



Royal Netherlands Institute for Sea Research

This is a preprint of:

Ruthrauff, D.R.; Dekinga, A.; Gill, R.E. & Piersma, T. (2018). Energetic solutions of Rock Sandpipers to harsh winter conditions rely on prey quality. *Ibis*, 160, 397-412

Published version: <https://dx.doi.org/10.1111/ibi.12534>

Link NIOZ Repository: <http://www.vliz.be/imis?module=ref&refid=291241>

[Article begins on next page]

The NIOZ Repository gives free access to the digital collection of the work of the Royal Netherlands Institute for Sea Research. This archive is managed according to the principles of the [Open Access Movement](#), and the [Open Archive Initiative](#). Each publication should be cited to its original source - please use the reference as presented.

When using parts of, or whole publications in your own work, permission from the author(s) or copyright holder(s) is always needed.

RH: *Constraints during winter in a northerly shorebird*

1 **Energetic constraints of Rock Sandpipers at the northern extent of their**
2 **range emphasize unique attributes of their benthic prey**

3

4 DANIEL R. RUTHRAUFF,^{1,2,3*} ANNE DEKINGA,² ROBERT E. GILL, JR.,¹ &
5 THEUNIS PIERSMA^{2,3}

6

7 ¹*Alaska Science Center, U.S. Geological Survey, 4210 University Drive,*
8 *Anchorage, AK 99508, USA*

9

10 ²*Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea*
11 *Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands*

12

13 ³*Chair in Global Flyway Ecology, Conservation Ecology Group, Groningen*
14 *Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O.*
15 *Box 11103, 9700 CC Groningen, The Netherlands*

16

17 *Corresponding author. E-mail: druthrauff@usgs.gov

18

RH: *Constraints during winter in a northerly shorebird*

19 **SUMMARY**

20 Rock Sandpipers *Calidris p. ptilocnemis* have the most northerly nonbreeding
21 distribution of any shorebird in the Pacific Basin (upper Cook Inlet, Alaska [61°N,
22 151°W]). In terms of freezing temperatures, persistent winds, and pervasive ice,
23 this site is the harshest used by shorebirds during winter. We integrated
24 physiological, metabolic, behavioural, and environmental aspects of the
25 nonbreeding ecology of Rock Sandpipers at the northern extent of their range to
26 determine the relative importance of these factors in facilitating their unique
27 nonbreeding ecology. Not surprisingly, estimated daily energetic demands were
28 greatest (372 kJ) during the coldest periods of winter (January). These estimates
29 are over 7 times greater than basal metabolic rates, a scope of increase that
30 approaches the maximum sustained rate of energetic output by shorebirds during
31 periods of migration, but far exceeds these periods in duration. We assessed the
32 quality of their primary prey, the bivalve *Macoma balthica*, to determine the daily
33 foraging duration required by Rock Sandpipers to satisfy such energetic
34 demands. Based on size-specific estimates of *Macoma* quality, Rock Sandpipers
35 require $>17 \text{ h d}^{-1}$ of foraging time in upper Cook Inlet in January. This range
36 approaches the average daily duration of mudflat availability in this region (~18
37 h), a maximum value that annually decreases due to the accumulation of shore-
38 fast ice. Rock Sandpipers likely maximize access to foraging sites by following
39 the exposure of ice-free mudflats across the upper Cook Inlet region and by
40 selecting smaller, higher quality *Macoma* to minimize foraging times. Ultimately,

RH: *Constraints during winter in a northerly shorebird*

41 this unusual nonbreeding ecology hinges upon the high quality of their *Macoma*
42 prey resources. Compared to other sites across their range, *Macoma balthica*
43 from upper Cook Inlet have relatively light shells, potentially a result of the
44 region's depauperate invertebrate predator community. We posit that future
45 thermogenic benefits of a warming upper Cook Inlet climate to Rock Sandpipers
46 may be offset by impacts to *Macoma balthica* survival and quality.

47

48 **Keywords:** animal distribution, climate change, intake rates, *Macoma balthica*,
49 metabolic expenditure, resource quality, Rock Sandpiper, *Calidris ptilocnemis*

RH: *Constraints during winter in a northerly shorebird*

50 INTRODUCTION

51 Animal distributional patterns reflect a multitude of physical, social, and biological
52 interactions (MacArthur 1984, Brown 1995, Gaston 2003), but at the most
53 fundamental level an animal's distribution is determined simply by the species'
54 ability to survive in a given environment. This characteristic reflects an
55 organism's adaptive, ecophysiological response to its environment (Root 1988,
56 Spicer & Gaston 1999), and study of organisms at the limits of their geographic
57 ranges can elucidate factors shaping these limits (Gaston 2009, Sexton *et al.*
58 2009). At high northern latitudes during winter, environmental conditions are
59 often characterized by low temperatures and low availability of food resources.
60 From a physiological perspective, range limits in these environments are thus
61 often influenced by an animal's ability to satisfy high cold-induced energetic
62 demands in the face of low resource abundance.

63 Shorebirds (Charadriiformes, suborders Charadrii and Scolopaci) are a
64 globally distributed, highly diverse avian taxa (Piersma *et al.* 1996) that constitute
65 a conspicuous component of wetland and coastal ecosystems. Most shorebird
66 species use their highly sensitive bills to peck or probe in soft substrates for prey
67 resources, a mode of foraging that predisposes them to regions of the globe that
68 ensure access to ice-free habitats (Piersma 1996, Piersma *et al.* 1996).
69 Additionally, because shorebirds have relatively high metabolic rates (Kersten &
70 Piersma 1987), they risk starvation when subjected to extended periods without
71 access to food (Marcström & Mascher 1979, Davidson & Evans 1982,
72 Camphuysen *et al.* 1996). These traits effectively serve to constrain the

RH: *Constraints during winter in a northerly shorebird*

73 nonbreeding distribution of most shorebirds to shorelines in temperate and
74 tropical regions (Piersma 1996, Colwell 2010).

75 Despite their affinity for shoreline habitats during the nonbreeding season,
76 most shorebird species breed at inland sites, often at high northern latitudes, and
77 conduct long annual migrations between breeding and nonbreeding sites
78 (Piersma *et al.* 1996, van de Kam *et al.* 2004). Shorebirds are renowned for
79 conducting long-distance migrations (Piersma & Davidson 1992, Battley *et al.*
80 2000, Gill *et al.* 2009), a natural history characteristic that has evolved to exploit
81 ephemerally abundant resources at sites during a relatively brief (2–3 months)
82 breeding season (Colwell 2010). As the breeding season wanes and conditions
83 at these sites deteriorate, such migratory behaviour also avoids the risk of
84 starvation that shorebirds would otherwise face by remaining at high northern
85 latitudes during winter. The life history of shorebirds breeding at high northern
86 latitudes, then, is generally characterized by long migrations between breeding
87 sites with ephemerally abundant food resources and nonbreeding sites at
88 temperate or tropical locations with predictable food resources (Piersma *et al.*
89 1996, Colwell 2010).

90 A few species of shorebird serve as exceptions to these trends, however,
91 and spend the nonbreeding season at high latitude sites that experience cold,
92 dark winters (Cramp & Simmons 1983, Summers *et al.* 1990). One such
93 shorebird is the Rock Sandpiper *Calidris ptilocnemis*. Rock Sandpipers are
94 common residents of the North Pacific Basin (Gill *et al.* 2002), and are not
95 unusual in size, appearance, or habits compared to other shorebirds breeding at

RH: *Constraints during winter in a northerly shorebird*

96 high latitude sites. Rock Sandpipers are unique, however, for the range of
97 environmental conditions they experience across their nonbreeding distribution.
98 Rock Sandpipers comprise four subspecies (Conover 1944, Pruett & Winker
99 2005) that exhibit differential migration patterns, a trait that exposes each
100 subspecies to distinct environmental conditions. At one extreme, most *C. p.*
101 *tschuktschorum* individuals migrate relatively long distances between
102 comparatively benign nonbreeding sites along the Pacific Northwest coast of
103 North America and breeding sites in western Alaska and the Chukotka
104 Peninsula, Russia (Gill *et al.* 2002, Lappo *et al.* 2012). At the other extreme, *C. p.*
105 *quarta* and *C. p. couesi* are essentially non-migratory, distributed throughout their
106 annual cycle at sites in the Commander Islands (*C. p. quarta*) and the Aleutian
107 Archipelago and Alaska Peninsula (*C. p. couesi*; Gill *et al.* 2002, Lappo *et al.*
108 2012). Unique among North American shorebirds, the primary nonbreeding
109 location of the fourth subspecies, *C. p. ptilocnemis* (hereafter *ptilocnemis*), is
110 farther north (1–4° latitude) than its breeding grounds (Figure 1). *Ptilocnemis*
111 conducts an east-west migration between their central Bering Sea breeding
112 grounds (Gill *et al.* 2002, Ruthrauff *et al.* 2012) and their primary wintering range
113 in upper Cook Inlet, Alaska (Gill & Tibbitts 1999, Ruthrauff *et al.* 2013c).

114 The northern extent of the *ptilocnemis* nonbreeding range in Cook Inlet
115 (61°N, 151°W; Figure 1), represents the most northerly winter distribution of any
116 shorebird in the Pacific Basin (Ruthrauff *et al.* 2013c). Ruthrauff *et al.* (2013c)
117 demonstrated that environmental conditions at this site are also the coldest
118 experienced by any nonbreeding shorebird in the world. The average daily high

RH: *Constraints during winter in a northerly shorebird*

119 temperature in this region is $\leq 0^{\circ}\text{C}$ for nearly 140 consecutive days between early
120 November and mid-March (Ruthrauff *et al.* 2013c), and such cold induces high
121 metabolic demands in birds (Vézina *et al.* 2006, Swanson 2010, Ruthrauff *et al.*
122 2013a). For *ptilocnemis* in Cook Inlet, these energetic demands are satisfied by
123 the consumption of the bivalve *Macoma balthica* (Gill & Tibbitts 1999, Gill *et al.*
124 2002). *Macoma* occur in high densities in Cook Inlet (Ruthrauff *et al.* 2013c), but
125 are only accessible to *ptilocnemis* during periods of low tide. Cook Inlet
126 experiences tidal fluctuations of over 10 m (Oey *et al.* 2007) across mudflats that
127 extend up to 7 km at low tide; when coupled with the region's cold temperatures,
128 *ptilocnemis* foraging habitats are subject to both direct freezing as well as
129 coverage by sea and shore-fast ice (Ruthrauff *et al.* 2013c). Thus, *ptilocnemis*
130 must satisfy high daily energetic requirements by exploiting a feeding window
131 initiated by the exposure of the mudflats below shore-fast ice on falling tides,
132 hastened by the freezing of exposed mudflats, and terminated by coverage with
133 ice or a flooding tide.

