Ruthrauff, D.R., Dekinga, A., Gill, R.E., Gils, J.A. van & Piersma, T. (2015). Ways to be different: foraging adaptations that facilitate higher intake rates in a northerly wintering shorebird compared with a low-latitude conspecific. *Journal of Experimental Biology*, 218, 1188-1197

Published version: dx.doi.org/10.1242/jeb.108894

Link NIOZ Repository: www.vliz.be/nl/imis?module=ref&refid=246610

RH: Adaptive differences in foraging ecologies

Ways to be different: foraging adaptations that facilitate higher intake rates in a northerly-wintering shorebird compared to a low-latitude conspecific~~s~~

Daniel R. Ruthrauff[1,2,*], Anne Dekinga[2], Robert E. Gill, Jr.[1], Jan A. van Gils[2], and Theunis Piersma[2,3]

[1]U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA

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

[3]Chair in Global Flyway Ecology, Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

[*]Author for correspondence (druthrauff@usgs.gov)

SUMMARY

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~~40°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. T~~conducted ~~hree~~ experiments ~~addressed ~~to assess the behavioural, 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* consumed a wider range of prey sizes, had higher maximum rates of energy intake, processed shell waste at higher maximum rates, and handled prey more quickly. Notably, however, the two subspecies did not differ in their abilities to find buried prey. ~~Differences in~~ The subspecies were similar in size and had equally sized gizzards, but the more northern *ptilocnemis* individuals were 10–14% heavier than their same-sex *tschuktschorum* counterparts. The higher body mass in *ptilocnemis* likely resulted 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 behavioural or sensory aspects.~~ These results represent unique evidence of subspecific differences in feeding ecologies that support observed biogeographic patterns.~~

Key words: intake rate, foraging ecology, functional response, nonbreeding distribution, subspecific differences

INTRODUCTION

The ways in which animals satisfy their daily energy requirements ultimately influence~~s~~ nearly every aspect of their ecology (Piersma and van Gils, 2011; Stephens and Krebs, 1986). Given the imperative to remain in energy and nutrient balance, an animal's foraging ecology ~~is~~ will be subject to strong selection pressure that can reflect an optimization of behavioural, environmental, and physiological ~~stimuli~~ processes (Perry and Pianka, 1997). The differential phenotypic expression of these ~~stimuli~~ processes 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; Costa et al., 2008; Darimont et al., 2004; Luck and Daily, 2003), interspecific competition (Johnson, 2001; Switalski, 2003), and intraspecfic niche differentiation (Berumen et al., 2005; Bolnick et al., 2003; Smith and Skúlason, 1996; Svanbäck and Persson, 2004). 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 (Grant, 1999; Schluter, 1995).

Due to their relative ease of observation and diversity of foraging strategies, shorebirds (Charadriiformes) are common subjects of foraging studies (Colwell, 2010; Goss-Custard et al., 2006; van de Kam et al., 2004). During the nonbreeding season, shorebirds experience ~~relatively~~ high energetic demands (Kersten and Piersma, 1987; Wiersma and Piersma, 1994), a natural history trait that also makes shorebirds ideal study subjects of the interplay between an organism's foraging ecology and ~~their~~ its energetic requirements (Kvist and Lindström, 2003; van Gils et al., 2005a; 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 (Jeschke et al., 2002), constraints which in shorebirds are typically caused by prey handling (Zwarts and Esselink, 1989) or digestive (van Gils et al., 2003b; Zwarts and Dirksen, 1990) limitations. Such observations conform to the more general patterns first derived by Holling (1959) and elucidated in shorebirds by others (e.g. ~~(~~Duijns et al., 2014; Lourenço et al., 2010; Piersma et al., 1995). In its simplest form, observations are modeled by the equation:

$$\frac{N}{T} = \frac{aD}{1 + aT_hD}. \qquad (1)$$

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*; cm^2 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 (van Gils et al., 2003b; van Gils et al., 2005b; Wanink and Zwarts, 1985). Because molluscivorous shorebirds efficiently exploit ~~small~~ prey even at relatively low densities (Piersma et al., 1998), 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 (Yang et al., 2013; Zwarts and Blomert, 1992). 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; Piersma et al., 2003; Quaintenne et al., 2010; van Gils et al., 2003a; van Gils et al., 2005a).

Most previous studies comparing the foraging ecologies of closely~~-~~ related subjects examined differences in the context of sympatric niche differentiation (Benkman, 1993; Huey and Pianka, 1981; Kawamori and Matsushima, 2012; Labropoulou and Eleftheriou, 1997; Pulliam, 1985). Here, we compare two subspecies of the rock sandpiper (*Calidris p. ptilocnemis* [Coues; hereafter *ptilocnemis*] and *Calidris p. tschuktschorum* [Portenko; hereafter *tschuktschorum*]), subspecies that are equipped with nearly identical foraging 'tools' (i.e. body size, bill morphology, diets, foraging behaviours), but which endure strongly contrasting environmental conditions across their largely allopatric nonbreeding ranges (e.g. table 1 in ~~(~~Ruthrauff et al., 2013a). We conducted experimental foraging trials on ~~identically-maintained~~ captive individuals of both ~~rock sandpiper~~ subspecies maintained under identical conditions 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 prey (the bivalve *Macoma balthica* ~~(~~[L.]) 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 (van Gils et al., 2005b). ~~We~~ Next, we ~~next~~ conducted ~~long-term trials~~a second trial 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 both a bird's ability to crush hard-shelled molluscs in ~~their~~ its gizzards and ~~their~~ its 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., 2005c), 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 maximum rates of energy intake ~~and~~ by processing shell waste more quickly than *tschuktschorum*. Finally, we conducted a third trial~~s~~ 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~~ uses primarily mudflat habitats ~~and~~ while *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 lower T_s and a higher instantaneous area of discovery, *a* [Piersma et al., 1995]~~, and lower T_s~~), and handle and ~~consume~~ swallow ~~discovered~~ prey more quickly ~~compared to~~than *tschuktschorum* (~~i.e. they would have a~~ lower T_h). ~~Taken together, d~~Differences between the subspecies in these ~~trials~~ three experiments would provide measures of the ~~relative~~ importance of behavioural, physiological, and sensory aspects of rock sandpiper foraging ecology ~~on~~ relative to 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., 2013b) to ~40°N (Gabrielson and Lincoln, 1959; Paulson, 1993). There are four recognized subspecies of rock sandpiper (American Ornithologists' Union, 1957; Conover, 1944), 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 (Ruthrauff et al., 2013a; Vézina et al., 2011). Because the two subspecies do not differ in their intrinsic ~~energetic~~ metabolic 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., 2013b). The~~,~~ ~~sites~~ average daily temperatue in upper Cook Inlet is ≤0°C for nearly half the year, making this~~with~~ the coldest ~~winter temperatures regularly experienced~~site regularly used by ~~any~~ shorebirds~~ species~~ (Ruthrauff et al., 2013c). *Tschuktschorum*, in contrast, is distributed as far south as northern California, primarily on rocky intertidal habitats (~~~41~~40°N; Paulson, 1993; Gill et al., 2002). The subspecies exhibit contrasting phenotypic responses that reflect the distinct environmental conditions of their respective nonbreeding ranges. *Ptilocnemis* carries high fat stores and augments the size of digestive organs during winter in upper Cook Inlet, while *tschuktschorum* carries low fat stores and maintains smaller digestive organs at more southerly sites (Ruthrauff et al., 2013c). The two subspecies ~~probably~~ co-occur in small numbers where the southern~~at the~~ ~~extremes~~ limit of the *ptilocnemis* ~~their distribution~~range overlaps the northern limit of the *tschuktschorum* range~~s~~, 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* essentially constitutes ~~the bulk of~~the entirety of the *ptilocnemis* diet on the mudflats of upper Cook Inlet (Gill et al., 2002; Ruthrauff et al., 2013b), 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~~ Differences in diet and habitat affinities may naturally predispose the two subspecies to different foraging ecologies, but the ~~two~~ subspecies co-occur at migratory stopover sites~~, however,~~ where both consume *Macoma* (D. R. Ruthrauff and R. E. Gill, Jr., unpublished)~~, making this familiar food resource an ideal subject of comparative foraging trials between the two subspecies~~.

