Inlet, St. George, and Noatak and Kobuk Valley National Parks, this marked the beginning of our friendship and a great decade of working together. I thank Bob for the numerous work opportunities, snorts of scotch whisky, grammar lessons, harangues, hurrahs, and everything in between. I still recall the time in 2007 when Bob innocently but purposefully broached with me the topic of pursuing a PhD. I was encouraged to think that Bob believed I could do it, a vote of confidence that helped me on my way. And who better than Bob to guide me in the study of Rock Sandpipers? Bob has been researching Rock Sandpipers for nearly forty years, and it has been a pleasure to learn from the source. I truly could not have done this without Bob's help. Thank you, Bob, for all the support and encouragement.

I am very fortunate to have haphazardly fallen in with this amazing group of mentors. Not only did they all share with me their love of shorebirds, science, and conservation, but I also managed a nice group of friends along the way. Among Lee, Colleen, Brian, and Bob, I have also had the opportunity to meet and interact with numerous other inspiring folks. To Phil Battley, Mark Colwell, Dov Lank, David Melville, Pavel Tomkovich, and Nils Warnock, thank you all for the encouraging pushes, whether you knew you were pushing or not. The most recent links in this ever-growing chain of interactions belong to Anne Dekinga and Theunis Piersma. Bob and Brian helped to organize an international expedition in 2005, funded by the Swedish government, to study the migration ecology of shorebirds staging in Alaska. The bulk of the work occurred on the Yukon-Kuskokwim Delta, but I happened to be at a camp at Egegik Bay on the Alaska Peninsula. In 2004, Anne Dekinga visited in order to assess the suitability of Egegik as a site for capturing Bar-tailed Godwits, and we quickly hit it off. I suspect the wind, rain, and fresh air was abundantly suitable for a Frisian. Anne had such fun that Theunis and Petra de Goeij came to join us in Egegik the next year. I did not overlap long on that trip with Anne, Theunis, and Petra, but I can't think of a better way to get to know someone than in the intimate surroundings of a leaky plywood cabin, preferably surrounded by tens of thousands of migrating shorebirds—including, coincidentally, Rock Sandpipers. Theunis had long been impressed by the unusual winter ecology of Rock Sandpipers, but Alaska's cold, coupled with the birds' remote distributions, makes studying Rock Sandpipers in the wild logistically impractical. But Theunis had the idea to bring captive Rock Sandpipers to the Royal Netherlands Institute for Sea Research for experimental work, and offered me the opportunity to stay on Texel and properly study the birds for my PhD. Ultimately it was (and has been) Theunis' indomitable enthusiasm and conviction that made this work. There are always details to arrange, but Theunis made things happen, overcoming my cautious reluctance. And it was Anne who arranged the practicalities of the transport and subsequent experimental trials, and guided my way with the nuts-and-bolts of the entire operation. Anne helped resurrect NIOZ's respirometry equipment, taught me the ins and outs of a Soxhlet apparatus, tirelessly scraped mussels with me at Paal 9, drove me to France on a mission to harvest *Macoma*, and organized aquaria for the housing of thousands of *Macoma* and *Mya*. I could not have done this without Anne's know-how and generous assistance.

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Tijssen for taking me to see Sinterklass arrive in Oudeschild by boat from Spain, Theunis for a tour of both the clog museum and Koninklijk Eise Eisinga Planetarium, Ysbrand for explaining the intricacies of fierljeppen, and Anita Koolhaas for a tasting menu of cheeses and stompots. I thank Geert Aarts and Eldar Rakhimberdiev for helping ease my way into Program R, and Jan van Gils and Allert Bijleveld for assistance with experimental design and set-up. Petra de Goeij always lent a patient ear as I tussled with my latest dilemma, and I appreciated Henk van der Veer's welcoming attitude towards an Alaskan stranger bearing noisy captive shorebirds. Patrick Triplet and Faustine Simon were very helpful in guiding us to *Macoma* hotspots near Parc du Marquenterre, Baie de Somme, France. Eva Kok and Kees Camphuysen provided the Dutch translations within the dissertation, and I am grateful to have benefitted from Dick Visser's talents in arranging and designing the layout of this book. And because a man cannot live on inspiration alone, I am especially grateful for financial assistance throughout the project from Bob (US Geological Survey) and Theunis (NIOZ).

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