134 Numerous physiological (Ruthrauff *et al.* 2013b, 2015), metabolic
135 (Ruthrauff *et al.* 2013a), behavioural (Ruthrauff & Eskelin 2009, Ruthrauff *et al.*
136 2015), and environmental (Ruthrauff *et al.* 2013c) factors have been identified
137 that together support this unique nonbreeding life history. Herein we integrate
138 these various components across a range of climatological scenarios to model
139 potential energetic constraints facing *ptilocnemis* during their winter occupancy of
140 upper Cook Inlet, Alaska. We estimated *ptilocnemis*' daily energetic demands
141 and the concomitant foraging durations required to satisfy these demands.

RH: *Constraints during winter in a northerly shorebird*

142 Ruthrauff *et al.* (2015) hypothesized that the colonization of upper Cook Inlet by
143 *ptilocnemis* was a relatively recent phenomenon facilitated by recent climate
144 warming that both formed Cook Inlet as a physical feature (Schmoll *et al.* 1999,
145 Reger *et al.* 2007) and promoted its colonization by *Macoma balthica* (Schmoll *et*
146 *al.* 1972). We further demonstrate that *Macoma* from upper Cook Inlet possess
147 unique attributes compared to *Macoma* from other sites. These attributes
148 enhance their quality as prey, and ultimately permit the high-latitude nonbreeding
149 distribution of *ptilocnemis* Rock Sandpipers. Ironically, the climate warming that
150 enabled this unique occurrence may hasten its end: although future climate
151 warming will offer thermogenic relief to *ptilocnemis*, it may also promote
152 ecosystem changes that may negatively alter the quality of Cook Inlet *Macoma*
153 as prey resources.

154 **METHODS**

155 We estimated the energetic demands of *ptilocnemis* across the months when
156 *ptilocnemis* is present in upper Cook Inlet (October–April; Ruthrauff *et al.* 2013c).
157 We integrated summaries of long-term climatological and environmental
158 conditions in upper Cook Inlet along with interrelated ecological components that
159 reflect ecophysiological characteristics of *ptilocnemis* or their primary prey,
160 *Macoma balthica*. These components include presence/absence estimates of
161 *ptilocnemis* in upper Cook Inlet during winter, intake rates and size preferences
162 of *ptilocnemis* feeding on *Macoma*, lipid stores and sizes of relevant organ

RH: *Constraints during winter in a northerly shorebird*

163 groups of *ptilocnemis* during winter, and size-related estimates of *Macoma*
164 quality. We describe each of these components below.

165 **Climatological and environmental summaries**

166 Climatological summaries follow procedures outlined by Ruthrauff *et al.* (2013c)
167 to derive values for long-term (1952–2015) average and extreme temperatures
168 and average winds in upper Cook Inlet
169 ([http://www7.ncdc.noaa.gov/IPS/lcd/lcd.html?_page=1&state=](http://www7.ncdc.noaa.gov/IPS/lcd/lcd.html?_page=1&state=AK&stationID=26451&_target2=Next+%3E)
170 [AK&stationID=26451&_target2=Next+%3E](http://www7.ncdc.noaa.gov/IPS/lcd/lcd.html?_page=1&state=AK&stationID=26451&_target2=Next+%3E)). For these summaries, we used
171 datasets for Anchorage, Alaska, in upper Cook Inlet (Figure 1) and the site with
172 the region's most extensive historical climatological information. Ruthrauff *et al.*
173 (2013c) determined that temperatures at this location were representative of
174 those at nearby locations (within 100 km) primarily used by *ptilocnemis*. We
175 calculated monthly average estimates of solar insolation in upper Cook Inlet
176 using National Aeronautics and Space Administration
177 (<https://eosweb.larc.nasa.gov/sse/>) datasets, and estimated the average monthly
178 and historical extremes of shore-fast ice extent using National Ice Center
179 datasets (http://www.natice.noaa.gov/products/weekly_products.html) from the
180 period October 2006–April 2015 following procedures described by Ruthrauff *et*
181 *al.* (2013c).

182 To estimate the amount of time that mudflats were exposed and
183 potentially available for foraging to *ptilocnemis* each day, we analyzed archived
184 images from the Federal Aviation Administration (<http://avcams.faa.gov/>) taken

RH: *Constraints during winter in a northerly shorebird*

185 overlooking the northern portion of Redoubt Bay (Figure 1), one of the primary
186 sites used by *ptilocnemis* in upper Cook Inlet (Ruthrauff *et al.* 2013c). Given the
187 region's patterns of sediment input (Bartsch-Winkler & Ovenshine 1984),
188 currents (Johnson 2008), tidal inundation and subsurface geomorphologies (Oey
189 *et al.* 2007, Ezer & Liu 2010), we assumed that mudflat exposure processes at
190 Redoubt Bay were representative of those at other nearby sites also used by
191 Rock Sandpipers. Images were taken at 10-minute intervals, and we observed
192 diurnal images only on days during which the mudflats were clearly visible
193 throughout the entire day. The time period over which we analyzed images did
194 not contain shore-fast ice, and as such these summaries yield estimates of
195 maximum potential mudflat exposure.

196 **Rock Sandpiper occurrence in upper Cook Inlet**

197 The winter abundance and distribution of Rock Sandpipers in upper Cook Inlet
198 was summarized from 99 aerial surveys across 16 winter seasons by Ruthrauff
199 *et al.* (2013c). Ruthrauff *et al.* observed large numbers of *ptilocnemis* displaced
200 from preferred sites in northern Cook Inlet to less-commonly used southern sites
201 on two occasions, and these displacement events coincided with periods of
202 unusually low temperatures that deviated from long-term averages by as much
203 as 20°C (Ruthrauff *et al.* 2013c). Based on the distribution patterns during (i.e.,
204 southward displacements and decreasing survey totals) and immediately
205 following (i.e., northward movements and increasing survey totals) the periods of
206 deep cold, Ruthrauff *et al.* (2013c) assumed that the aberrantly low temperatures

RH: *Constraints during winter in a northerly shorebird*

207 created unsustainable energetic demands that precipitated the movement to less
208 thermally-demanding sites outside the survey area. For the purposes of this
209 model, we considered the environmental conditions during these two cold
210 periods as threshold values in our energetic model.

211 **Rock Sandpiper intake rates**

212 We applied estimates of long-term maximum prey intake rates for *ptilocnemis* to
213 determine the amount of foraging time required to satisfy energetic demands
214 under the various environmental scenarios. In molluscivorous shorebirds like
215 Rock Sandpipers, energy intake rates are constrained by the act of crushing and
216 processing shell waste (Piersma *et al.* 1993, van Gils *et al.* 2005b), and so we
217 modeled intake rates with respect to shell intake (mg s^{-1}). The intake rate of Rock
218 Sandpipers during winter is unknown, but van Gils *et al.* (2003) determined that
219 intake rates of *Macoma* in Red Knots *C. canutus*, a closely related shorebird
220 species, were accurately described as a function of fresh gizzard mass (g) by the
221 equation $\text{Intake} = 0.05 \times (\text{Gizzard Mass})^2$. We thus calculated intake rates based
222 on this relationship using the average winter gizzard mass value for *ptilocnemis*
223 (5.32 g) reported by Ruthrauff *et al.* (2013b).

224 ***Macoma* quality and Rock Sandpiper diet reconstruction**

225 To determine the quality of *Macoma balthica* as prey, we calculated the
226 relationships of both the ash-free dry mass (AFDM) of *Macoma* flesh and
227 *Macoma* shell mass (i.e., ballast) to *Macoma* shell length using standard
228 techniques (Zwarts 1991, van Gils *et al.* 2005b). For molluscivores like Rock

RH: *Constraints during winter in a northerly shorebird*

229 Sandpipers, quality is determined by the ratio of AFDM to shell ballast, and this
230 value varies as a function of *Macoma* shell length. We derived this relationship
231 from 98 *Macoma* (lengths 6.5–15.4 mm) collected at the mouth of the Kasilof
232 River (Figure 1) in upper Cook Inlet on 27 and 28 September 2011. To satisfy
233 model assumptions of linear regression, we calculated these relationships after
234 log transforming (base 10) values of shell length, AFDM, and shell ballast, and
235 back-transformed these estimates to yield outputs in mg. For comparative
236 purposes, we similarly determined the quality of 152 *Macoma balthica* (lengths
237 5.5–15.2 mm) collected from the Baie de Somme estuary, France (50.2°N,
238 1.6°E), on 9 and 10 March 2010.

239 We estimated prey size preferences using diet reconstruction techniques
240 (Dekinga & Piersma 1993). Because the hinges of *Macoma* shells are relatively
241 durable, they are preserved in the gizzards of molluscivorous shorebirds. We first
242 estimated the relationship between *Macoma* shell length and the height of each
243 hinge (i.e., ‘hinge plus top’ height, Dekinga & Piersma 1993) by fitting a two-
244 parameter power law function using the aforementioned 109 *Macoma* specimens
245 from upper Cook Inlet. We next removed hinges from the gut contents of eight
246 *ptilocnemis* specimens (two females, six males) collected in upper Cook Inlet on
247 15 January 1997 ($n = 4$ specimens) and 14 March 1998 ($n = 4$ specimens). We
248 measured all hinges and shell lengths using a 10X dissecting scope equipped
249 with digital measuring software (Leica Application Suite; Leica Microsystems,
250 Wetzlar, Germany). The bird specimens were collected approximately 100 km
251 north from where we collected the *Macoma* specimens, and we assumed that the

RH: *Constraints during winter in a northerly shorebird*

252 relationship between *Macoma* hinge height and *Macoma* shell length was similar
253 between these sites. We applied the relationship relating *Macoma* length to hinge
254 height to the hinges recovered from the *ptilocnemis* specimens to estimate the
255 lengths of the consumed *Macoma*.

