

**Geographic and intersexual variation in morphology
and diet of black oystercatchers (*Haematopus
bachmani*)**

**by
Hannah Roodenrijs**

B.Sc., University of California, Berkeley, 2017

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

in the
Department of Biological Sciences
Faculty of Science

© Hannah Roodenrijs 2023
SIMON FRASER UNIVERSITY
Spring 2023

Declaration of Committee

Name: Hannah Roodenrijs

Degree: Master of Science

Title: Geographic and intersexual variation in morphology and diet of black oystercatchers (*Haematopus bachmani*)

Committee: **Chair:** Kathleen Fitzpatrick
Senior Lecturer, Biological Sciences

David Green
Supervisor
Professor, Biological Sciences

Tony Williams
Committee Member
Professor, Biological Sciences

Robert Elnor
Committee Member
Adjunct Professor, Biological Sciences

Jonathan Moore
Examiner
Professor, Biological Sciences

Ethics Statement

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

- a. human research ethics approval from the Simon Fraser University Office of Research Ethics

or

- b. advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University

or has conducted the research

- c. as a co-investigator, collaborator, or research assistant in a research project approved in advance.

A copy of the approval letter has been filed with the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Simon Fraser University Library
Burnaby, British Columbia, Canada

Update Spring 2016

Abstract

Black oystercatchers (*Haematopus bachmani*) are an iconic species of the rocky intertidal coastline ranging from Baja California to Alaska. I evaluated three ecological hypotheses for geographic and intersexual variation in morphology of black oystercatchers across seven sites in Alaska and British Columbia. I found evidence consistent with Allen's but not Bergmann's rule; birds in Alaska have shorter bills and tarsi. Additionally, despite differences in migratory behavior, I observed no difference in the wing shape of birds in British Columbia and Alaska. Intersexual differences, particularly in bill length, were larger than regional differences in morphology. I therefore tested whether bill dimorphism results from selection for resource partitioning using a stable isotope diet analysis. I found site differences in the diet of this generalist predator but no evidence that males and females differed in diet. The results of this thesis highlight the importance of multiple drivers in patterns of morphology.

Keywords: Shorebird; Latitudinal gradients; Reversed sexual dimorphism; Resource partitioning

Acknowledgements

Nothing in life is accomplished alone, and that is most certainly the case in grad school. There are so many people that I owe an immense amount of gratitude for their support and guidance. First, I would like to thank my supervisor David Green for his continuous guidance and support, and for gently pushing me along in my thesis when procrastination got the better of me. I also thoroughly enjoyed our field season together in 2021 and never stopped being impressed at how quickly you could sprint across the islands to grab a bird. Thanks to you and Elsie for taking me in when I first moved here and letting me spend time with one of the cutest dogs in the world, Millie. Thank you to my committee members Tony Williams and Bob Elner. Tony, thank you for inviting me to your lab dinners and feeding me pizza, and challenging me with your hard questions. Bob thank you for your insights into my thesis throughout the process and valuable feedback. Though an unofficial part of the committee, many thanks to Mark Hipfner for his comments on my chapters.

The data collection for this thesis and project would not be possible without the support of a small army of wonderful people. Thank you to Lena Ware for being a huge part of getting this project started, this entire thesis would not be possible without your hard work. To Jesse Kemp for stepping out of your comfort zone and tackling the 2022 field season with me. To Cole Rankin for braving the Alaskan weather and waves to catch birds and collect samples for us. Thanks to Alice Domalik, Viv Pattison, and Nick Clyde from ECCC for bringing us out on the Little Dipper in Gulf Islands National Park and support in catching birds. Thank you to Mark Maftei and Jen Willoughby from Raincoast Education Society for the boat chauffeuring throughout the beautiful Barkley Sound and entertainment while waiting for birds to get caught. In Haida Gwaii our work could not have been done without the enthusiastic support of Jake Pattison who took us around in his boat, as well as Rian Dickson and others from Laskeek Bay Conservation Society. Thank you for giving me the opportunity to experience the magic of East Limestone Island. A big thanks to Christine Rock from BC FLNRO for helping us get all our permits together for Haida Gwaii work, assisting us in the field, and cooking us some delicious dinners while we were there. Thank you to the Council of Haida Nations for granting us the privilege of doing research on your incredibly special ancestral homelands. All data collected in Alaska is a part of the Gulf Watch program run by Dan

Esler, Heather Coletti, and Brian Robinson, and thank you to Caitlin Marsteller for helping me in the lab in Anchorage. I had several people help process and prep stable isotope samples. Thank you, Jesse Kemp for prepping all the feather and claw samples in 2019, Simon Amanuel in 2022, and Bowen Cai in 2023.

Community makes life brighter, and I am so grateful to have found a community of wonderful people here. The CWE and BISC department have brought so many kind, fun and intelligent humans into my life. Thank you, sweet friends, for the numerous (very) long lunches, interesting chats over beers, dinners, celebrations, game nights, and dance parties. Also, for getting me outside for ski trips, hikes, bike rides, and birding to take in the beauty of this place. I am so grateful to you all and I hope that wherever life leads us, we can all get together from time to time. Thank you to my dear friends Ally and Arianna for checking in with me regularly, making the effort to come visit, and being the best friends I could ask for. Thank you, Cole, for being a steady, loving, and supportive presence in my life through many big changes.

And of course, I would not be here without the unending love and support from my parents and sister, I love you all so much. Thank you for always encouraging me to follow this path to all the places it has taken me around the world, even if you sometimes had no idea what I was doing. I am here because you instilled a deep sense of curiosity and love for the natural world in me at a very young age. Thank you, Eva, for being my best friend and my rock, you are my guide in how to lead a meaningful and fulfilling life.

I respectfully acknowledge the nations on whose unceded and ancestral lands I have had the privilege of living and conducting research on. This includes but is not limited to: Dena'ina, Alutiiq/Sugpiaq, Haida, shishálh, Toquaht, Uchklesah, Huu ay aht, Yuułuʔiłʔatḥ, Kyuquot/Checklesath, čišaaʔatḥ (Tseshaht), W̱SÁNEĆ nations, səliłwətaʔt (Tseil-Waututh), kwikwəłəm (Kwikwetlem), Sk̓wxwú7mesh Úxwumixw (Squamish) and xʷməθkʷəy̍əm (Musqueam) Nations.

Table of Contents

Declaration of Committee	ii
Ethics Statement.....	iii
Abstract.....	iv
Acknowledgements.....	v
Table of Contents.....	vii
List of Tables.....	viii
List of Figures.....	ix
Chapter 1. General Introduction	1
References.....	4
Chapter 2. Latitudinal gradients in morphometrics and wing shape in black oystercatchers	7
2.1. Introduction	7
2.2. Methods	9
Study Area	9
Field Methods	10
Wing Shape Analysis.....	13
Statistical Analysis	13
2.3. Results	15
2.4. Discussion.....	19
2.5. References.....	23
Chapter 3. Reversed sexual dimorphism and resource partitioning in black oystercatchers	30
3.1. Introduction	30
3.2. Methods	32
Study Area	32
Field methods and sampling.....	32
Sample preparation and analysis	33
Statistical Analysis	34
3.3. Results	35
3.4. Discussion.....	40
3.5. References.....	45
Appendix A. Chapter 2 Supplementary Material	51
Appendix B. Chapter 3 Supplementary Material	55

List of Tables

Table 2.1. Morphometrics and mass variation of male and female black oystercatchers in Alaska and British Columbia. We report means \pm SD and ranges in brackets, and statistical tests with significant results in bold.	15
Table 3.1. Regional differences in carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope signatures of black oystercatchers and prey in Alaska and British Columbia. We report means \pm SD, sample sizes in brackets and statistical tests with significant results in bold.....	36

List of Figures

Figure 2.1. Study sites across Alaska, USA and British Columbia, Canada where we captured black oystercatchers from 2019-2022.	10
Figure 2.2. Schematics of how morphological measurements were collected in the field including: (A) wing length, (B) tail length, (C) toe length, (D) two tarsus measurements, and (E) five bill measurements.	12
Figure 2.3. Sex and regional variation in (A) tarsus length (mm) and (B) culmen length (mm) in Alaska and British Columbia. The outline curve of the violin plot represent the probability density of the data at each tarsus length and black dots represent the median of the data.	17
Figure 2.4. Sex and regional variation in (A) wing pointedness scores (C2) and (B) wing convexity scores (C3). The violin plot shows the probability density at a given score with the black dot representing the median.	18
Figure 3.1. Biplots of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic values of prey items and oystercatchers within each site in (A) the four sites in Alaska and (B) the three BC sites. The colored dots and bars represent means (± 1 SD) of each of the five prey items. The raw data for black oystercatchers are shown by the black symbols with the sexes shown by different symbols. The oystercatcher isotope signatures are adjusted by a diet-tissue discrimination factor of 3.4 ‰ for $\delta^{15}\text{N}$ and 0.2 ‰ for $\delta^{13}\text{C}$	37
Figure 3.2. Diet proportions of black oystercatchers within each site in (A) Alaska or (B) British Columbia. The bars represent the mean (\pm SD) of the population proportion of each prey item with the sexes indicated by the colors	39

Chapter 1.

General Introduction

Shorebirds are a diverse order of birds that exhibit remarkable variation in their biogeography, behavior, and morphology (Colwell 2010). Most shorebirds have broad geographic distributions with a few exceptions (e.g., Tuamotu sandpiper, *Prosobonia cancellate*; Pierce and Blauvelt 2004). Species with broad distributions can have populations that adapt to local climatic or ecological conditions (Weston et al. 2020). This provides an opportunity to study how intraspecific variation in morphology, behavior, and life history traits can be shaped by biotic or abiotic forces. Several ecogeographical rules describe morphological variation across gradients of latitude, altitude, and geographic range (Gaston et al. 2007). Two long-standing patterns of latitudinal gradients of morphology include Allen's (Allen 1877) and Bergmann's (Bergmann 1847) rules, in which appendage length decreases (Allen's rule) while body size increases (Bergmann's) with increasing latitude or altitude. McQueen et al. (2022) found that across thirty species of shorebirds in Australia, twenty-one and twenty-four conformed to Allen's and Bergmann's rules, respectively.