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~~experiments was 82.7 ±0.9 g for *ptilocnemis* females, 75.1 ±2.5 g for *ptilocnemis* males, 74.4 ±1.1 g for *tschuktschorum* females, and 64.8 ±3.2 g for *tschuktschorum* males. ~~The~~ Prior to commencing the experiments, the height and width of the birds' gizzards ~~of experimental birds~~ did not differ ~~by sex or subspecies~~ when individuals were maintained on ~~prior to the diet switch~~diets of soft fish chow (all comparisons between sexes and subspecies ~~all comparisons~~ *P* ≥~~>~~ 0.~~49~~53, *t* ≤ 0.66), ~~but~~ and ~~gizzards increased substantially when their~~

~~diets were switched to hard-shelled prey. T~~the height and width of experimental birds' gizzards increased an average of 35 ± 8% and 27 ±6%, respectively, ~~after switching diets~~when their diets were switched to hard-shelled prey (Fig. 1). ~~The~~ When maintained on hard-shelled prey, the gizzards of females ~~increased~~ were larger~~more t~~ than males ($P <$ 0.01, $t = 3.26$ for height, $P < 0.05$, $t = 2.93$ for width), but the gizzard sizes of the subspecies did not differ overall ($P = 0.79$, $t = -0.27$ for height, $P = 0.91$, $t = 0.12$ for width).

Experiment I: ~~Prey quality and s~~Prey choice~~ize selection~~

Prey quality was highest in the smallest *Macoma* size class (size 1; 2.~~80~~ 83 kJ g^{-1} shell), and ~~only~~ slightly lower in size 2 *Macoma* (2.~~69~~ 58 kJ g^{-1} shell). The larger size classes were progressively lower in quality: 2.~~30~~ 21 kJ g^{-1} shell for size 3, and ~~1.87~~2.01 kJ g^{-1} shell for size 4 (Fig. 2). In ~~prey size selection trials~~experiment I, ~~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~~ingested; 20 (14.3%) *Macoma* of the second largest size class (size 3) were consumed, and most of the two smallest sizes were consumed (114 [81.4%] and 125 [89.3%] ~~and 114 [81.4%]~~ for sizes ~~1~~ 2 and ~~2~~1, respectively). Small within-group sample sizes precluded statistical comparison, however, and w~~and w~~e display graphical summaries of the selection trials in Fig. 3. In general, *ptilocnemis* consumed more *Macoma* across a wider ~~size~~ range of sizes than *tschuktschorum* (Fig. 3).

Experiment II: Maximum intake rates of exposed prey

Experiment II demonstrated that maximum intake rates were higher for *ptilocnemis* compared to *tschuktschorum*, and that birds of both subspecies increased these rates when consuming smaller prey. ~~The model selection process demonstrated strong support for the effect of prey size on both ash-free dry mass (AFDM) and shell ballast intake rates.~~ The sum of model weights (Σw_i~~Σw_i~~) for models including *Macoma* size was 1.0 for analyses with both ash-free dry mass (AFDM) and shell ballast as~~both~~ response variables, and ~~but~~ models containing subspecies also ~~(Σw_i = 0.64 and 0.56 for AFDM and shell ballast,~~

~~respectively) and~~ exhibited strong support ($\Sigma w_i = 0.78$ and 0.79 for AFDM and shell ballast, respectively). The effect of sex ($\Sigma w_i = 0.27$~~$\Sigma wi = 0.30$~~ and 0.~~25~~21 for AFDM and shell ballast, respectively) on maximum intake rates received little~~as covariates received less~~ support. ~~This was further demonstrated by the model-averaged parameter estimates for these variables (Table 1);~~Accordingly, the only model-averaged parameter estimates with 95% confidence intervals that did not overlap zero were those for prey size and subspecies (Table 1). ~~had 95% confidence intervals that did not overlap zero.~~ Model-averaged ~~parameter~~ predictions~~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,~~ were lower ~~and that intake rates~~ for *tschuktschorum* ~~were lower~~ than ~~those for~~ *ptilocnemis* across all size classes (~~Table 1;~~ Fig. 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. Within each subspecies, the 95% confidence intervals on these estimates overlapped between females and males within each size class, but many estimates differed between *ptilocnemis* and *tschuktschorum* (Fig. 4). Maximum intake rates were higher for the two smaller size classes of *Macoma* than the two larger sizes; m~~M~~aximum rates of ballast intake were achieved for all birds at prey size class 2, but AFDM intake rates were highest at size class 1. There was broad overlap, however, between ~~nearly identical for~~ size classes 1 and 2 within each sex/subspecies group (Fig. 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 (Fig. 4).~~