256 **Model parameterization**

257 We used model 5 of Wiersma & Piersma (1994) to estimate the metabolic rate of
258 Rock Sandpipers across the range of environmental conditions described above.
259 This model estimates maintenance metabolic rates (Watts), defined as basal
260 metabolic rate (the energy consumption of a resting, postabsorptive animal in a
261 normothermic environment; IUPS Thermal Commission 2003) plus any extra
262 energetic demands associated with thermoregulation at environmental
263 temperatures below the thermoneutral zone (Wiersma & Piersma 1994). The
264 model integrates energetic costs associated with relevant environmental
265 conditions (e.g., wind, temperature, solar insolation; Evans 1976), as well as
266 microhabitat and thermal conductance (Wiersma & Piersma 1994). Ranges of
267 values for the first three variables are described above (see Climatological and
268 Environmental Summaries), while microhabitat-specific conductance parameters
269 derive from values in table 1 of Wiersma & Piersma (1994). In general,
270 observations of *ptilocnemis* in upper Cook Inlet primarily constitute closely
271 huddled roosting birds or loose groups of birds foraging on mudflats. Such
272 observations correspond to Wiersma & Piersma's 'Dense group' (i.e., roosting)
273 and 'Mudflat and bare salt marsh' (i.e., birds foraging in loose groups)

RH: *Constraints during winter in a northerly shorebird*

274 microhabitats (table 1, Wiersma & Piersma 1994). We used a value of 42.6°C
 275 (Ruthrauff *et al.* 2013a) for the body temperature of *ptilocnemis*, and used
 276 equation 8-15 from Calder (1996) to estimate thermal conductance of *ptilocnemis*
 277 as a function of body mass. We applied the average body mass value of
 278 *ptilocnemis* in upper Cook Inlet during winter (108.2 g) for this calculation
 279 (Ruthrauff *et al.* 2013b).

280 To further incorporate additional energetic demands associated with
 281 foraging behaviours (e.g., food processing [Piersma *et al.* 2003] and locomotion
 282 activities [Bruinzeel & Piersma 1998]), we applied results from doubly-labeled
 283 water experiments on Red Knots (Piersma *et al.* 2003) to estimate the proportion
 284 of the daily energy budget comprised by other activities associated with foraging
 285 behaviours. Piersma *et al.* (2003) determined that 32.3% of the energy budget of
 286 foraging Red Knots was constituted by food processing and 18.0% by foraging-
 287 related locomotion, and we augmented the maintenance metabolic rates
 288 estimated for foraging birds accordingly. We summed these behaviour-specific
 289 totals for each day to estimate average energetic demands in Watts, and
 290 converted these estimates into daily energetic equivalents (1 Watt = 3.6 kJ h⁻¹).

291 We implemented an energy balance approach to determine feeding
 292 durations. In its simplest form, we assumed that (energy intake) - (energy
 293 expenditure) = 0, where energy is expended either at rate M_F (foraging) or M_R
 294 (roosting). If T_F (h) is the total daily time spent foraging at a maximum energy
 295 intake rate I (kJ h⁻¹), our model is further parameterized as:

$$296 \quad (I \times T_F) - ((M_R \times (24 - T_F)) - (M_F \times T_F)) = 0 \quad \text{Equation 1}$$

RH: *Constraints during winter in a northerly shorebird*

297 We integrated our size-specific estimates of *Macoma* quality into calculations of *I*
298 by multiplying the estimate of maximum intake rate (g shell h^{-1}) by the estimates
299 of *Macoma* quality (kJ g^{-1} shell). We then solved for T_F to determine minimum
300 daily foraging durations necessary to satisfy estimated daily energy expenditures.

301 To link intake to metabolizable energy, we converted estimates of shell
302 ballast intake into their energetic equivalent (kJ g^{-1} shell ballast) assuming an
303 energy density of 22 kJ g^{-1} ash-free dry mass *Macoma* flesh (Zwarts & Wanink
304 1993, van Gils *et al.* 2005b), and an assimilation efficiency of 0.8 (Yang *et al.*
305 2013). We integrated these estimates across a range of representative shell
306 lengths determined by our diet reconstruction results. We conducted all analyses
307 in R version 3.1.2 (R Development Core Team 2014).

308 **RESULTS**

309 **Climatological and environmental setting**

310 The average daily temperature (the mean of each day's average high and low
311 temperature) and extreme temperatures during winter in upper Cook Inlet, Alaska
312 are plotted in Figure 2. The mean of the average daily temperatures are $\leq 0^\circ\text{C}$ for
313 the months November–March (Table 1). January is the coldest month, with the
314 daily temperature averaging -9.2°C . The average wind speed varies little over the
315 winter period ($\sim 3 \text{ m s}^{-1}$), but the amount of incident solar radiation varies by a
316 factor of about 25 between the months of December ($6.25 \text{ Watts m}^{-2}$) and April
317 ($165.42 \text{ Watts m}^{-2}$).

RH: *Constraints during winter in a northerly shorebird*

318 The extent of mudflat habitat in the regions of upper Cook Inlet used by
319 *ptilocnemis* is about 610 km² (Ruthrauff *et al.* 2013c). The average diurnal period
320 in the archived images of Redoubt Bay that we assessed was 11.3 ±0.2 SE h. Of
321 this period, 8.3 ±0.3 SE h constituted periods when mudflats were at least
322 minimally exposed. We extrapolated these values across a 24-h period, and
323 estimate that the average daily duration of mudflat exposure at Redoubt Bay is
324 17.7 ±0.5 SE h. Because we classified the mudflats as exposed in images when
325 any mudflat remained uncovered by water, this total serves as a maximum value
326 that decreases with accretion of shore-fast ice. The accumulation of shore-fast
327 ice in upper Cook Inlet tracks monthly temperatures in winter. Shore-fast ice is
328 typically present in upper Cook Inlet from November–March (Poole & Hufford
329 1982, Ruthrauff *et al.* 2013c), and averages ≥200 km² from December–March.
330 The maximum areal extent of shore-fast ice (271.1 ±53.7 SE km²) occurs in
331 January, a time coinciding with the winter season's coldest temperatures.

332 ***Macoma* quality and *ptilocnemis* diet reconstruction**

333 The relationships describing AFDM (mg) and shell ballast (mg) as a function of
334 shell length for *Macoma balthica* from upper Cook Inlet are $\log_{10}(\text{AFDM}) =$
335 $3.00(\log_{10}(\text{shell length}) - 2.01$ and $\log_{10}(\text{shell ballast}) = 3.42(\log_{10}(\text{shell length}) -$
336 1.80 , respectively (Figure 3). Similar assessments of *Macoma balthica* collected
337 in Baie de Somme, France, are described by the relationships $\log_{10}(\text{AFDM}) =$
338 $3.10(\log_{10}(\text{shell length}) - 2.18$ and $\log_{10}(\text{shell ballast}) = 3.68(\log_{10}(\text{shell length}) -$
339 1.90 . The 95% confidence intervals on these estimated relationships are non-

RH: *Constraints during winter in a northerly shorebird*

340 overlapping between sites (Figure 3). AFDM estimates are higher for same-sized
341 *Macoma* from upper Cook Inlet compared to Baie de Somme, while the
342 estimates for shell mass are lower at upper Cook Inlet compared to Baie de
343 Somme.

344 The ratio of AFDM to shell mass, and thus quality, is highest in small
345 *Macoma* at both sites, and the ratio decreases with increasing shell size (Figure
346 3). Estimates of quality range from 3.49–5.02 kJ g⁻¹ shell for *Macoma* from upper
347 Cook Inlet and 1.87–3.39 kJ g⁻¹ shell for *Macoma* from Baie de Somme (Figure
348 3). Quality varied less by size for *Macoma* from upper Cook Inlet (30.4%
349 difference between maximum and minimum values) compared to Baie de
350 Somme (44.8%). The relationship of shell length (SL) to hinge + top height (HTH)
351 for *Macoma* from upper Cook Inlet is described by the equation $SL =$
352 $14.094(\text{HTH})^{.754}$. We recovered 347 hinges from the eight *ptilocnemis* specimens
353 (range 12–78 hinges per specimen), and applied this formula to estimate
354 *Macoma* lengths. Based on this relationship, the mean length of *Macoma*
355 consumed by the eight *ptilocnemis* specimens was 9.9 ± 0.1 SE mm (range 5.2–
356 15.0 mm; Figure 3). Temperatures on the days when the specimens were
357 collected (15 January 1997 and 14 March 1998) were similar, with equal high
358 (5°C) and similar average (1.1°C and -1.1°C, respectively) and low (-2.8°C and --
359 1.1°C, respectively) temperatures.

RH: *Constraints during winter in a northerly shorebird*

360 **Seasonal energetic thresholds**

361 Estimated behaviour-specific maintenance metabolic rates (Watts) across the
362 winter season are presented in Table 1. Average estimated metabolic rates are
363 greatest for *ptilocnemis* during January (2.51 ['roosting' scenario]–6.07 ['foraging'
364 scenario] Watts; Table 1) and lowest in April (1.90 ['roosting' scenario]–4.62
365 ['foraging' scenario] Watts; Table 1). Ruthrauff *et al.* (2013c) conducted two
366 surveys under unusually cold conditions during which they detected relatively few
367 birds present in upper Cook Inlet, and only at less frequently used southern sites.
368 The average temperature for the week preceding these two surveys was 10.6°C
369 colder than normal, and the average minimum temperature during these periods
370 was -27.5°C. Metabolic rate estimates during these cold periods ranged from
371 3.00 ('roosting' scenarios)–7.27 ('foraging' scenarios) Watts. In contrast,
372 *ptilocnemis* was distributed at the frequently used, more northern sites during
373 surveys conducted immediately prior to and following these 'cold period'
374 observations (Ruthrauff *et al.* 2013c). The daily average temperatures during
375 these periods were just 0.5°C below long-term averages and minimum
376 temperatures averaged -16.0°C. Estimated metabolic rates during these periods
377 were ~18% lower (2.46 ['roosting' scenarios]–5.97 ['foraging' scenarios] Watts)
378 during these 'normal' periods preceding and following the 'cold' observations.

379 **Estimated intake rates and minimum required foraging durations**

380 Following the technique of van Gils *et al.* (2003), we estimated that the intake
381 rate of *ptilocnemis* during winter in upper Cook Inlet was 1.42 mg shell s⁻¹ (see

RH: *Constraints during winter in a northerly shorebird*

382 Methods). We applied this value to determine the minimum foraging duration
383 required by *ptilocnemis* to satisfy their daily energetic demands. We estimated
384 daily minimum foraging durations for five sizes of *Macoma*: 6.5 mm (size of
385 smallest *Macoma* in samples used to calculate quality estimates, Figure 2), 8.3
386 mm and 11.4 mm (interquartile values based on diet reconstruction, Figure 3),
387 9.9 mm (mean value based on diet reconstruction, Figure 3), and 15.0 mm
388 (upper limit based on diet reconstruction, Figure 3). Estimated daily minimum
389 foraging durations increase as average winter temperatures decrease (Figure 2),
390 are shortest for birds feeding on the smallest (i.e., highest quality) *Macoma* (6.5
391 mm), and longest for birds consuming the largest (i.e., lowest quality) *Macoma*
392 (15.0 mm). Within a *Macoma* size class, estimates of required foraging durations
393 approximately double between the lowest and highest estimates across the
394 season (Figure 2). Across all sizes of *Macoma*, the day with the shortest
395 estimated foraging time is 30 April, while the day with the longest estimated
396 foraging time is 9 January (Figure 2).