Shorebirds demonstrate tremendous variation in migration strategies which has contributed to our understanding of avian migration. For example, bar-tailed godwits are obligate migrants and have adapted to shrink non-essential organs to fly up to 11,000 miles nonstop (Gill et al. 2005). Additionally, there are numerous species that exhibit intraspecific variation in migration strategies such as differential and partial migration (Colwell 2010). Western sandpipers undertake differential migration where females migrate further south than males in the nonbreeding period (Nebel et al. 2002). Several species display partial migration where certain individuals migrate while some remain resident year-round, such as Eurasian oystercatchers (*Haematopus ostralegus*; Méndez et al. 2020). The diversity of migratory strategies in shorebirds can facilitate studies on the influence of migration on wing morphology. For instance, Minias et al. (2015) found that the wing shape of sixteen shorebird species migrating through eastern Europe varied with migration distance, where those with more pointed wings migrated longer distances. Inter- and intraspecific variation in migration behavior in shorebirds has

provided insight into morphological and physiological adaptations that allow species or individuals to migrate.

Some of the most fascinating alternative mating systems in vertebrates occur in the shorebird family. For example, Ruffs (*Calidris pugnax*) are the only known bird species to have a polymorphism in male mating strategies, where three male morphs play different roles in the polygynous system (Baguette et al. 2022, Küpper 2021). Jacanas (Jacanidae; Emlen and Wrege 2004), spotted sandpipers (*Actitis macularia*; Oring et al. 1983), and phalaropes (*Phalaropus*; Reynolds 1985) all partake in a polyandrous mating system in which females defend territories or fight for males and provide little to no parental care. Despite these alternative strategies, most shorebird species are monogamous, yet within these species there exists a large variation in size and plumage dimorphism (Jehl and Murray 1986). The number of species that display reversed sexual dimorphism, in which the female is larger than the male, is one of the highest of any bird order (Jönsson and Alerstam 1990). Several hypotheses have been proposed for why this phenomenon evolved, and shorebirds are a model group on which to test them due to the diversity of size dimorphisms (Jehl and Murray 1986). Some hypotheses for reversed sexual dimorphism argue that smaller males are better able to perform agile display flights, or that larger females produce larger eggs and healthier chicks (Jehl and Murray 1986; Jönsson and Alerstam 1990). Other theories focus on an ecological basis, arguing that size differences between males and females allow for resource partitioning to reduce competition (Mueller 1990). Evidence for most hypotheses have been found within the shorebird order, though there is still much debate over the main selective forces for reversed sexual dimorphism.

Black oystercatchers (*Haematopus bachmani*) are a large shorebird species with a unique ecology that provides an opportunity to test long-standing patterns and hypotheses for morphological variation. The extended year-round distribution of black oystercatchers from Baja California to Alaska spans about thirty degrees of latitude, which may lead to adaptation to local environmental conditions (Andres and Falxa 2020). Evidence of site-specific variation has been found in parts of their range (Guzetti et al. 2008), but latitudinal gradients in their morphology are not yet understood. Additionally, black oystercatchers are partial migrants where about half of all individuals breeding in Alaska migrate, while others in Alaska and the rest of the range remain resident year-round (Johnson et al. 2010). Studies on other partial migrants have

demonstrated that migration can drive the evolution of wing shape, where migrants have longer, more pointed wings than residents (Perez-Tris and Telleria 2003; but see Green et al. 2009). Finally, despite monomorphic plumage, black oystercatchers exhibit marked reversed sexual dimorphism, particularly in bill length (Andres and Falxa 2020). Bill dimorphism between the sexes, at 9% difference is larger than other body morphology (Chapter 1), suggesting that resource partitioning may be a driving factor in the evolution of reversed sexual dimorphism of black oystercatchers (Nebel and Thompson 2011). In this thesis, I test several hypotheses of geographic and intersexual variation in morphology of black oystercatchers.

References

- Allen JA (1877) The influence of Physical conditions in the genesis of species. *Radical Rev* 1: 108–140.
- Andres, B.A. and G. A. Falxa (2020). Black Oystercatcher (*Haematopus bachmani*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.blkoys.01>
- Baguette, M.; Bataille, B.; Stevens, V.M. (2022). Evolutionary Ecology of Fixed Alternative Male Mating Strategies in the Ruff (*Calidris pugnax*). *Diversity* 14(4), 307. <https://doi.org/10.3390/d14040307>
- Bergmann, C. (1847). Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. – Göttinger Studien 1, 595–708.
- Colwell, M.A. (2010). *Shorebird ecology, conservation, and management*. University of California Press
- Stephen T. Emlen, Peter H. Wrege, Size Dimorphism, Intrasexual Competition, and Sexual Selection in Wattled Jacana (*Jacana Jacana*), A Sex-Role-Reversed Shorebird in Panama, *The Auk*, Volume 121, Issue 2, 1 April 2004, Pages 391–403, <https://doi.org/10.1093/auk/121.2.391>
- Gaston, K. J., Chown, S. L., & Evans, K. L. (2008). Ecogeographical rules: Elements of a synthesis. *Journal of Biogeography*, 35(3), 483–500. <https://doi.org/10.1111/j.1365-2699.2007.01772.x>
- Gill, R.E., Piersma, T., Hufford, G., Servranckx, R., Riegen, A. (2005). Crossing the Ultimate Ecological Barrier: Evidence for an 11 000-km-Long Nonstop Flight from Alaska to New Zealand and Eastern Australia by Bar-Tailed Godwits, *The Condor*, 107(1) ,1–20, <https://doi.org/10.1093/condor/107.1.1>
- Green, D. J., Whitehome, I. B. J., Taylor, A. L., & Drake, E. L. (2009). Wing Morphology Varies with Age but not Migratory Habit in American Dippers. *The Wilson Journal of Ornithology*, 121(1), 141–147. <https://doi.org/10.1676/07-163.1>
- Guzzetti, B. M., Talbot, S. L., Tessler, D. F., Gill, V. A., & Murphy, E. C. (2008). Secrets in the eyes of Black Oystercatchers: A new sexing technique. *Journal of Field Ornithology*, 79(2), 215–223. <https://doi.org/10.1111/j.1557-9263.2008.00167.x>
- Hockey, P., G. M. Kirwan, and P. F. D. Boesman (2020). Pied Oystercatcher (*Haematopus longirostris*), version 1.0. In Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.pieoys1.01>

- Jehl, J.R., Murray, B.G. (1986). The Evolution of Normal and Reverse Sexual Size Dimorphism in Shorebirds and other Birds. In: Johnston, R.F. (eds). *Current Ornithology*, vol 3. Springer, Boston, MA. https://doi.org/10.1007/978-1-4615-6784-4_1
- Johnson, M., Clarkson, P., Goldstein, M. I., Haig, S. M., Lanctot, R. B., Tessler, D. F., & Zwiefelhofer, D. (2010). Seasonal Movements, Winter Range Use, and Migratory Connectivity of the Black Oystercatcher. *The Condor*, 112(4), 731–743. <https://doi.org/10.1525/cond.2010.090215>
- Jönsson, P. E., & Alerstam, T. (1990). The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. *Biological Journal of the Linnean Society*, 41(4), 301–314. <https://doi.org/10.1111/j.1095-8312.1990.tb00838.x>
- Küpper, C. (2021). Ruff Shorebird, The. In: Shackelford, T.K., Weekes-Shackelford, V.A. (eds) *Encyclopedia of Evolutionary Psychological Science*. Springer, Cham. https://doi.org/10.1007/978-3-319-19650-3_3414
- McQueen, A., Klaassen, M., Tattersall, G. J., Atkinson, R., Jessop, R., Hassell, C. J., Christie, M., Victorian Wader Study Group, Australasian Wader Studies Group, & Symonds, M. R. E. (2022). Thermal adaptation best explains Bergmann’s and Allen’s Rules across ecologically diverse shorebirds. *Nature Communications*, 13(1), 4727. <https://doi.org/10.1038/s41467-022-32108-3>
- Méndez, V., Alves, J. A., Þórisson, B., Marca, A., Gunnarsson, T. G., & Gill, J. A. (2020). Individual variation in migratory behavior in a subarctic partial migrant shorebird. *Behavioral Ecology*, 31(3), 672–679. <https://doi.org/10.1093/beheco/araa010>
- Minias, P., Meissner, W., Włodarczyk, R., Ożarowska, A., Piasecka, A., Kaczmarek, K., & Janiszewski, T. (2015). Wing shape and migration in shorebirds: A comparative study. *Ibis*, 157(3), 528–535. <https://doi.org/10.1111/ibi.12262>
- Mueller, H. C. (1990). The Evolution of Reversed Sexual Dimorphism in Size in Monogamous Species of Birds. *Biological Reviews*, 65(4), 553–585. <https://doi.org/10.1111/j.1469-185X.1990.tb01238.x>
- Nebel, S., Lank, D. B., O’Hara, P. D., Fernández, G., Haase, B., Delgado, F., Estela, F.A., Evans Ogden, L.J., Harrington, B., Kus, B. E., Lyons, J. E., Francine Mercier, Ortego, B., Takekawa, J. Y., Warnock, N., & Warnock, S. E. (2002). Western Sandpipers (*Calidris mauri*) during the Nonbreeding Season: Spatial Segregation on a Hemispheric Scale. *The Auk*, 119(4), 922–928. <https://doi.org/10.2307/4090223>
- Nebel, S., & Thompson, G. J. (2011). The evolution of sexual bill-size dimorphism in shorebirds: A morphometric test of the resource partitioning hypothesis. *Evolutionary Ecology Research*, 13, 35–44.