Formatted: Not Superscript/ Subscript

Formatted: Subscript

Experiment III: Functional response to buried prey

The model selection process of search time yielded strong support for ~~models including~~the influence of two-way interactions ($\Sigma w_i = 0.99$~~$\Sigma w_i = 0.99$~~). Model-averaged parameter estimates indicated a strong interaction between sex and *Macoma* size, with males requiring more time to find larger prey (Table 2). ~~Similarly, search time decreased as prey density increased, t~~T*schuktschorum* required more search time to discover *Macoma* than *ptilocnemis*, and birds required more time to find large ~~size 2~~ *Macoma* (size 2; ~~than size 1 (~~Table 2). For small ~~-~~*Macoma* (size 1), model-averaged predictions of search time for females and males of both subspecies were similar and decreased as prey densities increased (Fig. 5, ~~upper~~ lower ~~half~~panel). For large *Macoma*, however, males of both subspecies (but especially *tschuktschorum*) required more time than females to find prey (Fig. 5, ~~lower~~ upper ~~half~~panel). Due to the interaction between sex and prey size in search times, we calculated the instantaneous area of discovery (*a*) only for small *Macoma* (size 1). Instantaneous area of discovery is inversely related to search time as a function of density (see Materials and Methods). Because search time decreased as density increased at a rate slightly less than -1 (Table 2, Fig. 5), this indicated that instantaneous area of discovery likewise declined as *Macoma* density increased. This decline was reflected by decreasing point estimates for *a* as densities increased, but the 95% confidence intervals on these estimates overlapped broadly across the range of densities in our trials. The confidence intervals on these estimates also overlapped across sex/subspecies groups. At densities of 208 *Macoma* m^{-2}, estimates of *a* (cm^2 s^{-1}) were 22.3 (13.7–30.9 [95% confidence interval]) for *ptilocnemis* females, 18.2 (13.7–22.6) for *ptilocnemis* males, 17.1 (11.0–23.2) for *tschuktschorum* females, and 24.1 (13.2–35.0) for *tschuktschorum* males.

Formatted: Subscript

~~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 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~~ After bringing a prey item to the surface of the sand, sandpipers~~larger prey~~ required more ~~handling~~ time ~~for rock sandpipers~~to handle large prey than small~~er~~ prey, and these times did not vary by prey density (Fig. 6). The model selection process yielded strong support for an effect of *Macoma* size (Σw_i~~Σw_i~~ = 1) on handling time and limited support for differences between the two subspecies (Σw_i~~Σw_i~~ = 0.5). ~~Along with estimates of the intercept, these~~Accordingly, prey size class and subspecies were the only variables in the handling time analysis with ~~model-averaged estimates and~~ 95% confidence intervals of parameter estimates that did not overlap zero. Parameter estimates indicated that large~~r~~ *Macoma* required more handling time~~ before swallowing than small *Macoma*~~, and that *tschuktschorum* handled *Macoma* longer than *ptilocnemis* (Table 2). ~~These patterns were evident in plots of model-averaged prediction estimates; d~~T~~espite overlap in estimated 95% confidence intervals, t~~he 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~~ (Fig. 6), but confidence intervals on these estimates overlapped across groups. Prey handling times averaged about five times longer ~~(2.2–3.2 s)~~ for large *Macoma* (2.2–3.2 s) compared to small *Macoma* (0.4–0.6 s), and the 95% confidence intervals did not overlap between the two size classes (Fig. 6).~~Within a size class, handling time did not vary by prey density (Fig. 6), satisfying the second key assumption of Holling's model (Holling, 1959).~~

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~~discover buried prey via probing. 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. *Ptilocnemis* had higher ~~AFDM intake rates and~~ shell processing capacities than *tschuktschorum*, which led to higher maximum AFDM intake rates (Table 1, Fig. 4). *Ptilocnemis*~~,~~ were also more effective at handling prey (T_h; Table 2, Fig. 6), and could consume larger prey than *tschuktschorum* (Fig. 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 2, Fig. 5).~~ Taken together, these differences ~~between the subspecies~~ reflect the greater importance of high sustained rates of energy intake for *ptilocnemis* compared to *tschuktschorum*.

The lack of obvious difference in instantaneous ~~search area~~area of discovery between the subspecies, however, is more difficult to interpret than differences in processing capacities. Such similarity may represent a relatively low importance of habitat-specific foraging adaptations (i.e. ~~remote sense~~tactile vs. visual cues) in rock sandpipers. For example,~~;~~ with prey densities in upper Cook Inlet exceeding 400 *Macoma* m^{-2} (Ruthrauff et al., 2013b), detecting prey by probing ~~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~~area of discovery may instead reflect the shared importance of this trait between the subspecies. Affirming these distinct 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~~ For digestively constrained foragers like rock sandpipers, maximum intake rates are ~~primarily~~ determined primarily by the physical capacity of a bird’s digestive ‘machinery,’~~,~~ and reflect physiological aspects of their foraging ecology (Battley and Piersma, 2005; McWilliams and Karasov, 2001). For example, van Gils et al. (2005a; 2005b) determined that red knots (*C. canutus* [L.]) selected foraging patches based on the density and diversity of the benthic prey community, and that these choices reflected the size, and hence processing capacity, of their gizzards. ~~Alternatively~~In contrast, prey handling potentially represents a mix of behavioural (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. *P*~~*ptilocnemis* females and males were ~ 10–14% heavier than their same-sex *tschuktschorum* counterparts~~ (see Results)~~. Such differences in body mass suggest that physiological processes unrelated to structural size influence differences in ~~aspects of rock sandpiper foraging ecologies, especially~~ maximum intake rates. As indicated by ultrasound measurements (Fig. 1), 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. ~~(~~Battley and Piersma, 2005; Diamond, 2002; Dykstra and Karasov, 1992). ~~For example,~~ 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, we propose that differences in body mass between the trial birds reflects a hypertrophy of digestive organs that facilitate higher intake rates in *ptilocnemis*. In a similar~~in a~~ comparison of nonbreeding populations of the closely ~~-~~related purple sandpiper (*C.* ~~*maritima*~~*maritima* [Brünnich])~~ from Norway and Scotland~~, Summers et al. (1998) detected no difference in stomach mass (~~primarily~~ composed primarily of gizzard) between individuals from Norway and Scotland~~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~~ necessary 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 (Clissold et al., 2013; Dykstra and Karasov, 1992; Price et al., 2013; Starck, 1999). However, given the identical holding conditions of our experimental setup, differences between the subspecies noted here~~in~~ ~~instead appear to~~likely ~~reflect~~ represent intrinsic adaptations rather than phenotypic responses.