397 For insights into scenarios when *ptilocnemis* was potentially unable to
398 meet their energetic demands over the course of a day, we estimated the
399 foraging durations for *ptilocnemis* during the two aforementioned periods of
400 extreme cold when birds were displaced from northern sites to more southerly
401 sites (see above). Estimated minimum foraging durations ranged from 25.3–96.7
402 h across the different sizes of *Macoma*. These estimates are $\geq 30\%$ higher than
403 the maximum estimated durations under average conditions (9 January; Figure
404 2). To similarly assess impacts of prey quality, we calculated the minimum

RH: *Constraints during winter in a northerly shorebird*

405 required foraging duration for *ptilocnemis* hypothetically feeding on lower quality
406 *Macoma* (i.e., *Macoma* from Baie de Somme, France). These estimates were
407 ≥ 2.4 times higher than those for birds feeding on same-sized *Macoma* from
408 upper Cook Inlet (Figure 2).

409 **DISCUSSION**

410 Our results elucidate several unique aspects of the winter ecology of Rock
411 Sandpiper. First, Rock Sandpipers wintering in upper Cook Inlet, Alaska,
412 consistently expend energy at very high rates. Given the limited exposure of
413 mudflat foraging habitats, the consistently long estimated foraging durations
414 imply that Rock Sandpipers likely move between sites in Cook Inlet across tidal
415 cycles to maximize their access to *Macoma* and satisfy their energetic demands.
416 Secondly, although Rock Sandpipers exhibit numerous unusual physiological
417 traits that facilitate their exploitation of Cook Inlet during winter, their ability to
418 exist at this site is ultimately dictated by the quality of their benthic prey
419 resources. Finally, the quality of their *Macoma* prey strongly contrasts with those
420 from other sites throughout the organism's range. These differences combined
421 have important implications for the persistence of this unusual winter ecology and
422 while these results require validation in a natural setting, they nonetheless
423 underscore many of the unusual environmental and ecophysiological factors that
424 support this unique winter ecology.

RH: *Constraints during winter in a northerly shorebird*

425 **Energetic cost of wintering in upper Cook Inlet, Alaska**

426 Shorebird species are renowned for their ability to sustain high levels of
427 metabolic output (Kersten & Piersma 1987, Piersma 2011), feats that are
428 heretofore recognized primarily for shorebirds during migrations spanning
429 periods <10 days (e.g., Pennycuick & Battley 2003, Gill *et al.* 2005). Such
430 observations yield estimated maximum sustained outputs 8–10 times above
431 basal metabolic rates (Piersma 2011). *Ptilocnemis* Rock Sandpipers represent a
432 unique addition to these observations, due both to the duration and seasonal
433 timing of their metabolic output. We estimate that *ptilocnemis* must feed for ≥ 12 h
434 d^{-1} during the majority of winter in upper Cook Inlet, regardless of which size
435 *Macoma* they consume (Figure 2), and that the estimated metabolic rates during
436 these foraging periods exceed basal metabolic rate (0.85 Watt; Ruthrauff *et al.*
437 2013a) by a factor of 5.4–7.1 (April and January, respectively; Table 1). Thus,
438 although the levels of metabolic output are lower than those of shorebirds during
439 active migration, they are nonetheless very high in an absolute sense (Hammond
440 & Diamond 1997, Piersma 2011), and unprecedented in duration for a shorebird
441 species.

442 Ruthrauff *et al.* (2013c) demonstrated that *ptilocnemis* are predictable and
443 abundant inhabitants of upper Cook Inlet under typical winter conditions, and
444 stochastic periods of low temperatures offer insight into climatic thresholds
445 beyond which *ptilocnemis* cannot apparently occupy upper Cook Inlet. Such cold
446 not only increases thermogenic costs, but also increases the amount of shore-
447 fast ice and decreases the amount of time that exposed mudflats remain

RH: *Constraints during winter in a northerly shorebird*

448 unfrozen. The estimated minimum required foraging times during the two ‘cold
449 period’ observations were more than double the maximum values estimated
450 under average conditions (January 9, the coldest day of the year in upper Cook
451 Inlet; Figure 2), and these estimates also greatly exceeded the maximum
452 duration of mudflat exposure under ice-free conditions. Even during periods of
453 ‘normal’ cold in December, January, and February, estimated foraging durations
454 routinely approach (i.e., 6.5 mm *Macoma*) and exceed thresholds (all other
455 *Macoma* size classes) dictated by mudflat availability or 24-h ceilings (Figure 2).

456 These results indicate that Rock Sandpipers regularly face energetic
457 constraints while occupying upper Cook Inlet. To assess the plausibility of these
458 estimates, we compared metabolic rate estimates derived using Wiersma and
459 Piersma’s (1994) model to laboratory-derived measures of *ptilocnemis* at
460 temperatures ranging from 5°– -20°C (Ruthrauff *et al.* 2013a). On average,
461 estimates derived following Wiersma and Piersma’s method were just 1.9%
462 higher than those directly measured via respirometry. Our derivation of *Macoma*
463 shell intake rates based on fresh gizzard mass derives from work on Red Knots
464 (van Gils *et al.* 2003) and yields an estimate (1.42 mg shell s⁻¹) that is in
465 accordance with laboratory-derived estimates (1.22 mg shell s⁻¹; Ruthrauff *et al.*
466 2015). The estimate implemented herein is ~14% higher than those derived
467 under experimental settings, but the latter value was measured in Rock
468 Sandpipers maintained at 14°C. Birds experience their lowest metabolic
469 demands under normothermic conditions (Scholander *et al.* 1950, Swanson
470 2010), and it is likely that the gizzard sizes, and hence shell processing abilities,

RH: *Constraints during winter in a northerly shorebird*

471 were not maximized during these experimental trials. In contrast, the *ptilocnemis*
472 specimens from which we derived our estimates were collected in the middle of
473 winter. Ruthrauff *et al.* (2013b) documented a significant increase in gizzard
474 mass from fall to winter in wild Rock Sandpipers, a phenotypically flexible
475 increase that they attributed to the increased foraging demands experienced by
476 birds in winter.

477 Beyond scrutinizing underlying physiological model assumptions, are
478 these estimates of minimum foraging durations reasonable in an ecological
479 context? From December–February, the value for the maximum duration of
480 mudflat exposure at Redoubt Bay (17.7 h d^{-1}) exceeds the estimated foraging
481 durations for *ptilocnemis* feeding on all but the smallest *Macoma* size classes
482 (Figure 2), seemingly placing strong prey-size constraints on Rock Sandpipers.
483 Other evidence suggests, however, that our metabolic estimates are potentially
484 high because *ptilocnemis* possesses certain physiological traits (e.g., dense
485 plumage, high lipid stores; Ruthrauff *et al.* 2013b) that potentially lower metabolic
486 costs. For instance, Piersma's (1996) shorebird-specific model relating body
487 mass and plumage underestimates the actual plumage mass of *ptilocnemis*
488 during winter (table 2, Ruthrauff *et al.* 2013b) by 33.1%. Furthermore, average
489 lipid stores in *ptilocnemis* are among the highest reported for shorebirds during
490 winter, constituting 18.2% of winter body mass (Ruthrauff *et al.* 2013b). Although
491 likely of importance primarily as energy stores (Blem 1990), high lipid stores
492 undoubtedly offer insulative gain as well. These two factors likely lower
493 conductance values for *ptilocnemis* in their natural settings, but the estimate of

RH: *Constraints during winter in a northerly shorebird*

494 conductance that we applied in this exercise is calculated based on body mass
495 alone (Calder 1996). Wiersma and Piersma's (1994) model is sensitive to such
496 adjustments; in our model, a 10% reduction in the conductance parameter results
497 in $\geq 11\%$ decrease in foraging durations, a reduction of $\geq 1.01 \text{ h d}^{-1}$ across all
498 *Macoma* size classes.

499 Similarly, *ptilocnemis* undoubtedly makes behavioural adjustments that
500 help minimize foraging durations. In a similar tidally-structured feeding
501 environment, van Gils *et al.* (2005a) describe how Red Knots in the Dutch
502 Wadden Sea forage for nearly 17 h d^{-1} by moving east from their roost with the
503 rising tide. Given the relatively small size of the upper Cook Inlet region ($\sim 50 \text{ km}$
504 $\times \sim 170 \text{ km}$), it is likely that *ptilocnemis* moves between sites on rising and falling
505 tides, day and night, to maximize their exposure to ice-free mudflat foraging
506 habitats. Indeed, anecdotal observations of *ptilocnemis* moving within and
507 between embayments to access exposed mudflats support this prediction (REG
508 unpubl.). We likewise predict that *ptilocnemis* birds select the highest quality (i.e.,
509 the smallest) *Macoma* when energetic demands are greatest. Based on hinge
510 remains, we estimated that the average size of *Macoma* consumed by
511 *ptilocnemis* was 9.9 mm. Interestingly, this size is $\sim 20\%$ lower in quality
512 compared to 6.5 mm *Macoma* (Figure 3). We believe that relatively low energetic
513 demands driven by mild environmental conditions during the specimen collection
514 period (see *Macoma* quality and *ptilocnemis* diet reconstruction) likely moderated
515 pressure to select small *Macoma*.

RH: *Constraints during winter in a northerly shorebird*

516 Estimates of metabolic rates of foraging birds are double those of roosting
517 birds (Table 1), and these values are ultimately the primary determinant of the
518 estimated foraging durations. In our model implementation, we assumed that the
519 costs of foraging-related behaviours noted by Piersma *et al.* (2003) increased in
520 proportion to the estimates of maintenance metabolic rates of foraging birds. The
521 accuracy of these estimates is difficult to assess due to the dearth of information
522 concerning behaviour-specific metabolic rates (but see Weathers *et al.* 1984,
523 Goldstein 1988, Bruinzeel & Piersma 1998). Piersma *et al.* (2003) measured
524 these values in birds at normothermic temperatures, and it may be that these
525 added costs are static and do not necessarily increase in concert with
526 maintenance metabolic demands as temperatures decline. The accuracy of this
527 assumption strongly affects our estimates of metabolic rates of foraging Rock
528 Sandpipers. Nonetheless, our model assumptions are based primarily on
529 empirically derived species-specific information, and potential inaccuracies (e.g.,
530 unrealistically high conductance values, inaccurate estimation of foraging
531 metabolic rates) derive from the best available information. Future studies should
532 view these aspects of our model as testable factors of this energetically
533 'expensive' winter ecology.