- Oring, L., Lank, D., Maxson, S. (1983). Population Studies of the Polyandrous Spotted Sandpiper. *The Auk*. 100. 272-285. 10.1093/auk/100.2.272.
- Perez-Tris, J., & Telleria, J. L. (2003). Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. *Journal of Avian Biology*, 32, 207-213. <https://doi.org/10.1111/j.0908-8857.2001.320301.x>
- Pierce, R.J., Blanvillain, C. (2004). Current status of the endangered Tuamotu Sandpiper or Titi *Prosobonia cancellate* and recommended actions for its recovery. *Wader Study Group Bulletin*, 105, 93-100.
- Reynolds, J.D. (1987), Mating system and nesting biology of the Red-necked Phalarope *Phalaropus lobatus*: what constrains polyandry?. *Ibis*, 129: 225-242. <https://doi.org/10.1111/j.1474-919X.1987.tb03203.x>
- Tessler, D. F., Johnson, J. A., Andres, B. A., Thomas, S., & Lanctot, R. B. (2014). A global assessment of the conservation status of the Black Oystercatcher *Haematopus bachmani*. *International Wader Studies* 20: 83–96.
- Weston, M. A., Clarke, K., Maguire, G. S., & Sumner, J. (2020). Morphological and molecular evidence of population divergence in a widespread shorebird across its southern mainland Australian distribution. *Conservation Genetics*, 21(4), 757–770. <https://doi.org/10.1007/s10592-020-01286-2>

Chapter 2.

Latitudinal gradients in morphometrics and wing shape in black oystercatchers

2.1. Introduction

Latitudinal variation in climatic and environmental conditions can impose selection pressures that drive latitudinal gradients in morphology, life history, and behavior (James 1970, Cody 1970, Laurila et al. 2008, Díaz et al. 2013, Bansal and Thacker 2021). Latitudinal patterns of morphology have been described in a diverse array of taxa from mammals (Alhajeri et al. 2020) to birds (Symonds and Tattersall 2010), and reptiles (Jaffe et al. 2016). Two of the earliest latitudinal patterns of morphology to be described (Allen 1887, Bergmann 1847) are now so established they are referred to as Allen's Rule and Bergmann's Rule, respectively. Bergmann's rule refers to a general ecogeographical pattern that within a broadly distributed clade, populations and species with larger individuals are found in colder environments and higher latitudes whereas populations and species with smaller individuals are found in aquatic environments and at lower latitudes. Bergmann (1847) suggested that this pattern arises because large-bodied endotherms have a lower surface area to volume ratio and better heat retention than small-bodied endotherms making them better adapted to colder climates. In several reviews involving hundreds of species, most bird species followed expected patterns of Bergmann's rule in body mass and/or linear measurements (Ashton 2002, Meiri and Dayan 2003).

Allen's rule, an extension of Bergmann's rule, states that endothermic animals living in colder climates usually have shorter and rounder limbs, tails, and ears that allow them to retain more heat than closely related species in warmer climates (Allen 1887). In several avian families such as Spheniscidae (penguins), Laridae (gulls), and Sternidae (terns), bill length and bill surface area decrease with increasing latitude and decreasing minimum temperature (reviewed by Symonds and Tattersall 2010). Although widely documented across species, Allen's rule is also supported within a species. For example, in Australia, Pied Oystercatcher (*Haematopus longirostris*) populations at higher latitudes had shorter bills than those at lower latitudes (McQueen et al. 2022).

Recent studies on birds have shown that the highly vascularized bill can aid in thermoregulation and quickly dissipate heat after physical exertion (Tattersal et al. 2017; Schraft et al. 2019). Despite the prevalence of these general patterns, critics have questioned the proposed mechanism suggesting that the thermoregulatory benefits associated with variation in body and appendage size would be small (Scholander 1955) and that alternative mechanisms for this pattern such as primary productivity (Rosenzweig 1968, Geist 1987) or the predictability of climate (Boyce 1979, Ashton 2002) were more plausible. Regardless of the mechanism, these widely observed latitudinal patterns of morphology can be useful in grouping species into subspecies or groups of different breeding origins when captured in a sympatric nonbreeding region (Delingat et al. 2011, Maggini et al. 2016, Ross and Bouzat 2014).

Harsher winter climates at higher latitudes can select for migratory life histories, and comparative studies show that the proportion of migrants and migration distance increases with latitude both across and within species (Slud 1976, Newton and Dale 1996, Berthold 1999, Sommveille et al. 2013). For example, in American Oystercatchers (*Haematopus palliatus*) all individuals breeding at the north end of the range migrate while nearly all birds in the southern end are year-round residents (Murphy et al. 2017). Morphological adaptations for migration occur in a range of taxa (Lockwood et al. 1998, Chapman et al. 2015, Flockhart et al. 2017). In birds, longer, more pointed wings with greater convexity reduce drag and allow for more energetically efficient flight during migration (Lockwood et al. 1998). With more migratory individuals and longer migration distance at higher latitudes, wing shape can also follow a latitudinal gradient within and across species (Fiedler 2005). Interspecific differences in wing length, pointedness, and convexity have been observed between species within a clade that vary in their migration distance (Marchetti et al. 1995, Minias et al. 2015). Intra-specific differences in wing shape can be more pronounced in species with distinct sub-populations or those where migration is a fixed rather than a facultative trait (Mulvihill and Chandler 1991, Fiedler 2004, Ożarowska et al. 2021, Pérez-Tris et al. 1999, Egbert and Belthoff 2003, Förschler and Bairlein 2011). Wing shape variation linked to migratory strategies has been used to distinguish between migrant and residents when both are present in the same area (Perez-Tris et al. 1999, De la Hera et al. 2007).

Black oystercatchers (*Haematopus bachmani*) are a large, partially migratory shorebird found along the west coast of North America from Baja California to the

Aleutian Islands in Alaska (from about 26°N to 60°N latitude, Tessler et al. 2014). Black oystercatchers are also sexually dimorphic with females being generally larger than males. Studies have also documented geographical variation in bill morphology, wing length, and mass among breeding populations in Alaska (Guzzetti et al. 2008). The migration strategy in this species varies with latitude: in Alaska, at least 50% of breeding individuals are estimated to migrate south for the nonbreeding season (C. Rankin pers. comm, Johnson 2010), whereas birds breeding in British Columbia, Canada, are thought to be almost entirely sedentary (Johnson 2010, Ware 2021). In this study, we examine whether latitudinal variation in climate and migratory behavior are associated with differences in morphology and wing shape of black oystercatcher populations in British Columbia and Alaska. Based on Allen's and Bergmann's rules, we predicted that birds captured in northern latitudes (in Alaska) would have larger bodies with shorter legs and bills to minimize heat loss. Due to the larger proportion of migrants in Alaska, we predicted birds in Alaska would have more pointed and concave wings for efficiency in migration.

2.2. Methods

Study Area

We studied black oystercatchers across British Columbia (BC), Canada, and Alaska, USA (Figure 2.1). We captured birds at five sites in British Columbia in Gulf Islands National Park and Preserve (48.77°N, -123.34°W), Pacific Rim National Park (48.94°N, -125.28°W), the Sunshine Coast Regional District (49.44°N, -123.65°W), and Masset Inlet (53.63°N, 132.33°W) and Skidegate Inlet (53.21°N, -132.11°W) in Haida Gwaii. In Alaska, we captured birds across four sites in Katmai National Park (58.23°N, -154.14°W), Kachemak Bay State Park (59.61°N, -151.23 °W), Kenai Fjords National Park (59.72 °N, -149.70°W), and Western Prince William Sound (60.19 °N, -147.91°W). We conducted fieldwork either in the spring (March-April) or summer (June-July) in BC and in the summer (June-August) in Alaska. All capture and handling of birds was conducted under permits provided by Simon Fraser University animal care and local and federal permits (Canada banding permit number 10667 Y, animal use permit number 1218-2021).

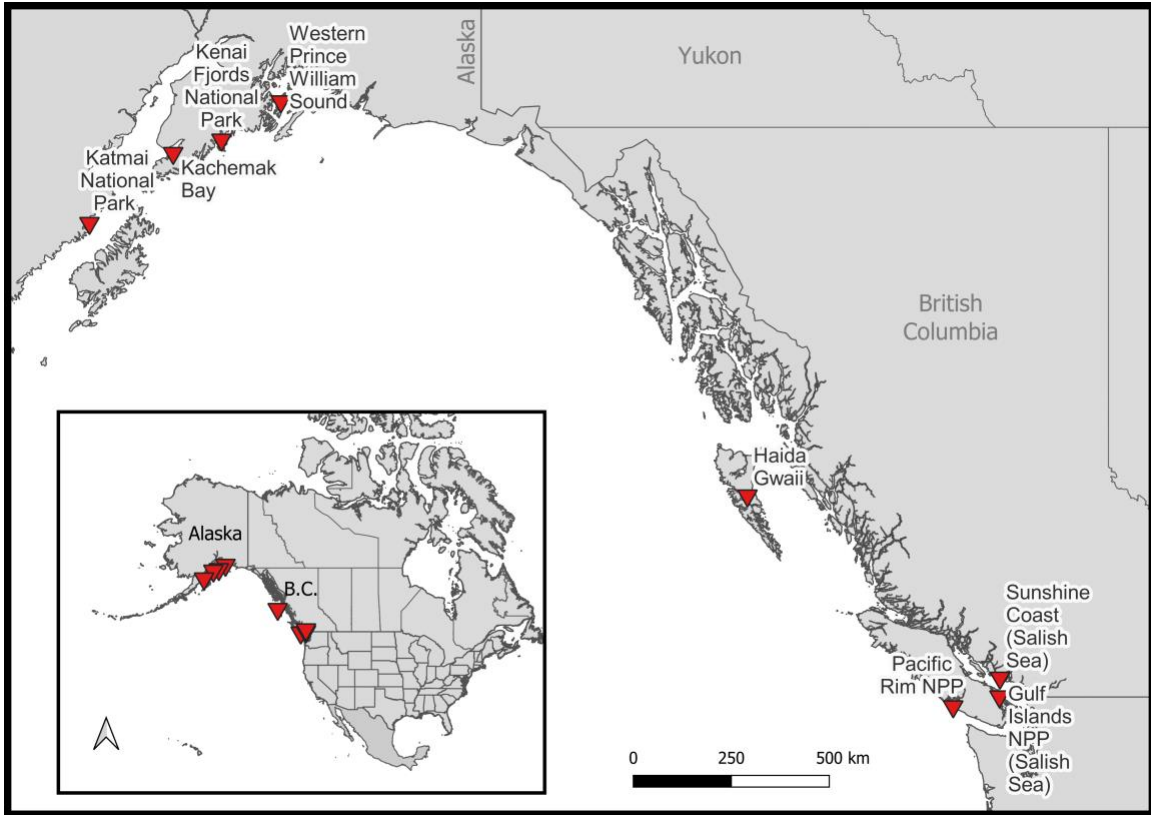


Figure 2.1. Study sites across Alaska, USA and British Columbia, Canada where we captured black oystercatchers from 2019-2022.