We noted apparent differences between the subspecies in the time necessary to find buried *Macoma* (T_s; Table 2, Fig. 5). ~~In the functional response trials, i~~It was counterintuitive, however, that larger prey items with a greater cross-sectional area should seemingly have been more difficult to find by~~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*,~~ When buried prey were encountered during these trials, ~~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. For trials involving~~-~~ large *Macoma* (size 2), however, ~~Just as shorebirds do in the wild, these~~ birds would ~~then~~ often assess the size of the *Macoma* while the prey ~~still sat~~remained 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~~ these 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 behaviours 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~~S~~ s~~maller rock sandpipers (especially *tschuktschorum* males) ~~more often~~appeared to reject~~ed~~ large buried *Macoma* ~~in the functional response trials~~more often than did larger birds, a result that was reflected by an ~~perceived~~ increase in search time (Table 2, Fig. 5) and by the observed ~~positive~~ interaction between sex and *Macoma* size (i.e. longest search times for males ~~and~~ with large *Macoma*~~s~~; Table 2). These findings were meaningful in the context of prey-~~-~~size thresholds, but obscured unbiased assessment of instantaneous ~~search~~ area of discovery. 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~~calculate *a*. Contrary to our prediction based on nonbreeding habitat preferences, 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.

~~As such~~For animals facing potential bottlenecks in prey intake, 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). ~~Because AFDM and shell ballast are allometric, non-linear functions of shell length (Fig. 2), the ratio of AFDM to ballast decreases as *Macoma* size increases. For instance, m~~Model results indicate that a female *ptilocnemis* ~~rock sandpiper~~ exploiting *Macoma* at a density of 208 individuals m^{-2} 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~~profitability in terms of energy intake (1.~~03~~29 mg AFDM s^{-1} for ~~size 2~~large *Macoma* compared to 0.~~83~~77 mg AFDM s^{-1} for ~~size 1~~small *Macoma*). For digestively constrained foragers like rock sandpipers, however, ~~rates of~~ energy intake rates over longer durations are better predicted ~~over longer durations~~ as a function of prey quality (Quaintenne et al., 2010; van Gils et al., 2005b), a relationship that maximizes the ratio of energy to shell ballast. ~~In the aforementioned example, short-term r~~Rates of ballast intake for the same bird consuming large *Macoma* are nearly ~~30% higher~~double those ~~(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~~small *Macoma* (10.54 mg shell ballast s^{-1} compared to 5.30 mg shell ballast s^{-1}). Thus, ~~long-term~~ for digestively constrained foragers, prey selection on the basis of energy per unit shell ballast maximizes energy intake ~~with respect to ballast intake, effectively prolonging~~ by 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 (Fig. 4), but the highest ballast intake rates occurred at the second size class ~~alone~~ (Fig. 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~~easier to crush (Piersma et al., 1993) and provide the highest ratio of energy to shell waste (Fig. 2). In the size-selection trials, ~~the~~ smaller-~~st~~ sized *Macoma* were consumed in preference to ~~the~~ larger sizes (Fig. 3), ~~supporting~~ consistent with our prediction that prey-size preferences would reflect prey quality. These preferences were evident for males and females of both subspecies (Fig. 3).

The differences between the subspecies in intake rates, handling efficiencies, and prey size choices have obvious consequences for ~~birds~~ animals attempting to satisfy high energetic demands in cold ~~nonbreeding~~ environments, and these~~. 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., 2013b), 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 (Goss-Custard et al., 2006; van Gils et al., 2005b), we predict that *ptilocnemis* rock sandpipers in upper Cook Inlet feed on *Macoma* of high quality (i.e. ~~relatively~~ small sizes) 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 unique~~high-latitude~~ nonbreeding distribution of *ptilocnemis* rock sandpipers.

Studies of other organisms have demonstrated that such traits can evolve over a matter of generations (Hendry and Kinnison, 1999; Schluter, 2000), and it is instructive to explore the timescale of these aspects of *ptilocnemis*' foraging ecology. The rock sandpiper is among several polymorphic Beringian endemic species (e.g. Abbott and Brochmann, 2003; Cook et al., 2005; Dawson et al., 2013; Pruett and Winker, 2005) whose polymorphy has been shaped by rapid, dynamic geologic processes throughout the region (Hopkins, 1959; Hopkins, 1973). The final formation of Cook Inlet as a geographic feature is believed to have occurred ~14,000 YBP (Reger et al., 2007; Schmoll et al., 1999), and fossil evidence indicates immediate colonization of the region thereafter by *Macoma* (Schmoll et al., 1972). Cook Inlet is the most northerly site in the region with abundant benthic food supplies that occur in the absence of permanent sea or shore-fast ice during winter (Ruthrauff et al., 2013b). It may be that rapid climate warming within the last century (Hinzman et al., 2005; Moritz et al., 2002; Serreze et al., 2000) only recently established ice-free mudflats and sufficiently relaxed energetic demands to permit the winter occupancy of Cook Inlet by *ptilocnemis*. ~~Such adaptations represent unique evidence among shorebirds of intrinsic foraging-related adaptations to divergent physiological stimuli between conspecifics.~~Regardless of their inception, such apparently intrinsic differences in foraging ecologies reflect the discrete processes by which environmental conditions lead to adaptive differences between closely related organisms (Reznick and Ghalambor, 2001; Schluter, 1996), and underscore the many aspects of foraging performance that can promote adaptive radiations (Grant and Grant, 1993; Liem, 1980; MacArthur, 1958; Schluter, 1993).

MATERIALS AND 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 (61.3°~~ 19′~~N, 165.8°~~ 47′~~W), and ~~acclimated the birds to captivity prior to ~~transport~~ing~~ed them to the Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands, on 21 September 2009. Transport of the birds to The Netherlands was authorized by the United States Fish and Wildlife Service (permit MB 789758), and followed United States Geological Survey animal care and use permit 2008-22. We determined the subspecific identity of birds based on diagnostic plumage characteristics of the wing and mantle (Gill et al., 2002), and sex from blood samples 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, we conducted experiments ~~maximum feeding rate trials were conducted~~ in outdoor aviaries. The mean temperature (± s.e.m.) over the experimental period in 2010 was 4.1 ±0.5°C in February, 8.4 ±0.6°C in March, and 9.8 ±0.6°C in April. In 2011, we conducted ~~, 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 s~~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~~ a preferred bivalve prey of rock sandpipers (Gill et al., 2002), and we ~~exclusively~~ used only *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*~~ AFDM and shell mass (i.e. ballast) using standard techniques (van Gils et al., 2005b; Zwarts, 1991). To satisfy underlying model assumptions, we calculated these relationships after ~~log -~~transforming ~~(base 10) values of~~ AFDM, ~~and~~ shell ballast, and shell length using $\log_{10}$ transformations (Fig. 2). 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} AFDM *Macoma* flesh (van Gils et al., 2005b; Zwarts and Wanink, 1993), 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 A.D., and birds were measured using a system that ensured that A.D. was ignorant of the identity of each bird as ~~they were~~it was measured. ~~Care~~ Care and handling of the birds and all experimental procedures complied with the Dutch Law on Experimental Welfare and the animal welfare guidelines of the Royal Netherlands Academy of Arts and Sciences (DEC permit NIOZ 09.01).