534 **Impact of *Macoma* quality on *ptilocnemis* winter ecology**

535 An unanticipated result from this study was the important role of prey quality in
536 enabling *ptilocnemis*' unique nonbreeding ecology. Given Ruthrauff *et al.*'s
537 (2013c) observations of *ptilocnemis* abandonment of upper Cook Inlet during

RH: *Constraints during winter in a northerly shorebird*

538 stochastic periods of cold, it is likely that *ptilocnemis* regularly feeds at maximum
539 rates with little buffer to accommodate increased energetic demands. As a
540 corollary, when faced with invariant metabolic demands but lower quality prey,
541 the only way to decrease foraging durations is via commensurate increases in
542 intake rates. Such an adjustment is unlikely for *ptilocnemis* in upper Cook Inlet. In
543 order for foraging durations of *ptilocnemis* feeding on low-quality prey (e.g.,
544 *Macoma* from Baie de Somme, France) to match those of *ptilocnemis* feeding on
545 high-quality prey (e.g., *Macoma* from Kasilof, Alaska), maximum intake rates
546 would need to increase by $\geq 62\%$, requiring an increase in gizzard mass of $\geq 28\%$.
547 Although shorebirds demonstrate an impressive ability to regulate the size of
548 their gizzard in response to energetic demands (Landys-Ciannelli *et al.* 2003,
549 Battley & Piersma 2005, van Gils *et al.* 2005a), such an adjustment is unlikely
550 given that *ptilocnemis* is already operating near the limit of its energetic
551 thresholds in upper Cook Inlet and so its gizzard size is likewise expected to
552 approach a physiological maximum.

553 Our estimates of quality for *Macoma* from Baie de Somme, France, are
554 similar to other published estimates from the Atlantic Basin (e.g., van Gils *et al.*
555 2005a, 2005b, Quaintenne *et al.* 2010), and we believe that these estimates are
556 lower than those for *Macoma* from upper Cook Inlet due to site-specific
557 differences in the presence of invertebrate predators (e.g., decapods [crabs,
558 shrimp], gastropods [snails]). Armored invertebrates can rapidly augment their
559 shells in response to predation pressure (Trussell 1996, Trussell & Smith 2000),
560 and we propose that *Macoma* from upper Cook Inlet possess relatively light

RH: *Constraints during winter in a northerly shorebird*

561 shells due to a relaxed selection pressure on this attribute compared to other
562 sites with a more diverse benthic predator community (e.g., Vermeij 1978, 1982).
563 Although foraging shorebirds undoubtedly exert selection pressure for heavier,
564 stronger shells on their bivalve prey, Rock Sandpipers crush in their gizzard any
565 *Macoma* that they are able to swallow (Ruthrauff *et al.* 2015). It is believed that
566 infaunal bivalves instead attempt to avoid shorebird predation principally by
567 adjusting their burying depth (Zwarts & Blomert 1992, Zwarts *et al.* 1992, Zwarts
568 & Wanink 1993, Edelaar *et al.* 2003). Heavier shells, especially in small-sized
569 *Macoma* that are still easily consumed by shorebirds, likely play a relatively
570 greater role in reducing predation by invertebrates (e.g., Beukema *et al.* 1998,
571 van der Veer *et al.* 1998, Hiddink *et al.* 2002). Such bivalve predators are
572 prevalent and abundant at lower latitude sites throughout the range of *Macoma*
573 *balthica* (e.g., Commito 1982, Beukema *et al.* 1998, Hiddink *et al.* 2002, Seitz *et*
574 *al.* 2003) but are apparently very uncommon or altogether absent from upper
575 Cook Inlet's mudflats (Lees *et al.*, 2001; DRR and REG pers. obs.).

576 **Implications of a warming climate**

577 Given that *ptilocnemis* appear to function at or near their metabolic limits for
578 months at a time during winter in upper Cook Inlet, projected warming of high-
579 latitude regions due to climate change (0.3°–4.8°C over the next century; IPCC
580 2013) has positive implications for the species. Warming temperatures will relax
581 thermogenic costs, which will in turn decrease daily energetic demands and
582 foraging durations. In addition, warming winters will decrease the extent of shore-

RH: *Constraints during winter in a northerly shorebird*

583 fast ice covering *ptilocnemis*' foraging habitats. Thus, warming winter
584 temperatures would appear to relax certain physiological and environmental
585 constraints and enable *ptilocnemis* to more easily exploit foraging opportunities
586 between falling and rising tides.

587 Such warming comes with potential costs, however, that could negatively
588 impact the quality of *Macoma*. Climate warming can permit range expansions
589 (McCarty 2001, Walther *et al.* 2002, Parmesan & Yohe 2003) or invasive
590 introductions (Dukes & Mooney 1999, Rahel & Olden 2008) of organisms, and
591 such ecosystem changes in Cook Inlet could alter the quality of *Macoma* as
592 *ptilocnemis* prey. As noted above, we believe that the absence of invertebrate
593 predators currently accounts for the high quality of *Macoma* in Cook Inlet, Alaska.
594 Bartsch-Winkler & Ovenshine (1984) proposed that glacier-derived sediments in
595 western Cook Inlet decrease local primary productivity; in conjunction with
596 dominant current patterns, this may impede the immigration and survival of
597 planktonic larvae in the region (Foster *et al.* 2010). The scouring action of tidally-
598 driven sea ice and exposure to cold winter temperatures likely further decreases
599 the current suitability of upper Cook Inlet's mudflats to such invertebrate
600 predators. Future impacts of climate warming on these physical processes in
601 upper Cook Inlet are unknown, but given our estimates for *ptilocnemis* birds
602 feeding on low quality prey (Figure 2), any thermogenic benefits due to projected
603 warming would potentially be counteracted by deterioration in *Macoma* quality.

604 Cook Inlet is a relatively recent (~14,000 YBP; Karlstrom 1964, Schmoll *et*
605 *al.* 1972) geographic feature formed by retreating glaciers during Holocene

RH: *Constraints during winter in a northerly shorebird*

606 warming (Schmoll *et al.* 1999). Thus, the winter occupancy of upper Cook Inlet
607 by *ptilocnemis* is a tangibly recent phenomenon; that *ptilocnemis* uses this site to
608 the exclusion of other shorebird species is curious. Given the abundance of high
609 quality prey, why do no other shorebird species occur in upper Cook Inlet during
610 winter? Assuming that *ptilocnemis* maximizes fitness by employing a northerly-
611 wintering life history (e.g., Stearns 1992), quantifying the interaction between the
612 aforementioned environmental (e.g., temperature, wind, ice), physiological (e.g.,
613 intake rates, insulative adjustments), and behavioural (e.g., irruptive movements,
614 small-scale site selection) factors under natural field conditions is necessary to
615 understand the adaptive significance and continued persistence of this unusual
616 nonbreeding distribution.

617 **ACKNOWLEDGEMENTS**

618 We thank Colleen Handel for discussions on estimating foraging durations and
619 insights on implementing our model approach, and Sander Holthuijsen for
620 assistance with *Macoma* samples. Any use of trade, product, or firm names is for
621 descriptive purposes only and does not imply endorsement by the U.S.
622 Government.

623 **REFERENCES**

624 **Bartsch-Winkler, S., & Ovenshine, A.T.** 1984. Macrotidal subarctic
625 environment of Turnagain and Knik Arms, upper Cook Inlet, Alaska:
626 sedimentology of the intertidal zone. *J. Sediment. Petrol.* **54**: 1221–1238.

RH: *Constraints during winter in a northerly shorebird*

- 627 **Battley, P.F., & Piersma, T.** 2005. Adaptive interplay between feeding ecology
628 and features of the digestive tract in birds. In Starck, J. M. & Wang, T. (eds)
629 *Physiological and Ecological Adaptations to Feeding in Vertebrates*: 201–
630 228. Enfield: Science Publishers.
- 631 **Battley, P.F., Piersma, T., Dietz, M.W., Tang, S., Dekinga, A., & Hulsman, K.**
632 2000. Empirical evidence for differential organ reductions during trans-
633 oceanic bird flight. *Proc. R. Soc. London B* **267**: 191–195.
- 634 **Beukema, J.J., Honkoop, P.J.C., & Dekker, R.** 1998. Recruitment in *Macoma*
635 *balthica* after mild and cold winters and its possible control by egg
636 production and shrimp predation. *Hydrobiologia*: 23–34.
- 637 **Blem, C.R.** 1990. Avian energy storage. *Curr. Ornithol.* **7**: 59–113.
- 638 **Brown, J.H.** 1995. *Macroecology*. Chicago: University of Chicago Press.
- 639 **Bruinzeel, L.W., & Piersma, T.** 1998. Cost reduction in the cold: heat generated
640 by terrestrial locomotion partly substitutes for thermoregulation costs in Knot
641 *Calidris canutus*. *Ibis* **140**: 323–328.
- 642 **Calder, W.A., III.** 1996. *Size, Function, and Life History*. Mineola: Dover.
- 643 **Camphuysen, K., Ens, B.J., Heg, D., Hulscher, J.B., van der Meer, J., & Smit,**
644 **C.J.** 1996. Oystercatcher *Haematopus ostralegus* winter mortality in The
645 Netherlands: the effect of severe weather and food supply. *Ardea* **84A**: 469–
646 492.
- 647 **Colwell, M.A.** 2010. *Shorebird Ecology, Conservation, and Management*.