Field Methods

We captured black oystercatchers using noose mats and noose lines with decoys (Mad River Decoys) and a remote speaker playing black oystercatcher calls (Foxpro Inferno). We targeted territorial individuals and pairs with active capture techniques, and individuals in flocks with passive capture techniques. We banded each bird with a USGS stainless steel band on the right tarsus, and two green plastic bands with a unique alpha-numeric on each tibia (Haggie Engraving, Millington, MD). For each bird captured, we determined age based on plumage and the color of the bill and eye (Pyle 2008). We assigned sex of individuals by the extent of a black fleck in the iris of the eye. Guzetti et al. (2008) showed that sexing birds by eye fleck was concordant with molecular sexing in 94% of individuals. Females usually have a distinct eye fleck (category 3), and males have little to no eye fleck (category 1; see Figure 1.1 in Guzetti et al. 2008). For birds with intermediate eye fleck scores (category 2), we assigned sex using information on the sex of their mate and culmen and tarsus length.

For each bird captured we recorded ten morphological measurements (Figure 2.2). We weighed birds to the nearest 5 grams using a spring balance (Pesola Medio 1000g), and measured the wing chord, tail length, and length of the middle toe to the nearest mm using a 1 mm-unit ruler. We measured tarsus in two ways using 0.1 mm-unit calipers (SPI Polymid Dial 150mm); diagonal tarsus from the interstitial joint to the last leg scale before the toes (Pyle 1997), and maximum tarsus length from the lower hind edge of the tibia to the heel of the foot. We described bill morphology with five measurements using 0.1 mm-unit calipers (SPI Polymid Dial 150mm): the length of the exposed culmen from the edge of the feathers to the tip, length of bill and head combined, bill depth at the nares, bill width at the nares, and depth of the bill at the tip.

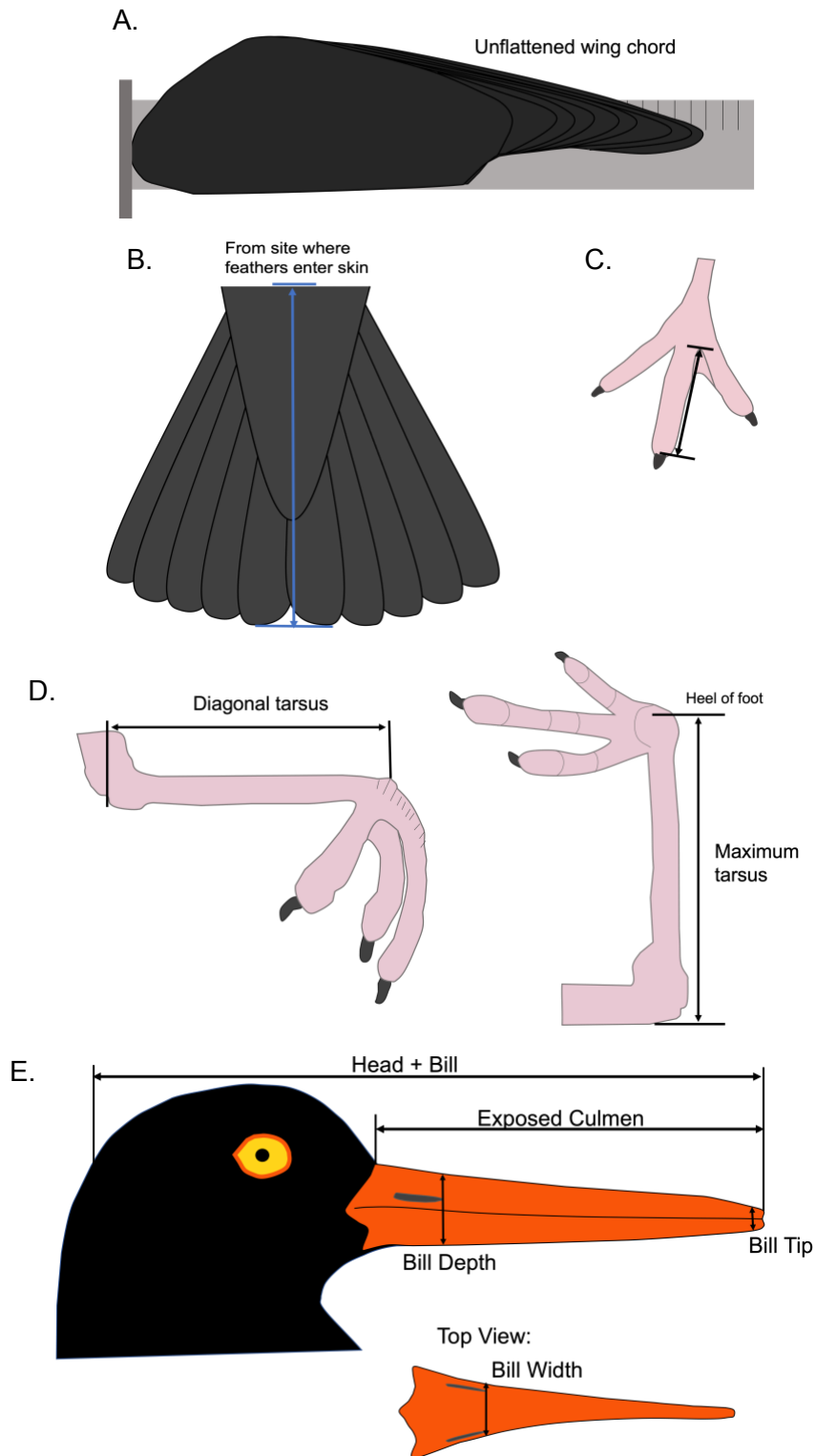


Figure 2.2. Schematics of how morphological measurements were collected in the field including: (A) wing length, (B) tail length, (C) toe length, (D) two tarsus measurements, and (E) five bill measurements.

Wing Shape Analysis

To minimize handling time, we photographed the wing of each bird in the folded position on a board next to a ruler. Photos of folded wings were taken at every site except Haida Gwaii and Sunshine Coast in 2019. We estimated the difference in length of each adjacent primary feather (Evered 1990) using FIJI image processing software (Schindelin et al. 2012). We used these differences and the wing chord measured in the field to calculate the length of each primary that was visible in the photo (following Evered 1990). We were able to measure the length of six to ten primaries per bird from photos, depending on the extent of molt the wing was in at the time of capture. We determined the lengths of the nine outer primaries for 58 birds, and the length of the eight, seven and six outer primaries for 77, 98 and 111 birds, respectively. The innermost primary (P1) was often covered by the secondaries and rarely visible.

We quantified the wing shape of each bird using a size-constrained components analysis (SCCA), as described by Lockwood et al. (1998), using R code available from Stojanovic et al. (2020). Size-constrained components analysis takes the length of the primary feathers and calculates three measures of wing shape: the isometric size of the wing or overall wing size (C1), the pointedness of the wing (C2), and the convexity of the wing (C3). Initially, we quantified the wing shape of birds for which we had the measurements of at least the nine outermost primary feathers measured (P10-2). In this SCCA, the C2 score was strongly influenced by the loadings from the three outer primaries (P10, P9, and P8) whereas the C3 score was strongly influenced by the middle three primaries (P7, P6, and P5; Table A.1). We also estimated the wing shape for birds for which we had lengths of the 7 outer primaries (P10-P4). In this SCCA the C2 and C3 scores were also heavily influenced by the length of the three outer primaries and three middle primaries, respectively (Table A.1). Further, C2 scores and C3 scores obtained with the smaller and larger sample were highly correlated ($r > 0.95$ for C2 and $r > 0.60$ for C3). We therefore used wing shape estimates from the second SCCA in subsequent analyses.

Statistical Analysis

There was considerable collinearity in the morphological measures and mass (Figure A.1). The two tarsus measures were correlated ($r = 0.61$), so we retained only

one, the diagonal tarsus length (hereafter tarsus length) in subsequent analyses. The five bill morphology measures were also highly correlated (Figure A.2), so we retained only the exposed culmen length (hereafter referred to as culmen length) and bill depth as measures of bill shape. In BC, birds caught in March were, on average, 13.8 grams heavier than birds caught in June and July ($t = -1.54$, $p = 0.13$). We adjusted the mass of birds to account for seasonal differences in mass prior to analysis.

We evaluated Bergmann's and Allen's rule by comparing the morphology of birds captured in BC and Alaska using adjusted mass and 6 morphological measures: wing, tail, toe, tarsus, culmen, and bill depth. Mass, wing length, and tail length provide a measurement of overall body size (James 1970), while toe, tarsus, culmen and bill depth are linear measures of appendages whose length may influence heat retention (Nudds and Oswald 2007, Symonds and Tattersall 2010).

We first evaluated whether there was any evidence for regional differences in morphology using a MANOVA that controlled for sex differences in morphology. We subsequently used linear mixed models to evaluate regional variation in each of the seven measurements while accounting for both sex differences and finer scale geographic variation associated with site. In these models we used the individual morphological trait as the independent variable with sex, region, and an interaction between sex and region as fixed effects and site as a random term. In the model for mass, we included an additional fixed effect of season of capture (Spring or Summer). Finally, we used a set of ANOVAs to further explore site specific variation in the morphology of black oystercatchers in BC and Alaska, separately.

We next evaluated whether there was evidence for regional differences in the wing shape of black oystercatchers. In these linear mixed models, we used wing pointedness (C2) and wing convexity (C3) as the independent variables, sex, region, and an interaction between sex and region as fixed effects and site as a random term.