Experiment~~al Trial~~s

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~~up 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* ~~fe~~male in these trials. ~~We held four birds per aviary, and provided constant access to fresh and salt water. We~~ For all trials, we removed food from the aviaries at 0800 h to ensure that birds were hungry and foraged in a motivated manner ~~during all feeding trials~~. Trials commenced at 1400 h, 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 *ad libitum*.

Experiment I: Prey choice

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 ± s.e.m. lengths

7.5 ±0.1 mm, 8.8 ±0.1 mm, 11.4 ±0.1 mm and 13.5 ±0.1 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, and w~~. W~~e 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 w~~ Trials lasted 15 min, and we counted the number of each size class that was consumed upon completion of each trial. ~~Trials lasted 15 min, and w~~We performed one trial per bird per day across three consecutive days. 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.

Experiment II: Maximum intake rate of exposed prey

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-min trial. We conducted two trials per size class for each bird, and performed one trial per bird per day across ~~eight~~ 8 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~~prey consumptions.

~~During the maximum intake trials, o~~One *ptilocnemis* male never consumed any *Macoma* in the eight maximum intake 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, which~~. These two birds~~ never consumed any size 4 *Macoma*. Thus, no prey were consumed in 16 of 64 maximum intake trials. In another trial involving a *tschuktschorum* male,~~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-min long trials. On no occasions were birds able to consume all the *Macoma* provided during a trial, and the average ± s.e.m. 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.

Experiment III: Functional response to buried prey

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 X 60 cm long X 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 X 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 behaviours 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~~10 min or once five *Macoma* had been consumed, whichever was first. We performed one trial per bird per day~~ across a period of 20 days~~.

Birds consumed no prey in 3 of 144 functional response trials. In ~~only 19~~an additional 16~~ of 144~~ trials, ~~did~~ birds consumed ~~fewer than 5~~1–4 *Macoma* in the 10-min trial period. M~~; as with the maximum intake trials, m~~ost (*n* = ~~14~~11) of these trials involved male *tschuktschorum* subjects; t~~. T~~hese 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. ~~Trials where no *Macoma* were consumed were removed from all subsequent analyses.~~

Video analysis and statistical analyses

Across all three experimental trials, we removed observations in which no *Macoma* were consumed from all subsequent analyses. V~~Across all trials, v~~ideo observation conditions were excellent during trials, 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 behaviours using JWatcher software (Blumstein and Daniel, 2007). In the maximum intake rate trials, we divided ~~the~~ (number of *Macoma* consumed -1) by ~~over~~ the duration between the consumption of the first and last *Macoma* in each trial. We applied the results of our *Macoma* prey quality assessments ~~(i.e. mg AFDM and mg shell ballast as functions of shell length)~~ to the mean *Macoma* size ~~for~~ of 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). W~~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 of discovery a using the formula

$$a = \frac{1}{T_s D}. \qquad (2)$$

following ~~(~~Lourenço et al. (~~,~~ 2010) and ~~;~~ van Gils et al. (~~,~~ 2005b). We determined T_s for each *Macoma* that was consumed, and accounted for the depletion of prey when integrating density (D) in our estimates of a. Search time and ~~,~~ handling time ~~, and instantaneous search area~~ were the response variables in the functional response trials.

We fitted generalized linear mixed-effects models to assess the effect of relevant biological parameters on the foraging behaviours 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. ~~(~~McKechnie and Wolf, 2004; West et al., 2002) that might affect intake rates. For the functional response trials we included sex, subspecies, *Macoma* size, and *Macoma* density as explanatory variables. 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. To better fit underlying model assumptions, we transformed search time, handling time, ~~instantaneous search area,~~ and *Macoma* density using ~~base-10~~ log$_{10}$ 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 calculated model-averaged parameter estimates using ~~averaged our model results in proportion to~~ Akaike weights ~~to generate overall parameter and prediction estimates a~~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~~1.0 (R Core Team, 2014), fit mixed-effects models using the lme4 package (Bates et al., 2014), and averaged model outputs using the AICcmodavg package (Mazerolle, 2014). ~~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 ± s.e.m.

ACKNOWLEDGEMENTS

Allert Bijleveld, Maarten Brugge, Ysbrand Galama, Sander Holthuijsen, Rim Lucassen, Andy Reeves, and John Terenzi were instrumental in helping to collect, sort, and maintain the bivalves used in ~~our~~ the trials. Dick Visser assisted with figures, and Anneke Bol provided genetics-based sexing results. Colleen Handel, Robert Ricklefs, and three anonymous reviewers provided comments that greatly improved the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

AUTHOR CONTRIBUTIONS

All authors contributed to the conceptual approach of the study; D.R.R., A.D., and R.E.G. collected data, and D.R.R. wrote the manuscript with important input from R.E.G., J.A.v.G., and T.P.

COMPETING INTERESTS

No competing interests declared.

FUNDING

This research was funded by the U.S. Geological Survey's Ecosystems Mission Area and by the Marine Ecology Department at NIOZ Royal Netherlands Institute for Sea Research. J.A.v.G. was supported by an NWO VIDI grant (864.09.002).

REFERENCES

Abbott, R. J. and Brochmann, C. (2003). History and evolution of the arctic flora: in the footsteps of Eric Hultén. *Mol. Ecol.* **12**, 299–313.

American Ornithologists' Union (1957). *Check-list of North American birds*. 5th ed. American Orithologists' Union.

Bates, D., Maechler, M., Bolker, B. and Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Battley, P. F. and Piersma, T. (2005). Adaptive interplay between feeding ecology and features of the digestive tract in birds. In *Physiological and Ecological Adaptations to Feeding in Vertebrates* (ed. J. M. Starck and T. Wang), pp. 201–228. Enfield, NH: Science Publishers.

Benkman, C. W. (1993). Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. *Ecol. Monogr.* **63**, 305–325.

Blumstein, D. T. and Daniel, J. C. (2007). *Quantifying Behavior the JWatcher Way*. Sunderland, MA: Sinauer Associates, Inc.

Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. 2nd ed. New York, NY: Springer-Verlag.

Clissold, F. J., Brown, Z. P. and Simpson, S. J. (2013). Protein-induced mass increase of the gastrointestinal tract of locusts improves net nutrient uptake via larger meals rather than more efficient nutrient absorption. *J. Exp. Biol.* **216**, 329–337.

Colwell, M. A. (2010). *Shorebird Ecology, Conservation, and Management*. Berkeley, CA: University of California Press.

Conover, B. (1944). The North Pacific allies of the Purple Sandpiper. *Zool. Ser. F. Museum Nat. Hist.* **29**, 169–179.