RH: *Constraints during winter in a northerly shorebird*

- 648 Berkeley: University of California Press.
- 649 **Commito, J.A.** 1982. Effects of *Lunatia heros* predation on the population
650 dynamics of *Mya arenaria* and *Macoma balthica* in Maine, USA. *Mar. Biol.*
651 **69**: 187–193.
- 652 **Conover, B.** 1944. The North Pacific allies of the Purple Sandpiper. *Zool. Ser. F.*
653 *Museum Nat. Hist.* **29**: 169–179.
- 654 **Cramp, S., & Simmons, K.E.L.** 1983. The birds of the western Palearctic. In S.
655 Cramp, S. & Simmons, K. E. L. (eds) *Handbook of the Birds of Europe the*
656 *Middle East and North Africa. Vol. 3: waders to gulls.* Oxford: Oxford
657 University Press.
- 658 **Davidson, N.C., & Evans, P.R.** 1982. Mortality of Redshanks and
659 Oystercatchers from starvation during severe weather. *Bird Study* **29**: 183–
660 188.
- 661 **Dekinga, A., & Piersma, T.** 1993. Reconstructing diet composition on the basis
662 of faeces in a mollusc-eating wader, the Knot *Calidris canutus*. *Bird Study*
663 **40**: 144–156.
- 664 **Dukes, J.S., & Mooney, H. A.** 1999. Does global change increase the success
665 of biological invaders? *Trends Ecol. Evol.* **14**: 135–139.
- 666 **Edelaar, P., Drent, J., & de Goeij, P.** 2003. A double test of the parasite
667 manipulation hypothesis in a burrowing bivalve. *Oecologia* **134**: 66–71.
- 668 **Evans, P.R.** 1976. Energy balance and optimal foraging strategies in shorebirds:

RH: *Constraints during winter in a northerly shorebird*

669 some implications for their distributions and movements in the non-breeding
670 season. *Ardea* **64**: 117–139.

671 **Ezer, T., & Liu, H.** 2010. On the dynamics and morphology of extensive tidal
672 mudflats: integrating remote sensing data with an inundation model of Cook
673 Inlet, Alaska. *Ocean Dyn.* **60**: 1307–1318.

674 **Foster, N.R., Lees, D.C., Lindstrom, S.C., & Saupe, S.** 2010. Evaluating a
675 potential relict Arctic invertebrate and algal community on the west side of
676 Cook Inlet. Final report, OCS Study MMS 2010-005. Fairbanks: Coastal
677 Marine Institute, University of Alaska.

678 **Gaston, K.J.** 2003. *The Structure and Dynamics of Geographic Ranges*. Oxford:
679 Oxford University Press.

680 **Gaston, K.J.** 2009. Geographic range limits: achieving synthesis. *Proc. R. Soc.*
681 *London B* **276**: 1395–1406.

682 **Gill, R.E., Jr., Piersma, T., Hufford, G.L., Servranckx, R., & Riegen, A.C.**
683 2005. Crossing the ultimate ecological barrier: evidence for an 11,000-km-
684 long nonstop flight from Alaska To New Zealand and eastern Australia By
685 Bar-tailed Godwits. *Condor* **107**: 1–20.

686 **Gill, R.E., Jr., & Tibbitts, T.L.** 1999. Seasonal shorebird use of intertidal
687 habitats in Cook Inlet, Alaska. Anchorage, Alaska. Final report, OCS Study
688 MMS 99-0012. Anchorage, Alaska: U.S. Department of the Interior.

689 **Gill, R.E., Jr., Tibbitts, T.L., Douglas, D.C., Handel, C.M., Mulcahy, D.M.,**
690 **Gottschalck, J.C., Warnock, N., McCaffery, B.J., Battley, P.F., &**

RH: *Constraints during winter in a northerly shorebird*

- 691 **Piersma, T.** 2009. Extreme endurance flights by landbirds crossing the
692 Pacific Ocean: ecological corridor rather than barrier?. *Proc. R. Soc. London*
693 *B* **276**: 447–457.
- 694 **Gill, R.E., [Jr.], Tomkovich, P.S., & McCaffery, B.J.** 2002. Rock Sandpiper
695 (*Calidris ptilocnemis*). In Poole, A., and Gill, F. (eds) *The Birds of North*
696 *America Online, No. 686*. Philadelphia, Pennsylvania: The Birds of North
697 America, Inc.
- 698 **Goldstein, D.L.** 1988. Estimates of daily energy expenditure in birds: the time-
699 energy budget as an integrator of laboratory and field studies. *Am. Zool.* **28**:
700 829–844.
- 701 **Hammond, K., & Diamond, J.** 1997. Maximal sustained energy budgets in
702 humans and animals. *Nature* **386**: 457–462.
- 703 **Hiddink, J.G., Marijnissen, S.A.E., Troost, K., & Wolff, W.J.** 2002. Predation
704 on 0-group and older year classes of the bivalve *Macoma balthica*:
705 interaction of size selection and intertidal distribution of epibenthic predators.
706 *J. Exp. Mar. Bio. Ecol.* **269**: 223–248.
- 707 **IPCC.** 2013. *Climate Change 2013: The Physical Science Basis. Contributions of*
708 *Working Group I to the Fifth Assessment Report of the Intergovernmental*
709 *Panel on Climate Change*. Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M.,
710 Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V. & Midgley, P. M.
711 (eds). Cambridge: Cambridge University Press.
- 712 **IUPS Thermal Commission.** 2003. Glossary of terms for thermal physiology. *J.*

RH: *Constraints during winter in a northerly shorebird*

- 713 *Therm. Biol.* **28**: 75–106.
- 714 **Johnson, M.** 2008. Water and ice dynamics in Cook Inlet. Final report, OCS
715 Study MMS 2008-061. Fairbanks: Coastal Marine Institute, University of
716 Alaska.
- 717 **Karlstrom, T.N.V.** 1964. Quaternary geology of the Kenai Lowland and glacial
718 history of the Cook Inlet region, Alaska. U.S. Geological Survey Professional
719 Paper 443.
- 720 **Kersten, M., & Piersma, T.** 1987. High levels of energy expenditure in
721 shorebirds: metabolic adaptations to an energetically expensive way of life.
722 *Ardea* **75**: 175–187.
- 723 **Landys-Ciannelli, M.M., Piersma, T., & Jukema, J.** 2003. Strategic size
724 changes of internal organs and muscle tissue in the Bar-tailed Godwit during
725 fat storage on a spring stopover site. *Funct. Ecol.* **17**: 151–159.
- 726 **Lappo, E., Tomkovich, P.S., & Syroechkovski, E.** 2012. Rock Sandpiper. In
727 *Atlas of Breeding Waders in the Russian Arctic*: 286–289. Moscow:
728 Publishing House 000.
- 729 **Lees, D.C., Driskell, W.B., Payne, J.R., & Hayes, M.O.** 2001. Intertidal
730 reconnaissance survey in upper Cook Inlet. Final report. Kenai, Alaska:
731 Cook Inlet Regional Citizens Advisory Council.
- 732 **MacArthur, R.H.** 1984. *Geographical Ecology: Patterns in the Distribution of*
733 *Species* Princeton: Princeton University Press.

RH: *Constraints during winter in a northerly shorebird*

- 734 **Marcström, V., & Mascher, J.W.** 1979. Weights and fat in Lapwings *Vanellus*
735 *vanellus* and Oystercatchers *Haematopus ostralegus* starved to death during
736 a cold spell in spring. *Ornis Scand.* **10**: 235–240.
- 737 **McCarty, J.P.** 2001. Ecological consequences of recent climate change.
738 *Conserv. Biol.* **15**: 320–331.
- 739 **Oey, L.-Y., Ezer, T., Hu, C., & Muller-Karger, F.E.** 2007. Baroclinic tidal flows
740 and inundation processes in Cook Inlet, Alaska: numerical modeling and
741 satellite observations. *Ocean Dyn.* **57**: 205–221.
- 742 **Parmesan, C., & Yohe, G.** 2003. A globally coherent fingerprint of climate
743 change impacts across natural systems. *Nature* **421**: 37–42.
- 744 **Pennycuik, C.J., & Battley, P.F.** 2003. Burning the engine: a time-marching
745 computation of fat and protein consumption in a 5420-km flight by Great
746 Knots, *Calidris tenuirostris*. *Oikos* **103**: 323–332.
- 747 **Piersma, T.** 1996. Energetic constraints on the non-breeding distribution of
748 coastal shorebirds. *Int. Wader Stud.* **8**: 122–135.
- 749 **Piersma, T.** 2011. Why marathon migrants get away with high metabolic ceilings:
750 towards an ecology of physiological restraint. *J. Exp. Biol.* **214**: 295–302.
- 751 **Piersma, T., & Davidson, N.C.** 1992. The migration and annual cycles of five
752 subspecies of Knots in perspective. *Wader Study Gr. Bull.* **64**: 187–197.
- 753 **Piersma, T., Dekinga, A., van Gils, J.A., Achterkamp, B., & Visser, G.H.**
754 2003. Cost-benefit analysis of mollusc eating in a shorebird I. Foraging and

RH: *Constraints during winter in a northerly shorebird*

- 755 processing costs estimated by the doubly labelled water method. *J. Exp.*
756 *Biol.* **206**: 3361–3368.
- 757 **Piersma, T., van Gils, J.A., & Wiersma, P.** 1996. Family Scolopacidae
758 (Sandpipers, Snipes, and Phalaropes). In del Hoyo, J., Elliott, A., & Sargatal,
759 J. (eds) *Handbook of the Birds of the World - Volume 3*: 444–533.
760 Barcelona: Lynx Edicions.
- 761 **Piersma, T., Koolhaas, A., & Dekinga, A.** 1993. Interactions between stomach
762 structure and diet choice in shorebirds. *Auk* **110**: 552–564.
- 763 **Poole, F.W., & Hufford, G.L.** 1982. Meteorological and oceanographic factors
764 affecting sea ice in Cook Inlet. *J. Geophys. Res.* **87**: 2061–2070.
- 765 **Pruett, C.L., & Winker, K.S.** 2005. Biological impacts of climatic change on a
766 Beringian endemic: cryptic refugia in the establishment and differentiation of
767 the Rock Sandpiper (*Calidris ptilocnemis*). *Clim. Change* **68**: 219–240.
- 768 **Quaintenne, G., van Gils, J.A., Bocher, P., Dekinga, A., & Piersma, T.** 2010.
769 Diet selection in a molluscivore shorebird across Western Europe: does it
770 show short- or long-term intake rate-maximization? *J. Anim. Ecol.* **79**: 53–62.
- 771 **R Core Team.** 2014. *R: A Language and Environment for Statistical Computing*.
772 Vienna: R Foundation for Statistical Computing.
- 773 **Rahel, F.J., & Olden, J.D.** 2008. Assessing the effects of climate change on
774 aquatic invasive species. *Conserv. Biol.* **22**: 521–533.
- 775 **Reger, R.D., Sturmman, A.G., Berg, E.E., & Burns, P.A.C.** 2007. *A guide to the*