Finally, we used linear discriminant analyses (LDAs) to evaluate whether we could use morphological measurements and wing shape to distinguish between males or females captured in BC and Alaska. We ran separate LDAs for each sex using the MASS package (Venables and Ripley 2002) after confirming the assumption of heteroskedasticity (Box's M test for females: $\text{Chi-Sq} = 35.2$, $\text{df} = 36$, $p = 0.51$; males: Chi-

Sq= 30.7, df= 36, p=0.72). We randomly assigned 75% of the data to a “training” dataset to run the models and tested the model accuracy using the remaining 25% of the data in the “test” dataset. Sample sizes for the body morphometrics and wing shape differed so initial LDAs included only the six body morphometrics and mass. Further LDAs added the C2 and C3 scores to test if their addition improved model accuracy.

2.3. Results

Body morphometrics and wing shape data were collected for 194 individual birds over three years in 2019 (n=110), 2020 (n= 28), and 2021 (n=57). Time spent in the field was limited in 2020 due to restrictions imposed during the COVID-19 pandemic. In BC and Alaska 95 and 99 individuals were captured, respectively. Females (n=99, 51%) and males (n=95, 49%) were nearly equally represented among the total birds captured.

Both sex and regional differences in the morphometrics of black oystercatchers were evident (MANOVA; sex: F=47.01, p<0.0001; region: F=7.40, p<0.0001). Females were generally larger than males in both Alaska and BC (Table 2.1). Females weighed 5.4% more, and had wing, tail, toe, tarsus, and culmen lengths that were 2-9% longer than males.

Black oystercatchers in Alaska had shorter tarsi and bills than those in BC (Table 2.1, Figure 2.3). Tarsus and culmen length of birds in BC were 2.2% larger than those in Alaska. There were no regional differences in toe or bill depth (Table 2.1). There was no evidence that birds in Alaska have larger bodies than those in BC: mass, wing length, tail length did not vary regionally (Table 2.1).

Table 2.1. Morphometrics and mass variation of male and female black oystercatchers in Alaska and British Columbia. We report means \pm SD and ranges in brackets, and statistical tests with significant results in bold.

	Alaska		British Columbia		Linear Mixed Model Results					
	Male (n=55)	Female (n=59)	Male (n=47)	Female (n=49)	Sex		Region		Region*Sex	
					t	p	t	p	t	p
Wing	247.1 \pm 5.8 (235-261)	251.6 \pm 8.6 (235-280)	246.4 \pm 4.9 (234-256)	253.6 \pm 5.0 (245-268)	-3.53	0.0005	1.55	0.121	-1.48	0.139
Tail	101.8 \pm 4.3 (94-110)	103.7 \pm 4.4 (93-113)	98.8 \pm 4.8 (90-112)	101.8 \pm 4.6 (92-115)	-2.19	0.03	-1.62	0.135	-0.82	0.413
Toe	44.0 \pm 2.0 (40-50)	44.8 \pm 2.0 (39-49)	43.6 \pm 1.6 (40-47)	45.2 \pm 2.0 (40-50)	-2.21	0.029	0.49	0.636	-1.26	0.209
Tarsus	51.9 \pm 1.8 (48-56.7)	53.1 \pm 2.0 (47.1-56.9)	52.6 \pm 1.9 (47.2-56.5)	54.6 \pm 1.7 (51.6-59.6)	-3.43	0.0008	2.58	0.030	-1.70	0.091
Culmen	69.5 \pm 2.7 (64.6-76.2)	76.2 \pm 3.3 (71.3-83)	70.8 \pm 3.2 (64.3-77.9)	77.7 \pm 3.3 (67-84)	-11.89	<0.0001	2.67	0.017	-0.12	0.906
Bill Depth	12.3 \pm 0.6 (11.3-14.2)	12.6 \pm 0.7 (11.1-14.2)	12.4 \pm 0.7 (11.1-14.1)	12.6 \pm 0.5 (11.4-14.1)	-2.21	0.028	-0.87	0.408	0.18	0.859
Mass	557.0 \pm 26 (500-597)	593.3 \pm 39 (525-702)	583.5 \pm 39 (500-692)	613.5 \pm 44 (525-717)	-4.74	<0.0001	0.69	0.500	0.70	0.486

There was evidence of finer-scale variation in morphology with overall differences between sites and sex (MANOVA; site: $F = 2.68$ $p < 0.0001$, sex: $F = 45.34$, $p < 0.0001$). However, ANOVAs on each morphological trait by site and sex showed that these site differences only occurred in BC and not Alaska (Table A.2). All morphological measurements except tail and toe were significantly different among sites in BC (Table A.2).

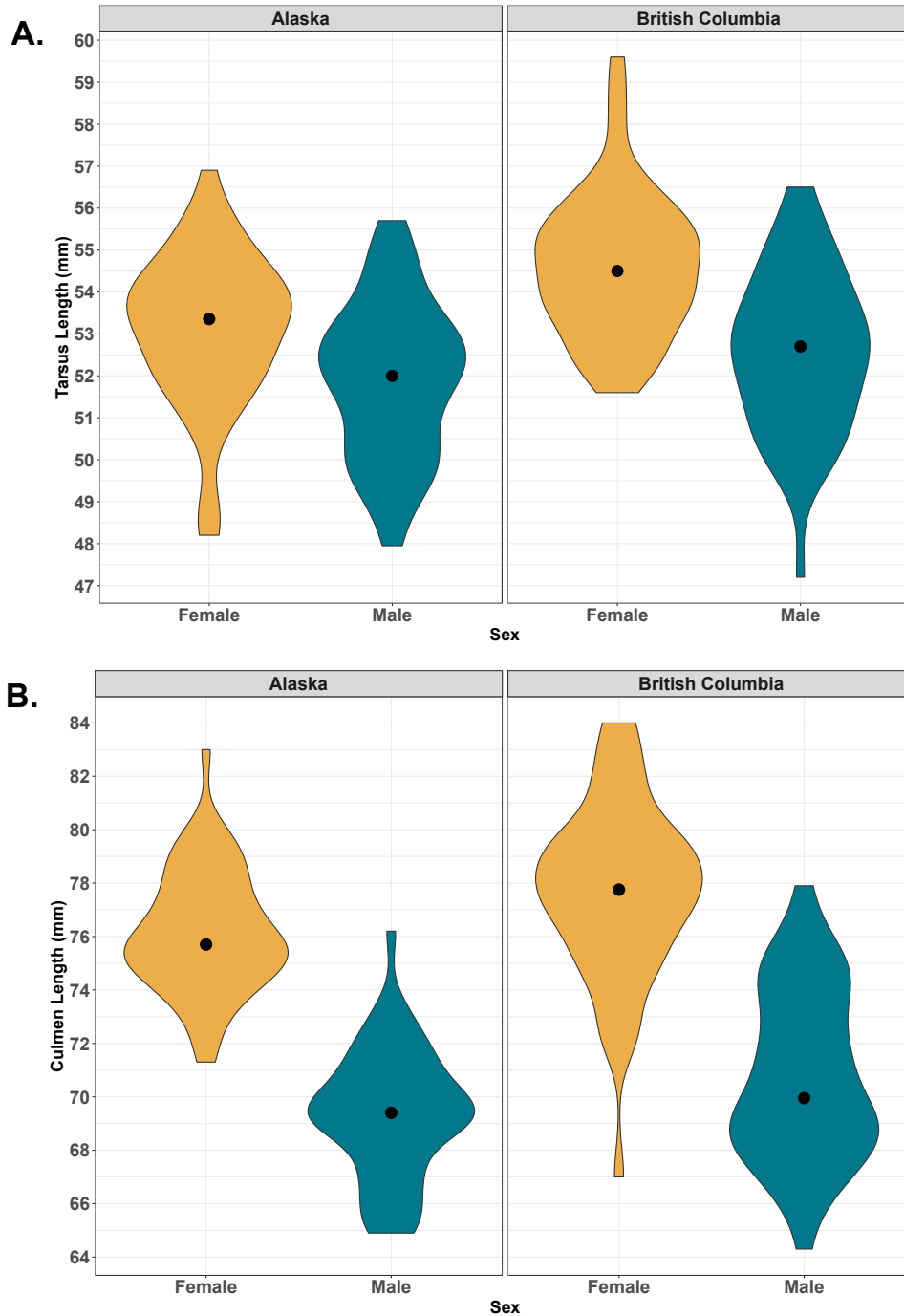


Figure 2.3. Sex and regional variation in (A) tarsus length (mm) and (B) culmen length (mm) in Alaska and British Columbia. The outline curve of the violin plot represent the probability density of the data at each tarsus length and black dots represent the median of the data.

We were able to calculate C2 and C3 scores of 95 birds. There were no differences in wing pointedness (C2) scores between BC and Alaska (region: $t=-2.13$, $p=0.06$; region*sex: $t=1.88$, $p=0.06$; Figure 2.4 A). Similarly, there were no differences in

wing convexity between Alaska and BC (region: $t=0.62$, $p=0.54$; region*sex: $t=-0.038$, $p=0.97$; Figure 2.4. B). Female and male wing shape did not differ (C2: $t=0.35$, $p=0.72$; C3: sex: $t=-1.71$, $p=0.09$; Figure 2.4).