Cook, J. A., Hoberg, E. P., Koehler, A., Henttonen, H., Wickström, L., Haukisalmi, V., Galbreath, K., Chernyavski, F., Dokuchaev, N., Macdonald, S. O., et al. (2005). Beringia: intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *Mammal Study* **30**, S33–S44.

Dawson, N. G., Hope, A. G., Talbot, S. L. and Cook, J. A. (2013). A multilocus evaluation of ermine (*Mustela erminea*) across the Holarctic, testing hypotheses of

Pleistocene diversification in response to climate change. *J. Biogeogr.* http://doi.wiley.com/10.1111/jbi.12221.

Dekinga, A., Dietz, M. W., Koolhaas, A. and Piersma, T. (2001). Time course and reversibility of changes in the gizzards of red knots alternately eating hard and soft food. *J. Exp. Biol.* **204**, 2167–2173.

Diamond, J. (2002). Quantitative evolutionary design. *J. Physiol.* **542**, 337–345.

Dietz, M. W., Dekinga, A., Piersma, T. and Verhulst, S. (1999). Estimating organ size in small migrating shorebirds with ultrasonography: an intercalibration exercise. *Physiol. Biochem. Zool.* **72**, 28–37.

Duijns, S., Knot, I. E., Piersma, T. and van Gils, J. A. (2014). Field measurements give biased estimates of functional response parameters, but help explain foraging distributions. *J. Anim. Ecol.* http://www.ncbi.nlm.nih.gov/pubmed/25327649.

Dykstra, C. R. and Karasov, W. H. (1992). Changes in gut structure and function of house wrens (*Troglodytes aedon*) in response to increased energy demands. *Physiol. Zool.* **65**, 422–442.

Gabrielson, I. N. and Lincoln, F. C. (1959). *The Birds of Alaska*. Harrisburg, PA: Stackpole Co.

Gill, R. E., Tomkovich, P. S. and McCaffery, B. J. (2002). Rock Sandpiper. In *The Birds of North America Online* (ed. A. Poole), Ithaca NY: Cornell Lab of Ornithology.

Goss-Custard, J. D., West, A. D., Yates, M. G., Caldow, R. W. G., Stillman, R. A., Bardsley, L., Castilla, J., Castro, M., Dierschke, V., Le V. dit Durell, S. E. A., et al. (2006). Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biol. Rev. Camb. Philos. Soc.* **81**, 501–529.

Grant, P. R. (1999). *Ecology and Evolution of Darwin's Finches*. 2nd edition. Princeton, NJ: Princeton University Press.

Grant, B. R. and Grant, P. R. (1993). Evolution of Darwin's finches caused by a rare climatic event. *Proc. Biol. Sci.* **251**, 111–117.

Griffiths, R., Daan, S. and Dijkstra, C. (1996). Sex identification in birds using two CHD genes. *Proc. Biol. Sci.* **263**, 1251–1256.

Hassell, M. P. (1982). What is searching efficiency? *Ann. Appl. Biol.* **101**, 170−175.

Hendry, A. P. and Kinnison, M. T. (1999). The pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**, 1637–1653.

Hinzman, L. D., Bettez, N. D., Bolton, W. R., Chapin III, F. S., Dyurgerov, M. B., Fastie, C. L., Griffith, B., Hollister, R. D., Hope, A., Huntington, H. P., et al. (2005). Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Clim. Change* **72**, 251–298.

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**, 385–398.

Hopkins, D. M. (1959). Cenozoic history of the Bering Land Bridge. *Science* **129**, 1519–1528.

Hopkins, D. M. (1973). Sea level history in Beringia during the past 250,000 years. *Quat. Res.* **3**, 520–540.

Huey, R. B. and Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology* **62**, 991–999.

Jeschke, J. M., Kopp, M. and Tollrian, R. (2002). Predator functional responses: discriminating between handling and digesting prey. *Ecol. Monogr.* **72**, 95–112.

Kawamori, A. and Matsushima, T. (2012). Sympatric divergence of risk sensitivity and diet menus in three species of tit. *Anim. Behav.* **84**, 1001–1012.

Kersten, M. and Piersma, T. (1987). High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* **75**, 175–187.

Kvist, A. and Lindström, Å. (2003). Gluttony in migratory waders − unprecedented energy assimilation rates in vertebrates. *Oikos* **103**, 397−402.

Labropoulou, M. and Eleftheriou, A. (1997). The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. *J. Fish Biol.* **50**, 324–340.

Liem, K. F. (1980). Adaptive significance of intra- and interspecific differences in the feeding repertoires of Cichlid fishes. *Am. Zool.* **20**, 295–314.

Lourenço, P. M., Mandema, F. S., Hooijmeijer, J. C. E. W., Granadeiro, J. P. and Piersma, T. (2010). Site selection and resource depletion in black-tailed godwits *Limosa l. limosa* eating rice during northward migration. *J. Anim. Ecol.* **79**, 522–528.

MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**, 599–619.

Mazerolle, M. J. (2014). AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-1.

McKechnie, A. E. and Wolf, B. O. (2004). The allometry of avian basal metabolic rate: good predictions need good data. *Physiol. Biochem. Zool.* **77**, 502–521.

McWilliams, S. R. and Karasov, W. H. (2001). Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comp. Biochem. Physiol.* **128**, 579–593.

Moritz, R. E., Bitz, C. M. and Steig, E. J. (2002). Dynamics of recent climate change in the Arctic. *Science* **297**, 1497–1502.

Paulson, D. (1993). *Shorebirds of the Pacific Northwest*. Seattle, WA: University of Washington Press.

Perry, G. and Pianka, E. R. (1997). Animal foraging: past, present and future. *Trends Ecol. Evol.* **12**, 360−364.

Formatted: Dutch (Netherlands)

Piersma, T. and van Gils, J. A. (2011). *The Flexible Phenotype. A Body-Centred Integration of Ecology, Physiology, and Behaviour*. Oxford: Oxford University Press.

Piersma, T., Koolhaas, A. and Dekinga, A. (1993). Interactions between stomach structure and diet choice in shorebirds. *Auk* **110**, 552–564.

Formatted: Dutch (Netherlands)

Piersma, T., van Gils, J. A., de Goeij, P. and van der Meer, J. (1995). Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *J. Anim. Ecol.* **64**, 493–504.

Formatted: Dutch (Netherlands)

Piersma, T., Aelst, R., Kurk, K., Berkhoudt, H. and Maas, L. R. M. (1998). A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proc. Biol. Sci.* **265**, 1377–1383.

Formatted: Dutch (Netherlands)

Piersma, T., Dekinga, A., van Gils, J. A., Achterkamp, B. and Visser, G. H. (2003). Cost-benefit analysis of mollusc eating in a shorebird I. Foraging and processing costs estimated by the doubly labelled water method. *J. Exp. Biol.* **206**, 3361−3368.