RH: *Constraints during winter in a northerly shorebird*

- 776 *Late Quaternary History of Northern and Western Kenai Peninsula, Alaska.*
777 Anchorage: State of Alaska Department of Resources, Division of Geological
778 and Geophysical Surveys.
- 779 **Root, T.** 1988. Energy constraints on avian distributions and abundances.
780 *Ecology* **69**: 330–339.
- 781 **Ruthrauff, D.R., Dekinga, A., Gill, R.E., Jr., van Gils, J.A., & Piersma, T.**
782 2015. Ways to be different: foraging adaptations that facilitate higher intake
783 rates in a northerly-wintering shorebird compared to a low-latitude
784 conspecific. *J. Exp. Biol.* **218**: 1188–1197.
- 785 **Ruthrauff, D.R., Dekinga, A., Gill, R.E., Jr., & Piersma, T.** 2013a. Identical
786 metabolic rate and thermal conductance in Rock Sandpiper (*Calidris*
787 *ptilocnemis*) subspecies with contrasting nonbreeding life histories. *Auk*
788 **130**: 60–68.
- 789 **Ruthrauff, D.R., Dekinga, A., Gill, R.E., Jr., Summers, R.W., & Piersma, T.**
790 2013b. Ecological correlates of variable organ sizes and fat loads in the
791 most northerly-wintering shorebirds. *Can. J. Zool.* **91**: 698–705.
- 792 **Ruthrauff, D.R., & Eskelin, T.** 2009. Observations of body-icing on Rock
793 Sandpipers during winter in upper Cook Inlet, Alaska. *Wader Study Gr. Bull.*
794 **116**: 88–90.
- 795 **Ruthrauff, D.R., Gill, R.E., Jr., & Tibbitts, T.L.** 2013c. Coping with the cold: an
796 ecological context for the abundance and distribution of Rock Sandpipers
797 during winter in upper Cook Inlet, Alaska. *Arctic* **66**: 269–278.

RH: *Constraints during winter in a northerly shorebird*

- 798 **Ruthrauff, D.R., Tibbitts, T.L., Gill, R.E., Jr., Dementyev, M.N., & Handel,**
799 **C.M.** 2012. Small population size of the Pribilof Rock Sandpiper confirmed
800 through distance-sampling surveys in Alaska. *Condor* **114**: 544–551.
- 801 **Schmoll, H.R., Szabo, B.J., Rubin, M., & Dobrovolny, E.** 1972. Radiometric
802 dating of marine shells from the Bootlegger Cove Clay, Anchorage area,
803 Alaska. *Geol. Soc. Am. Bull.* **83**: 1107–1114.
- 804 **Schmoll, H.R., Yehle, L.A., & Updike, R.G.** 1999. Summary of Quaternary
805 geology of the Municipality of Anchorage, Alaska. *Quat. Int.* **60**: 3–36.
- 806 **Scholander, P., Hock, R., Walters, V., Johnson, F., & Irving, L.** 1950. Heat
807 regulation in some arctic and tropical mammals and birds. *Biol. Bull.* **99**:
808 237–258.
- 809 **Seitz, R.D., Marshall Jr., L.S., Hines, A.H., & Clark, K.L.** 2003. Effects of
810 hypoxia on predator-prey dynamics of the Blue Crab *Callinectes sapidus* and
811 the Baltic Clam *Macoma balthica* in Chesapeake Bay. *Mar. Ecol. Prog. Ser.*
812 **257**: 179–188.
- 813 **Sexton, J.P., McIntyre, P.J., Angert, A.L., & Rice, K.J.** 2009. Evolution and
814 ecology of species range limits. *Annu. Rev. Ecol. Evol. Syst.* **40**: 415–436.
- 815 **Spicer, J.I., & Gaston, K.J.** 1999. *Physiological Diversity and its Ecological*
816 *Implications*. Oxford: Blackwell Science Ltd.
- 817 **Stearns, S.C.** 1992. *The Evolution of Life Histories*. Oxford: Oxford University
818 Press.

RH: *Constraints during winter in a northerly shorebird*

- 819 **Summers, R.W., Strann, K.-B., Rae, R., & Heggas, J.** 1990. Wintering Purple
820 Sandpipers *Calidris maritima* in Troms county, northern Norway. *Ornis*
821 *Scand.* **21**: 248–254.
- 822 **Swanson, D.L.** 2010. Seasonal and metabolic variation in birds: functional and
823 mechanistic correlates. *Curr. Ornithol.* **17**: 75–129.
- 824 **Trussell, G.C.** 1996. Phenotypic plasticity in an intertidal snail: the role of a
825 common crab predator. *Evolution* **50**: 448–454.
- 826 **Trussell, G.C., & Smith, L.D.** 2000. Induced defenses in response to an
827 invading crab predator: an explanation of historical and geographic
828 phenotypic change. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 2123–2127.
- 829 **van de Kam, J., Ens, B., Piersma, T., & Zwarts, L.** 2004. *Shorebirds: An*
830 *Illustrated Behavioural Ecology*. Utrecht: KNNV Publishers.
- 831 **van der Veer, H.W., Feller, R.J., Weber, A., & Witte, J.I.** 1998. Importance of
832 predation by crustaceans upon bivalve spat in the intertidal zone of the
833 Dutch Wadden Sea as revealed by immunological assays of gut contents. *J.*
834 *Exp. Mar. Bio. Ecol.* **231**: 139–157.
- 835 **van Gils, J.A., Dekinga, A., Spaans, B., Vahl, W.K., & Piersma, T.** 2005a.
836 Digestive bottleneck affects foraging decisions in Red Knots *Calidris*
837 *canutus*. II. Patch choice and length of working day. *J. Anim. Ecol.* **74**: 120–
838 130.
- 839 **van Gils, J.A., Piersma, T., Dekinga, A., & Dietz, M.W.** 2003. Cost-benefit
840 analysis of mollusc-eating in a shorebird II. Optimizing gizzard size in the

RH: *Constraints during winter in a northerly shorebird*

- 841 face of seasonal demands. *J. Exp. Biol.* **206**: 3369–3380.
- 842 **van Gils, J.A., De Rooij, S.R., Van Belle, J., van der Meer, J., Dekinga, A.,**
843 **Piersma, T., & Drent, R.** 2005b. Digestive bottleneck affects foraging
844 decisions in Red Knots *Calidris canutus*. I. Prey choice. *J. Anim. Ecol.* **74**:
845 105–119.
- 846 **Vermeij, G.J.** 1978. *Biogeography and Adaptation: Patterns of Marine Life.*
847 Cambridge: Harvard University Press.
- 848 **Vermeij, G.J.** 1982. Phenotypic evolution in a poorly dispersing snail after arrival
849 of a predator. *Nature* **299**: 349–350.
- 850 **Vézina, F., Jalvingh, K.M., Dekinga, A., & Piersma, T.** 2006. Acclimation to
851 different thermal conditions in a northerly wintering shorebird is driven by
852 body mass-related changes in organ size. *J. Exp. Biol.* **209**: 3141–3154.
- 853 **Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee,**
854 **T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F.** 2002.
855 Ecological responses to recent climate change. *Nature* **416**: 389–395.
- 856 **Weathers, W.W., Buttemer, W.A., Hayworth, A.M., & Nagy, K.A.** 1984. An
857 evaluation of time-energy estimates of daily energy expenditure in birds..
858 *Auk* **101**: 459–472.
- 859 **Wiersma, P., & Piersma, T.** 1994. Effects of microhabitat, flocking, climate and
860 migratory goal on energy expenditure in the annual cycle of Red Knots.
861 *Condor* **96**: 257–279.

RH: *Constraints during winter in a northerly shorebird*

- 862 **Yang, H., Chen, B., Ma, Z., Hua, N., van Gils, J.A., Zhang, Z.-W., & Piersma,**
863 **T.** 2013. Economic design in a long-distance migrating molluscivore: how
864 fast-fuelling Red Knots in Bohai Bay, China, get away with small gizzards. *J.*
865 *Exp. Biol.* **216**: 3627–3636.
- 866 **Zwarts, L.** 1991. Seasonal variation in body condition of the bivalves *Macoma*
867 *balthica*, *Scrobicularia plana*, *Mya arenaria*, and *Cerastoderma edule* in the
868 Dutch Wadden Sea. *Netherlands J. Sea Res.* **28**: 231–245.
- 869 **Zwarts, L., & Blomert, A.-M.** 1992. Why Knot *Calidris canutus* take medium-
870 sized *Macoma balthica* when six prey species are available. *Mar. Ecol. Prog.*
871 *Ser.* **83**: 113–128.
- 872 **Zwarts, L., Blomert, A.-M., & Wanink, J.H.** 1992. Annual and seasonal variation
873 in the food supply harvestable by Knot *Calidris canutus* staging in the
874 Wadden Sea in late summer. *Mar. Ecol. Prog. Ser.* **83**: 129–139.
- 875 **Zwarts, L., & Wanink, J.H.** 1993. How the food supply harvestable by waders in
876 the Wadden Sea depends on the variation in energy density, body weight,
877 biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands*
878 *J. Sea Res.* **31**: 441–476.
- 879

RH: *Constraints during winter in a northerly shorebird*

880 **TABLES**

881 **Table 1.** Long-term average climatic conditions from October–April, upper Cook
 882 Inlet, Alaska, and concomitant maintenance metabolic rates for *ptilocnemis* Rock
 883 Sandpipers. Climate information summarized for Anchorage, Alaska, from 1 April
 884 1952–22 September 2015. Metabolic rate estimates are derived for two habitat-
 885 specific scenarios representing roosting and foraging behaviours; see Methods
 886 for full model parameterization.

Month	Climate Variable			Estimated Metabolic Rate (Watts)	
	Mean Temp. (°C)	Wind (m s ⁻¹)	Insolation (Watts m ⁻²)	Roosting	Foraging
October	1.6	3.00	57.50	1.97	4.79
November	-5.5	2.91	20.00	2.33	5.65
December	-8.5	2.82	6.25	2.48	5.98
January	-9.2	2.86	12.92	2.51	6.07
February	-7.0	3.08	40.83	2.41	5.87
March	-3.8	3.13	97.08	2.23	5.42
April	2.3	3.26	165.42	1.90	4.62

887

RH: *Constraints during winter in a northerly shorebird*

888 **FIGURE LEGENDS**

889 **Figure 1.** Primary North Pacific distribution of Rock Sandpiper *Calidris p.*
890 *ptilocnemis*. *Ptilocnemis* breeds on small islands in the central Bering Sea (box
891 with dashed border), and is distributed primarily in upper Cook Inlet, Alaska,
892 during the nonbreeding season (box, enlarged in inset to left). Inset: dashed line
893 delineates upper and lower Cook Inlet, and place names refer to upper Cook
894 Inlet locations mentioned in the text.