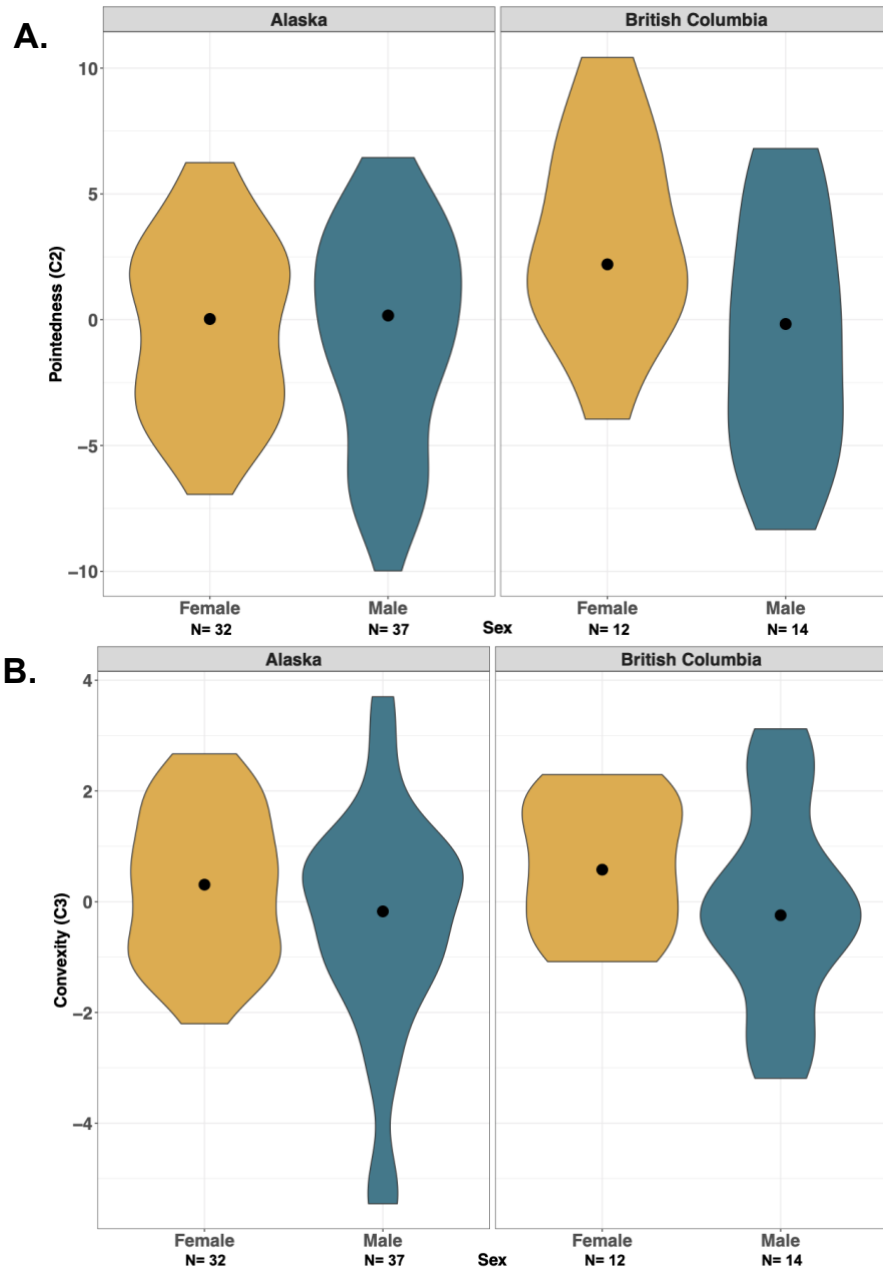


Figure 2.4. Sex and regional variation in (A) wing pointedness scores (C2) and (B) wing convexity scores (C3). The violin plot shows the probability density at a given score with the black dot representing the median.

The LDA confirmed that the six morphological traits differed between regions (females: $n = 92$, Wilks Lambda = 0.72, $p < 0.001$; males: $n = 88$, Wilks Lambda = 0.70, $p < 0.001$). However, the LDA had only a limited ability to successfully assign individuals to the correct region when using the six morphometrics and mass (females 78%, males 77%). The addition of wing shape metrics reduced the sample size in the LDA and reduced accuracy of assigning the region to individuals (70% for females and 66% for males).

2.4. Discussion

Avian morphology can be shaped by climatic conditions and the energetic demands of migration, both of which can vary with latitude. Here, we present evidence that geographical variation in the morphology of black oystercatchers in British Columbia and Alaska is consistent with Allen's rule. Tarsus and culmen are shorter in birds in Alaska than in BC. However, there is little evidence that black oystercatchers follow the patterns consistent with Bergmann's rule or for variation in wing shape between the two regions.

Bergmann's rule predicts that body sizes of individuals at higher latitudes will be larger than those at lower latitudes (Bergmann 1847). We found no evidence that black oystercatchers follow the predicted patterns of Bergmann's rule. In contrast, Meiri and Dayan (2003) found that most (72% of $n = 94$), but not all, species follow the pattern (Meiri and Dayan 2003). However, non-migratory species are more likely to comply with Bergmann's Rule than migrants, likely because they need to adapt to the variable annual conditions in one location while migrants can track warmer temperatures by relocating for the nonbreeding period (Meiri and Dayan 2003, McQueen et al. 2022). In our study, the mixture of both resident and migrant individuals included in the analysis may have made it more difficult to detect Bergmann's rule in black oystercatchers.

Allen's rule predicts that individuals at higher latitudes will have shorter extremities, and bill length and tarsus in many bird species follow the pattern (Symonds and Tattersall 2010). Bills can evolve to aid in thermoregulation, and individuals can dissipate excess metabolic heat after physical exertion through convective heat loss from these featherless extremities (Tattersall et al. 2017, Schraft et al. 2019). Schraft et al. (2019) found that tufted puffins can lose as much as 10-18% of their excess body

heat through their bills after energetically expensive flight. Legs can also aid in thermoregulation where shorter legs can keep birds in colder climates in the warmer 'boundary layer' close to the ground and out of wind that might dissipate heat more quickly (Cartar and Morrison 2005). We found that black oystercatchers in Alaska have shorter culmen and tarsi than those in British Columbia. Black oystercatchers in Alaska likely experience colder climates than those in BC, even during the breeding season, and reduced bill and leg size in Alaska may aid individuals in conserving heat by reducing convective heat loss through their bills and legs. Additionally, black oystercatchers are frequently seen employing heat saving behaviors such as bill tucking, lifting of one leg, or sitting (personal obs.). Behavioral thermoregulation follows a latitudinal gradient across many avian taxa including shorebirds, providing further evidence that the heat loss through these appendages can make a difference in body temperature regulation in colder climates (Pavlovic et al. 2018). Although culmen and tarsus lengths of black oystercatchers from Alaska were about 2% shorter than those in BC, these differences were much smaller than the differences between males and females. Sex differences in culmen and tarsus were about 9% and 3% respectively. This brings into question which mechanisms most strongly affect the morphology of bill and tarsus lengths.

Wing shape is argued to vary with migration, and the selective pressure of migration often leads to individuals with longer and more pointed wings (Lockwood 1998). With a higher proportion of migratory individuals and longer-distance migrants at higher latitudes, wing shape variation may follow a latitudinal gradient (Fielder 2005, Somveille et al. 2013). In this study, we found no evidence of differences in the wing shape of black oystercatchers in Alaska and British Columbia. Several factors may contribute to why we did not detect wing shape adaptations in these populations. Wing shape differences within a species may be less likely when migration is a facultative trait. In species such as blackcap warblers (*Sylvia atricapilla*) in Europe, migration is a fixed trait in some populations and the adaptations in wing shape for migration vary with migration distance (Fielder 2004, Ożarowska et al. 2021). In black oystercatchers, whether migration is facultative or obligate remains uncertain, and if the trait is not fixed the selection on wing shape for migration could be relaxed in this species (Tessler et al. 2014, Johnson 2010). Additionally, intra-specific variation in wing shape may be more apparent if all individuals in a population migrate long distances (in the range of 4000 km

or more: Förschler and Bairlein 2011). Black oystercatchers are partial migrants, and a portion of the population of this study were fitted with GPS tags and geolocators to record annual movements. Of this sample, 50% of the twenty-three individuals in Alaska migrated and those that did varied substantially in their migration distance between about 800 and 1600 km (C. Rankin pers comm). These distances are relatively small compared to other migratory species (ranging from 3000-7000 km in European shorebirds: Minias et al. 2015) and may not be long enough to select for longer, more pointed wings in black oystercatchers. Additionally, with the mix of both migrants and residents in the Alaska population, bimodality in wing shape may be expected in Alaska. Though there is some suggestion of bimodality in the probability distribution of wing pointedness (Figure 2.4 A), there is no evidence that individuals with more pointed wing scores are migrants in Alaska. Predation risk and territory defense can select for shorter, more rounded wing shapes (Swaddle and Lockwood 1998). Black oystercatchers are vulnerable to predation by avian predators such as peregrine falcons and bald eagles (Tessler et al. 2007). Adults spend much of their time defending territory during the breeding season, and pursuit of intruders and predators often involves complex aerial maneuvers (Andres and Falxa 2020). Predator avoidance and pursuit of intruders may select more for wings that aid in quick, explosive flight in black oystercatchers. Finally, small sample sizes and difference in timing of capture of some birds in British Columbia could affect our findings. Individuals captured in BC in the spring could have less feather wear and be less rounded than those captured in BC and Alaska in the summer. We did find that wing lengths of birds in BC were longer, on average, in the spring than the summer. However, restricting to only birds captured in the summer in BC in the analysis did not alter our conclusions. In black oystercatchers, wing shape may not be influenced by migration due to limited migration distance or another stronger selection force acting on wing shape.

Researchers have successfully used differences in morphology and wing shape to discriminate migrants from residents or individuals from different breeding origins when found in the same site (Pérez-Tris et al. 1999, Neto et al. 2013, Maggini 2016). Here, despite differences in morphology between birds in BC and Alaska, the linear discriminant analysis was limited in the accuracy of classifying birds as captured in British Columbia or Alaska. Though the predictions of region when using the six body morphometrics and mass was better than what would be expected by chance, the

accuracy of our analysis was much lower than other published studies using morphology in discriminant analysis (77-78% in our study compared to about 85-100% in other studies; de la Hera et al. 2007, Delingat et al. 2011, Neto et al. 2013, Maggini et al. 2016). Therefore, morphology cannot be used to distinguish between birds from the two regions. Limits in the ability to distinguish between birds from the two regions may come from the considerable variation in morphology both within and across sites. Particularly in British Columbia, we found significant differences in all traits but tail and toe length across sites (Table A.3). All black oystercatchers previously tracked in British Columbia exhibit only local movement (Ware 2021), which could lead to limited mixing between larger geographic areas in the province. Morphological variation among sites within regions showed no consistent pattern associated with latitude, longitude, and exposure. Intertidal invertebrate abundance can be highly variable locally (Zacharias and Roff 2001) and the morphological differences among sites, particularly in bill shape, could indicate adaptation to local prey availability.