Price, E. R., Ruff, L. J., Guerra, A. and Karasov, W. H. (2013). Cold exposure increases intestinal paracellular permeability to nutrients in the mouse. *J. Exp. Biol.* **216**, 4065−4070.

Pruett, C. L. and Winker, K. S. (2005). Biological impacts of climatic change on a Beringian endemic: cryptic refugia in the establishment and differentiation of the rock sandpiper (*Calidris ptilocnemis*). *Clim. Change* **68**, 219–240.

Pulliam, H. R. (1985). Foraging efficiency, resource partitioning, and the coexistence of sparrow species. *Ecology* **66**, 1829–1836.

Quaintenne, G., van Gils, J. A., Bocher, P., Dekinga, A. and Piersma, T. (2010). Diet selection in a molluscivore shorebird across western Europe: does it show short- or long-term intake rate-maximization? *J. Anim. Ecol.* **79**, 53–62.

R Development Core Team (2014). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reger, R. D., Sturmann, A. G., Berg, E. E. and Burns, P. A. C. (2007). *A Guide to the Late Quaternary History of Northern and Western Kenai Peninsula, Alasa*. Anchorage, Alaska: State of Alaska Department of Resources, Division of Geological and Geophysical Surveys.

Reznick, D. N. and Ghalambor, C. K. (2001). The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112–113**, 183–198.

Ruthrauff, D. R., Dekinga, A., Gill, R. E., Jr. and Piersma, T. (2013a). Identical metabolic rate and thermal conductance in rock sandpiper (*Calidris ptilocnemis*) subspecies with contrasting nonbreeeding life histories. *Auk* **130**, 60−68.

Ruthrauff, D. R., Gill, R. E., Jr. and Tibbitts, T. L. (2013b). Coping with the cold: an ecological context for the abundance and distribution of rock sandpipers during winter in upper Cook Inlet, Alaska. *Arctic* **66**, 269–278.

Ruthrauff, D. R., Dekinga, A., Gill, R. E., Jr., Summers, R. W. and Piersma, T. (2013c). Ecological correlates of variable organ sizes and fat loads in the most northerly-wintering shorebirds. *Can. J. Zool.* **91**, 698−705.

Schluter, D. (1993). Adaptive radiation in sticklebacks: size, shape, and habitat use efficiency. *Ecology* **74**, 699–709.

Schluter, D. (1995). Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology* **76**, 82–90.

Schluter, D. (1996). Ecological causes of adaptive radiation. *Am. Nat.* **148**, S40–S64.

Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford, UK: Oxford University Press.

Schmoll, H. R., Szabo, B. J., Rubin, M. and Dobrovolny, E. (1972). Radiometric dating of marine shells from the Bootlegger Cove Clay, Anchorage area, Alaska. *Geol. Soc. Am. Bull.* **83**, 1107–1114.

Schmoll, H. R., Yehle, L. A. and Updike, R. G. (1999). Summary of Quaternary geology of the Municipality of Anchorage, Alaska. *Quat. Int.* **60**, 3–36.

Serreze, M., Walsh, J., Chapin III, F. S., Osterkamp, T. E., Dyurgerov, M. B., Romanovsky, V. E., Oechel, W. C., Morison, J., Zhang, T. and Barry, R. (2000). Observational evidence of recent change in the northern high-latitude environment. *Clim. Change* **46**, 159–207.

Starck, J. M. (1999). Phenotypic flexibility of the avian gizzard: rapid, reversible and repeated changes of organ size in response to changes in dietary fibre content. *J. Exp. Biol.* **202**, 3171–3179.

Stephens, D. W. and Krebs, J. R. (1986). *Foraging Theory*. Princeton, NJ: Princeton University Press.

Summers, R. W., Piersma, T., Strann, K.-B. and Wiersma, P. (1998). How do purple sandpipers *Calidris maritima* survive the winter north of the Arctic circle? *Ardea* **86**, 51–58.

Formatted: Dutch (Netherlands)

van de Kam, J., Ens, B., Piersma, T. and Zwarts, L. (2004). *Shorebirds: An Illustrated Behavioural Ecology*. 2nd ed. Utrecht, NL: KNNV Publishers.

van Gils, J. A., Schenk, I. W., Bos, O. and Piersma, T. (2003a). Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *Am. Nat.* **161**, 777–793.

Formatted: Dutch (Netherlands)

van Gils, J. A., Piersma, T., Dekinga, A. and Dietz, M. W. (2003b). Cost-benefit analysis of mollusc-eating in a shorebird II. Optimizing gizzard size in the face of seasonal demands. *J. Exp. Biol.* **206**, 3369–3380.

Formatted: Dutch (Netherlands)

van Gils, J. A., Dekinga, A., Spaans, B., Vahl, W. K. and Piersma, T. (2005a). Digestive bottleneck affects foraging decisions in red knots *Calidris canut*us. II. Patch choice and length of working day. *J. Anim. Ecol.* **74**, 120–130.

Formatted: Dutch (Netherlands)

van Gils, J. A., De Rooij, S. R., Van Belle, J., van der Meer, J., Dekinga, A., Piersma, T. and Drent, R. (2005b). Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. I. Prey choice. *J. Anim. Ecol.* **74**, 105–119.

van Gils, J. A., Battley, P. F., Piersma, T. and Drent, R. (2005c). Reinterpretation of gizzard sizes of red knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. *Proc. Biol. Sci.* **272**, 2609–2618.

Vézina, F., Jalvingh, K. M., Dekinga, A. and Piersma, T. (2006). Acclimation to different thermal conditions in a northerly wintering shorebird is driven by body mass-related changes in organ size. *J. Exp. Biol.* **209**, 3141–3154.

Vézina, F., Dekinga, A. and Piersma, T. (2011). Shorebirds' seasonal adjustments in thermogenic capacity are reflected by changes in body bass: how preprogrammed and instantaneous acclimation work together. *Integr. Comp. Biol.* **51**, 394–408.

Wanink, J. and Zwarts, L. (1985). Does an optimally foraging oystercatcher obey the functional response? *Oecologia* **67**, 98–106.

West, G. B., Woodruff, W. H. and Brown, J. H. (2002). Allometric scaling of metabolic rate from molecules and mitochondria to cells and mammals. *Proc. Natl. Acad. Sci. USA* **99 Suppl. 1**, 2473–2478.

Wiersma, P. and Piersma, T. (1994). Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. *Condor* **96**, 257–279.

Yang, H., Chen, B., Ma, Z. -j., Hua, N., van Gils, J. A., Zhang, Z.-W. and Piersma, T. (2013). Economic design in a long-distance migrating molluscivore: how fast-fuelling red knots in Bohai Bay, China, get away with small gizzards. *J. Exp. Biol.* **216**, 3627–3636.