895

896 **Figure 2.** Upper figure: long-term daily average (solid line) and extreme
897 temperatures (small circles) during winter in Anchorage, Alaska (upper Cook
898 Inlet); dashed line delineates 0°C. Lower figure: predicted minimum foraging
899 durations necessary to satisfy estimated daily metabolic demands of Rock
900 Sandpipers (*Calidris p. ptilocnemis*) during winter in upper Cook Inlet, Alaska.
901 Estimates integrate average temperatures, wind speeds, and rates of solar
902 insolation. The increasing weights of the lines represent estimated foraging
903 durations for *ptilocnemis* feeding on 6.46 mm, 8.33 mm, 9.94 mm, 11.42 mm,
904 and 14.96 mm *Macoma*, respectively (see Results for rationale behind size
905 classes). Solid lines represent estimates for birds feeding on *Macoma* from upper
906 Cook Inlet, Alaska, and dashed line represents estimates for birds feeding on
907 lower-quality prey (6.46 mm *Macoma* from Baie de Somme, France). Shaded
908 region includes foraging durations that exceed the average daily maximum
909 duration of mudflat exposure at Redoubt Bay, Alaska, one of the primary
910 wintering sites used by *ptilocnemis* in upper Cook Inlet.

RH: *Constraints during winter in a northerly shorebird*

911

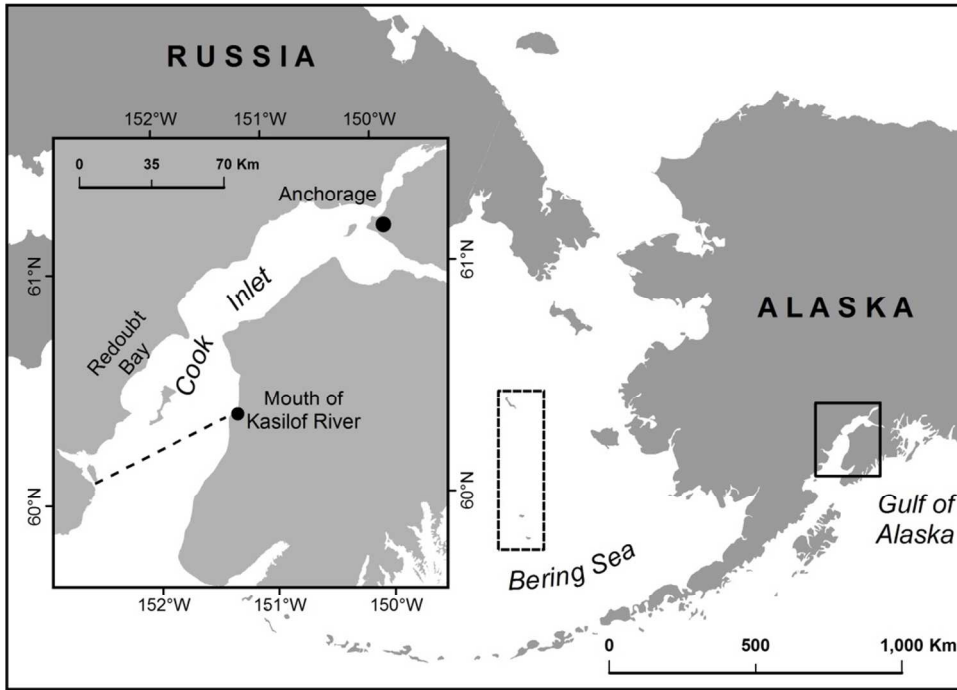
912 **Figure 3.** Characteristics of the bivalve *Macoma balthica*, primary prey of Rock
913 Sandpipers (*Calidris p. ptilocnemis*) in upper Cook Inlet, Alaska, during winter.
914 The left-hand scale on the lower figure represents the relationship between
915 *Macoma* shell length (mm) and ash-free dry mass (AFDM; triangles) and shell
916 mass (circles) for *Macoma* from Kasilof, Alaska (open symbols), and Baie de
917 Somme, France (filled symbols). Values are on \log_{10} scale, and dashed lines are
918 95% confidence intervals of these relationships described by linear regression.
919 The right-hand scale depicts estimates of *Macoma* quality (kJ g^{-1} dry shell mass)
920 as a function of shell length for *Macoma* from Kasilof, Alaska (dashed line), and
921 Baie de Somme, France (solid line). Values reflect metabolizable energy
922 estimated by applying an energy density of 22 kJ g^{-1} AFDM *Macoma* flesh and
923 an assimilation efficiency of 0.8 (see Methods). Boxplot (top) represents the size
924 distribution of *Macoma* consumed by *ptilocnemis* in upper Cook Inlet during
925 winter based on diet reconstruction techniques. Thick vertical line represents the
926 median, circle the mean, box the 25th and 75th percentiles, and whiskers the
927 range of values.

928

RH: Constraints during winter in a northerly shorebird

929 **FIGURES**

930 Figure 1.

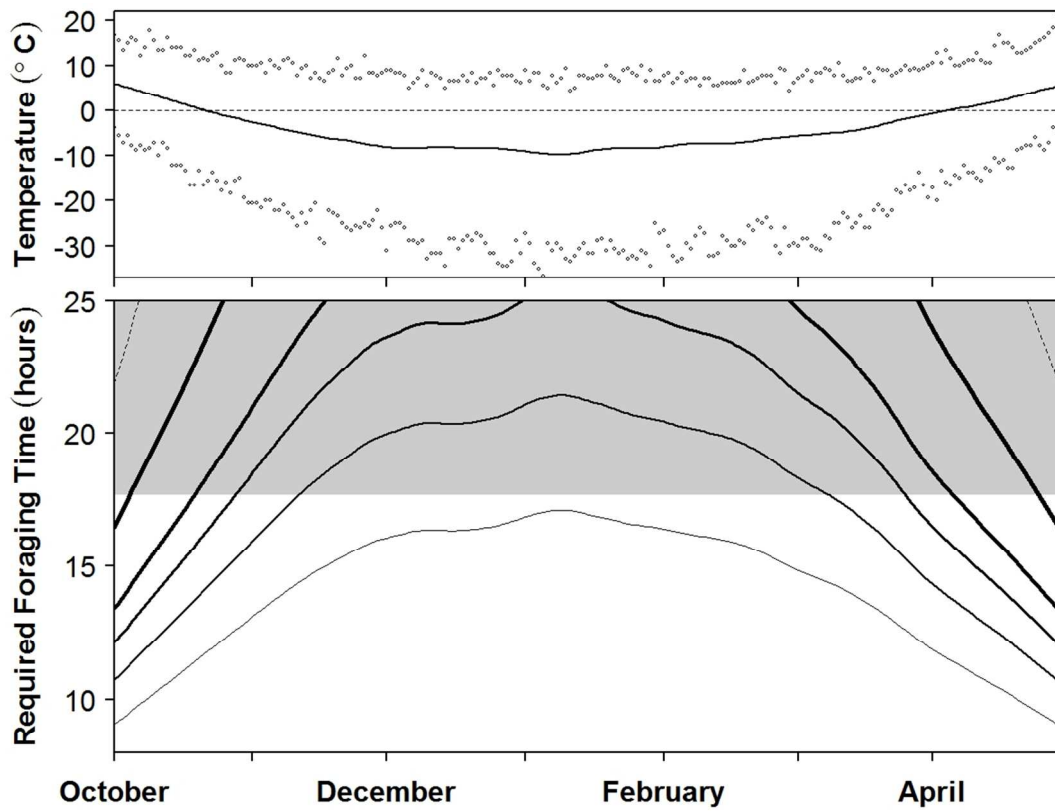


931

932

RH: Constraints during winter in a northerly shorebird

933 Figure 2.

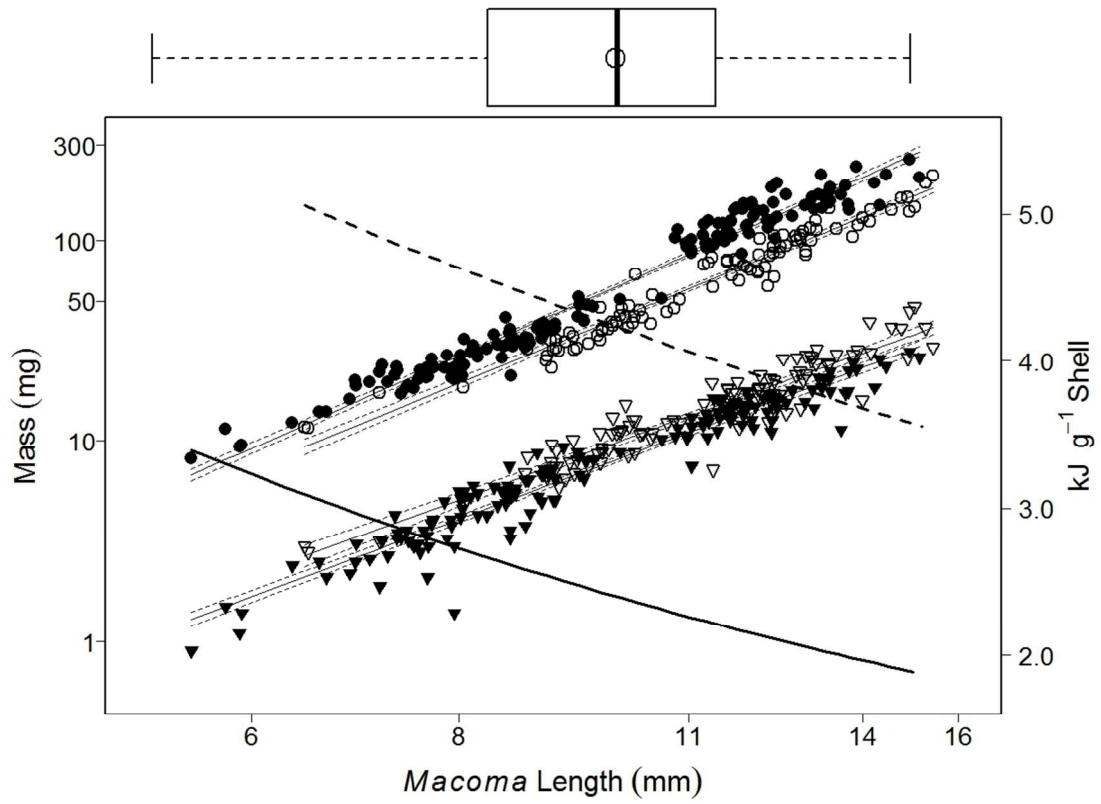


934

935

RH: Constraints during winter in a northerly shorebird

936 Figure 3.



937