Reverse sexual dimorphism has been well documented in shorebirds, and black oystercatchers are known to show reverse sexual dimorphism in body size and bill length (Andres and Falxa 2020). We found that intersexual variation in morphometrics and mass was greater than regional variation in these traits. Female birds had bills that were 9% and tarsi that were 3% bigger than males, whereas BC birds had bills and tarsi that were 2% larger than those in Alaska. The large intersexual variation in morphology in both BC and Alaska suggest a role for other drivers of black oystercatcher morphology. Reversed sexual size dimorphism been argued to evolve to reduce competition between the sexes and allow for resource partitioning (Nebel and Thompson 2011, Duijns et al. 2014). Alternatively, reversed sexual dimorphism could be driven by sexual selection where larger females could produce larger eggs (Selander 1972) or incubate more efficiently (Snyder and Wiley 1976). Additionally, smaller males could allow for more efficient foraging to provide for chick rearing (Jönson and Alerstam 1990) or better agility for courtship displays (Peters 1986). In black oystercatchers, resource partitioning or sexual selection may be stronger drivers of morphology than climate. In chapter two, I investigate a potential driver of these large morphological differences, particularly in bill length, between male and female black oystercatchers.

2.5. References

- Alhajeri, B. H., Fourcade, Y., Upham, N. S., & Alhaddad, H. (2020). A global test of Allen's rule in rodents. *Global Ecology and Biogeography*, 29(12), 2248–2260. <https://doi.org/10.1111/geb.13198>
- Allen JA (1877) The influence of Physical conditions in the genesis of species. *Radical Rev* 1: 108–140.
- Andres, B.A. and G. A. Falxa (2020). Black Oystercatcher (*Haematopus bachmani*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.blkoys.01>
- Ashton, K. G. (2002). Patterns of within-species body size variation of birds: Strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, 11(6), 505–523. <https://doi.org/10.1046/j.1466-822X.2002.00313.x>
- Bansal, U., & Thaker, M. (2021). Diet influences latitudinal gradients in life-history traits, but not reproductive output, in ectotherms. *Global Ecology and Biogeography*, 30(12), 2431–2441. <https://doi.org/10.1111/geb.13396>
- Bergmann, C. (1847). Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. – Göttinger Studien 1, 595–708
- Berthold, P. (1999). A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich*, 70(1), 1–11. <https://doi.org/10.1080/00306525.1999.9639744>
- Boyce, M. S. (1979). Seasonality and Patterns of Natural Selection for Life Histories. *The American Naturalist*, 114(4), 569–583.
- Cartar, R. V., & Morrison, R. I. G. (2005). Metabolic Correlates of Leg Length in Breeding Arctic Shorebirds: The Cost of Getting High. *Journal of Biogeography*, 32(3), 377–382.
- Carvalho Provinciato, I. C., Araújo, M. S., & Jahn, A. E. (2018). Drivers of wing shape in a widespread Neotropical bird: A dual role of sex-specific and migration-related functions. *Evolutionary Ecology*, 32(4), 379–393. <https://doi.org/10.1007/s10682-018-9945-4>
- Chapman, B. B., Brönmark, C., Nilsson, J.-Å., & Hansson, L.-A. (2011). The ecology and evolution of partial migration. *Oikos*, 120(12), 1764–1775. <https://doi.org/10.1111/j.1600-0706.2011.20131.x>
- Chesser, R. T. (1998). Further perspectives on the breeding distribution of migratory birds: South American austral migrant flycatchers. *Journal of Animal Ecology*, 67(1), 69–77. <https://doi.org/10.1046/j.1365-2656.1998.00179.x>

- Cody, M. L. (1966). A General Theory of Clutch Size. *Evolution*, 20(2), 174–184.
<https://doi.org/10.1111/j.1558-5646.1966.tb03353.x>
- Culumber, Z. W. (2022). Variation in behavioral traits across a broad latitudinal gradient in a livebearing fish. *Evolutionary Ecology*, 36(1), 75–91.
<https://doi.org/10.1007/s10682-021-10146-5>
- Cucco, M., & Bowman, R. (2018). Mass fluctuation in breeding females, males, and helpers of the Florida scrub-jay *Aphelocoma coerulescens*. *PeerJ*, 6, e5607.
<https://doi.org/10.7717/peerj.5607>
- de la Hera, I., Pérez-Tris, J., & Tellería, J. (2007). Testing the validity of discriminant function analyses based on bird morphology: The case of migratory and sedentary blackcaps *Sylvia atricapilla* wintering in southern Iberia. *Ardeola: Revista Ibérica de Ornitología*, 54, 81–91.
<https://doi.org/10.1080/00063659909461142>
- Delingat, J., Hobson, K. A., Dierschke, V., Schmaljohann, H., & Bairlein, F. (2011). Morphometrics and stable isotopes differentiate populations of Northern Wheatears (*Oenanthe oenanthe*). *Journal of Ornithology*, 152(2), 383–395.
<https://doi.org/10.1007/s10336-010-0599-4>
- Díaz, M., Møller, A. P., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Markó, G., & Tryjanowski, P. (2013). The Geography of Fear: A Latitudinal Gradient in Anti-Predator Escape Distances of Birds across Europe. *PLoS ONE*, 8(5), e64634. <https://doi.org/10.1371/journal.pone.0064634>
- Duijns, S., van Gils, J. A., Spaans, B., ten Horn, J., Brugge, M., & Piersma, T. (2014). Sex-specific winter distribution in a sexually dimorphic shorebird is explained by resource partitioning. *Ecology and Evolution*, 4(20), 4009–4018.
<https://doi.org/10.1002/ece3.1213>
- Egbert, J. R., & Belthoff, J. R. (2003). Wing Shape in house finches Differs Relative to Migratory Habit in Eastern and Western North America. *The Condor*, 105, 825–829. <https://doi.org/10.1093/condor/105.4.825>
- Evered, D. S. (1990). Measures of Wing Area and Wing Span from Wing Formula Data. *The Auk*, 107, 784–787. <https://doi-org.proxy.lib.sfu.ca/10.2307/4088014>
- Fiedler, W. (2005). Ecomorphology of the External Flight Apparatus of Blackcaps (*Sylvia atricapilla*) with Different Migration Behavior. *Annals of the New York Academy of Sciences*, 1046(1), 253–263. <https://doi.org/10.1196/annals.1343.022>
- Figuerola, J. (1999). A comparative study on the evolution of reversed size dimorphism in monogamous waders. *Biological Journal of the Linnean Society*, 67(1), 1–18.
<https://doi.org/10.1111/j.1095-8312.1999.tb01926.x>

- Flockhart, D. T. T., Fitz-gerald, B., Brower, L. P., Derbyshire, R., Altizer, S., Hobson, K. A., Wassenaar, L. I., & Norris, D. R. (2017). Migration distance as a selective episode for wing morphology in a migratory insect. *Movement Ecology*, 5(1), 7. <https://doi.org/10.1186/s40462-017-0098-9>
- Förschler, M. I., & Bairlein, F. (2011). Morphological Shifts of the External Flight Apparatus across the Range of a Passerine (Northern Wheatear) with Diverging Migratory Behaviour. *PLoS ONE*, 6(4), e18732. <https://doi.org/10.1371/journal.pone.0018732>
- Geist, V. (1987). Bergmann's rule is invalid. *Canadian Journal of Zoology*, 65(4), 1035–1038. <https://doi.org/10.1139/z87-164>
- Guzzetti, B. M., Talbot, S. L., Tessler, D. F., Gill, V. A., & Murphy, E. C. (2008). Secrets in the eyes of Black Oystercatchers: A new sexing technique. *Journal of Field Ornithology*, 79(2), 215–223. <https://doi.org/10.1111/j.1557-9263.2008.00167.x>
- James, F. C. (1970). Geographic Size Variation in Birds and Its Relationship to Climate. *Ecology*, 51(3), 365–390. <https://doi.org/10.2307/1935374>
- Johnson, M., Clarkson, P., Goldstein, M. I., Haig, S. M., Lanctot, R. B., Tessler, D. F., & Zwiefelhofer, D. (2010). Seasonal Movements, Winter Range Use, and Migratory Connectivity of the Black Oystercatcher. *The Condor*, 112(4), 731–743. <https://doi.org/10.1525/cond.2010.090215>
- Jönsson PE, Alerstam T. (1990). The adaptative significance of parental role division and sexual size dimorphism in breeding shorebirds. *Biological Journal of the Linnean Society* 41: 301-314.
- Laurila, A., Lindgren, B., & Laugen, A. T. (2008). Antipredator Defenses Along a Latitudinal Gradient in *Rana temporaria*. *Ecology*, 89(5), 1399–1413. <https://doi.org/10.1890/07-1521.1>
- Linek, N., Brzęk, P., Gienapp, P., O'Mara, M. T., Pokrovsky, I., Schmidt, A., Shipley, J. R., Taylor, J. R. E., Tiainen, J., Volkmer, T., Wikelski, M., & Partecke, J. (2021). A partial migrant relies upon a range-wide cue set but uses population-specific weighting for migratory timing. *Movement Ecology*, 9(1), 63. <https://doi.org/10.1186/s40462-021-00298-y>
- Lockwood, R., Swaddle, J. P., & Rayner, J. M. V. (1998). Avian Wingtip Shape Reconsidered: Wingtip Shape Indices and Morphological Adaptations to Migration. *Journal of Avian Biology*, 29(3), 273. <https://doi.org/10.2307/3677110>
- Maggini, I., Metzger, B., Voss, M., Voigt, C. C., & Bairlein, F. (2016). Morphometrics and stable isotopes differentiate wintering populations of a migratory bird. *Movement Ecology*, 4(1), 20. <https://doi.org/10.1186/s40462-016-0085-6>
- Mayr, E. (1956). Geographical Character Gradients and Climatic Adaptation. *Evolution*, 10(1), 105–108. <https://doi.org/10.2307/2406103>