Zwarts, L. (1991). Seasonal variation in body condition of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria*, and *Cerastoderma edule* in the Dutch Wadden Sea. *Netherlands J. Sea Res.* **28**, 231−245.

Zwarts, L. and Blomert, A.-M. (1992). Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Mar. Ecol. Prog. Ser.* **83**, 113–128.

Zwarts, L. and Dirksen, S. (1990). Digestive bottleneck limits the increase in food intake of whimbrels preparing for spring migration from the Banc d'Arguin, Mauritania. *Ardea* **78**, 257−278.

Zwarts, L. and Esselink, P. (1989). Versatility of male curlews *Numenius arquata* preying upon *Nereis diversicolor* deploying contrasting capture modes dependent on prey availability. *Mar. Ecol. Prog. Ser.* **56**, 255–269.

Zwarts, L. and Wanink, J. H. (1993). How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands J. Sea Res.* **31**, 441–476.

TABLES

Table 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 Fig. 2), 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}.

	Maximum Intake Rate Model Set~~:~~	
Parameter	Ash-free Dry Mass	Shell Ballast
Macoma Size 3[a]	-0.~~059~~ 073 (-0.~~074~~087– -0.~~045~~058)	-0.~~229~~ 285 (-0.~~343~~398– -0.~~116~~172)
Macoma Size 4[a]	-0.~~097~~ 111 (-0.~~114~~129– -0.~~079~~094)	-0.~~324~~ 537 (-0.~~464~~672– -0.~~183~~402)
Subspecies[b]	-0.028 (-0.~~053~~049– -0.~~002~~006)	-0.~~188~~ 207 (-0.~~375~~364– -0.~~001~~049)

[a] *Macoma* size 1 is the reference level.

[b] *Calidris p. ptilocnemis* is the reference level.

Table 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*$^{-1}$) and~~,~~ 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~~ model~~s~~ did not. Only parameters with confidence limits that do not overlap zero are shown; units for response variables are on the ~~base 10~~ $\log_{10}$ scale (see Methods).

	Functional Response Model Set~~:~~	
Parameter	Search Time	Handling Time
Male X Large *Macoma*	0.355 (0.141–0.570)	Not applicable
Log_{10}(*Macoma* Density)	-0.715 (-0.953– -0.476)	—
Subspecies[b]	0.162 (0.021–0.302)	0.206 (0.034–0.377)
Macoma Size[a]	0.301 (0.201–0.401)~~0.355 (0.141–0.570)~~	0.698 (0.650–0.746)
Intercept	2.517 (1.994–3.04)	-0.454 (~~-0.121 –~~-0.787– -0.121)

[a] ~~M~~Small *Macoma* (size ~~2~~ 1) is~~is~~ the reference level.

[b] *Calidris p. ptilocnemis* is the reference level.

FIGURE LEGENDS

Fig. 1. **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 ± s.e.m. 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.

Fig. 2. **Shell ballast (mg; open circles) and ash-free dry mass (mg; closed circles) as a function of shell length (mm) for *Macoma balthica*.** ~~Response v~~Variables are plotted on the ~~base-10~~ $\log_{10}$ scale ~~(see Methods)~~. Relationship calculated from *Macoma* collected at Baie de Somme, France, and used in trials to determine maximum intake rates of *ptilocnemis* and *tschuktschorum* rock sandpipers. The solid line (±95% confidence interval) describes the ~~polynomial~~ relationship $log_{10}(AFDM) = -$~~1.624~~$2.182 +$ ~~0.372~~$3.095 * log_{10}(\text{shell length})$ ~~$- 0.012*(\text{shell length})^2$~~, and the dotted line (±95% confidence interval) describes $log_{10}(\text{shell ballast}) = -1.902$~~0.684~~ $+$ ~~0.327~~$3.681 * log_{10}(\text{shell length})$ ~~$- 0.008*(\text{shell length})^2$~~. Back-transformed estimates of the ratio AFDM:shell ballast were multiplied by metabolizable energy content to ~~represent~~ calculate *Macoma* quality (kJ g^{-1} shell; see Materials and Methods), represented on the right-hand axis by the dot-dashed line. N~~; ‘+’ symbols~~umbers 1–4 ~~mark~~ denote quality estimates for ~~the four sizes of~~ *Macoma* size classes used in the prey choice and maximum intake~~se~~ trials.

Fig. 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; Fig. 3A)–4 (largest; Fig. 3D). Bars represent average ± s.e.m. proportion consumed of each size class across all trials. Only trials where at least one *Macoma* was consumed are depicted (n = 14 trials, ~~total~~involving two *ptilocnemis* females [one and three trials], two *ptilocnemis* males [two trials each], one *tschuktschorum* female [one trial], and two *tschuktschorum* males [one

and four trials]~~, comprising 4 trials each by *ptilocnemis* females and males, 1 trial involving a *tschuktschorum* female, and 5 involving *tschuktschorum* males~~).

Fig. 4. **Predicted intake rates of shell ballast (upper symbols; values > 0.~~30~~ 20 mg s^{-1}) and ash-free dry mass (lower symbols; values < 0.~~30~~ 20 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; Fig. 2). Values represent model-averaged predictions ± 95% confidence intervals. Predictions derive from analysis of 29 trials involving four *ptilocnemis* birds (two females [seven trials each] and two males [seven and eight trials]) and 17 trials involving three *tschuktschorum* birds (one female [seven trials] and two males [four and six trials]).

Fig. 5. **Predicted search time (s *Macoma*$^{-1}$) for female and male *ptilocnemis* and *tschuktschorum* rock sandpipers to find ~~buried small~~ large (upper ~~half~~panel) and ~~large~~ small (lower ~~half~~panel) buried *Macoma balthica*.** Values are on log$_{10}$ scale and 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. Estimates derive from analysis of 69 trials using large *Macoma* and 69 trials using small *Macoma*. Trials involved eight birds (two of each sex of each subspecies), and each bird participated in 7–9 trials per size class. Dashed lines represent slopes of -1.

Fig. 6. **Predicted handling time (s *Macoma*$^{-1}$) for female and male *ptilocnemis* and *tschuktschorum* rock sandpipers before swallowing ~~small~~ large (upper symbols; values > 1 s) ~~(Size 1)~~ and ~~large~~ small (lower symbols; values < 1 s) ~~(Size 2)~~ *Macoma balthica*.** Values are on log$_{10}$ scale and 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. Estimates derive from analysis of 70 trials using large *Macoma* and 71 trials using small *Macoma*. Trials involved same eight birds as in Fig. 5, and each bird participated in 8–9 trials per size class.

1022