- Marchetti, K., Price, T., & Richman, A. (1995). Correlates of Wing Morphology with Foraging Behaviour and Migration Distance in the Genus *Phylloscopus*. *Journal of Avian Biology*, 26(3), 177–181. <https://doi.org/10.2307/3677316>
- McQueen, A., Klaassen, M., Tattersall, G. J., Atkinson, R., Jessop, R., Hassell, C. J., Christie, M., Victorian Wader Study Group, Australasian Wader Studies Group, & Symonds, M. R. E. (2022). Thermal adaptation best explains Bergmann's and Allen's Rules across ecologically diverse shorebirds. *Nature Communications*, 13(1), 4727. <https://doi.org/10.1038/s41467-022-32108-3>
- Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, 30(3), 331–351. <https://doi.org/10.1046/j.1365-2699.2003.00837.x>
- Minias, P., Meissner, W., Włodarczyk, R., Ożarowska, A., Piasecka, A., Kaczmarek, K., & Janiszewski, T. (2015). Wing shape and migration in shorebirds: A comparative study. *Ibis*, 157(3), 528–535. <https://doi.org/10.1111/ibi.12262>
- Mulvihill, R. S., & Chandler, C. R. (1991). A Comparison of Wing Shape between Migratory and Sedentary Dark-Eyed Juncos (*Junco hyemalis*). *The Condor*, 93(1), 172–175. <https://doi.org/10.2307/1368620>
- Murphy, S. P., Virzi, T., & Sanders, F. (2017). Exploring Differences in Adult Survival and Site Fidelity of Migratory and Non-Migratory American Oystercatcher (*Haematopus palliatus*) Populations. *Waterbirds*, 40(sp1), 32–43. <https://doi.org/10.1675/063.040.sp105>
- Nebel, S., & Thompson, G. J. (2011). The evolution of sexual bill-size dimorphism in shorebirds: A morphometric test of the resource partitioning hypothesis. *Evolutionary Ecology Research*, 13, 35–44.
- Neto, J. M., Gordinho, L., Belda, E. J., Marín, M., Monrós, J. S., Fearon, P., & Crates, R. (2013). Phenotypic Divergence among West European Populations of Reed Bunting *Emberiza schoeniclus*: The Effects of Migratory and Foraging Behaviours. *PLoS ONE*, 8(5), e63248. <https://doi.org/10.1371/journal.pone.0063248>
- Newton, I., & Dale, L. (1996). Relationship between Migration and Latitude Among West European Birds. *Journal of Animal Ecology*, 65(2), 137–146. <https://doi.org/10.2307/5716>
- Nudds, R. L., & Oswald, S. A. (2007). An Interspecific Test of Allen's Rule: Evolutionary Implications for Endothermic Species. *Evolution*, 61(12), 2839–2848. <https://doi.org/10.1111/j.1558-5646.2007.00242.x>
- Ożarowska, A., Zaniewicz, G., & Meissner, W. (2021). Sex and age-specific differences in wing pointedness and wing length in blackcaps *Sylvia atricapilla* migrating through the southern Baltic coast. *Current Zoology*, 67(3), 271–277. <https://doi.org/10.1093/cz/zoaa065>

- Pavlovic, G., Weston, M. A., & Symonds, M. R. E. (2019). Morphology and geography predict the use of heat conservation behaviours across birds. *Functional Ecology*, 33(2), 286–296. <https://doi.org/10.1111/1365-2435.13233>
- Pérez-Tris, J., Carbonell, R., & Tellería, J. L. (1999). A method for differentiating between sedentary and migratory Blackcaps *Sylvia atricapilla* in wintering areas of southern Iberia. *Bird Study*, 46(3), 299–304. <https://doi.org/10.1080/00063659909461142>
- Perez-Tris, J., & Telleria, J. L. (2001). Age-related variation in wing shape of migratory and sedentary Blackcaps (*Sylvia atricapilla*). *Journal of Avian Biology*, 32, 207–213.
- Peters RH. (1986). *The ecological implications of body size*. Cambridge: Cambridge University Press.
- Pyle, P. (1997). Identification Guide to North American Birds, Part I: Columbidae to Ploceidae. Bolinas, CA: Slate Creek Press. ISBN 0961894024.
- Pyle, P. (2008). Identification Guide to North American Birds, Part II: Anatidae to Alcidae. Bolinas, CA: Slate Creek Press. ISBN 9780961894047.
- Rising, J. D., & Somers, K. M. (1989). The Measurement of Overall Body Size in Birds. *The Auk*, 106(4), 666–674.
- Ross, J. D., & Bouzat, J. L. (2014). Genetic and morphometric diversity in the Lark Sparrow (*Chondestes grammacus*) suggest discontinuous clinal variation across major breeding regions associated with previously characterized subspecies. *The Auk*, 131(3), 298–313. <https://doi.org/10.1642/AUK-13-246.1>
- Rosenzweig, M. L. (1968). The Strategy of Body Size in Mammalian Carnivores. *The American Midland Naturalist*, 80(2), 299–315. <https://doi.org/10.2307/2423529>
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak, P., & Cardona, A. (2012). Fiji: An open-source platform for biological-image analysis. *Nature Methods*, 9(7), 676–682. <https://doi.org/10.1038/nmeth.2019>
- Scholander, P. F. (1955). Evolution of Climatic Adaptation in Homeotherms. *Evolution*, 9(1), 15–26. <https://doi.org/10.2307/2405354>
- Schraft, H. A., Whelan, S., & Elliott, K. H. (2019). Huffin' and puffin: Seabirds use large bills to dissipate heat from energetically demanding flight. *Journal of Experimental Biology*, jeb.212563. <https://doi.org/10.1242/jeb.212563>

- Selander, R.K. (1972). Sexual Selection and Dimorphism in Birds. In B.G. Campbell (Ed.), *Sexual Selection and the Descent of Man*. (pp. 180-230). Transaction Publishers.
- Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., & Ericsson, G. (2012). From migration to nomadism: Movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, 22(7), 2007–2020. <https://doi.org/10.1890/12-0245.1>
- Slud, P. (1976). Geographic and climatic relationships of avifaunas with special reference to comparative distribution in the neotropics. *Smithsonian Contributions to Zoology*, 212, 1–149. <https://doi.org/10.5479/si.00810282.212>
- Snyder CG, Wiley JW. (1976). Sexual size dimorphism in hawks and owls of North America. *Ornithological Monographs* 20.
- Somveille M., Manica A., Butchart S.H.M., Rodrigues A.S.L. (2013). Mapping Global Diversity Patterns for Migratory Birds. *PloS ONE* 8(8): e70907. <https://doi.org/10.1371/journal.pone.0070907>
- Stojanovic, D., Neeman, T., & Heinsohn, R. (2020). Overlap in the wing shape of migratory, nomadic and sedentary grass parrots. *Journal of Avian Biology*, 51(12). <https://doi.org/10.1111/jav.02586>
- Swaddle, J. P., & Lockwood, R. (1998). Morphological Adaptations to Predation Risk in Passerines. *Journal of Avian Biology*, 29(2), 172–176. <https://doi.org/10.2307/3677195>
- Symonds, M. R. E., & Tattersall, G. J. (2010). Geographical Variation in Bill Size across Bird Species Provides Evidence for Allen's Rule. *The American Naturalist*, 176(2), 188–197. <https://doi.org/10.1086/653666>
- Tattersall, G. J., Arnaout, B., & Symonds, M. R. E. (2017). The evolution of the avian bill as a thermoregulatory organ. *Biological Reviews*, 92(3), 1630–1656. <https://doi.org/10.1111/brv.12299>
- Tessler, D.F., J.A. Johnson, B.A. Andres, S. Thomas, and R.B. Lanctot. 2007. Black Oystercatcher (*Haematopus bachmani*) Conservation Action Plan. International Black Oystercatcher Working Group, Alaska Department of Fish and Game, Anchorage, Alaska, U.S. Fish and Wildlife Service, Anchorage, Alaska, and Manomet Center for Conservation Sciences, Manomet, Massachusetts. 115 pp. (http://www.whsrn.org/shorebirds/conservation_plans.html)
- Tessler, D. F., Johnson, J. A., Andres, B. A., Thomas, S., & Lanctot, R. B. (2014). A global assessment of the conservation status of the Black Oystercatcher *Haematopus bachmani*. *International Wader Studies* 20: 83–96.
- Venables WN, Ripley BD (2002). *Modern Applied Statistics with S*, Fourth edition. Springer, New York. <https://www.stats.ox.ac.uk/pub/MASS4/>.

- Ware, L. (2021). Satellite telemetry reveals habitat selection decisions by black oystercatchers across seasonal, diel, and tidal cycles. [Master's Thesis, Simon Fraser University]. Summit Research Repository.
- Wiklund, C. G. (1996). Body Length and Wing Length Provide Univariate Estimates of Overall Body Size in the Merlin. *The Condor*, 98(3), 581–588.
<https://doi.org/10.2307/1369570>
- Zacharias, M. A., & Roff, J. C. (2001). Explanations of patterns of intertidal diversity at regional scales. *Journal of Biogeography*, 28(4), 471–483.
<https://doi.org/10.1046/j.1365-2699.2001.00559.x>
- Zwarts L., J.B. Hulscher, K. Koopman & P.M. Zegers (1996). Body weight in relation to variation in body size of Oystercatchers *Haematopus ostralegus*. *Ardea* 84A: 21-28.

Chapter 3.

Reversed sexual dimorphism and resource partitioning in black oystercatchers

3.1. Introduction

Reversed sexual dimorphism, where the female is larger than the male, has evolved in a diversity of avian orders including hawks (Accipitriformes), falcons (Falconiformes), and shorebirds (Charadriiformes; Mueller 1990). Reversed sexual dimorphism may arise through an increase in female size (Reynolds 1972, Andersson and Norberg 1981), decrease in male size (Jehl and Murray 1984), or a divergence in size between males and females (Ydenberg and Forbes 1991). Consequently, hypotheses regarding the evolution of reversed sexual dimorphism are often taxon-specific (for birds of prey see Reynolds 1972, Andersson and Norberg 1981, Mueller and Meyer 1985, Ydenberg and Forbes 1991, Krüger 2005; for shorebirds: Jehl and Murray 1984, Figuerola 1999; for gulls and alcid: Székely et al., 2000, Lindenfors et al. 2003). The hypotheses proposed can be broadly categorized as being ecological, the outcome of sex-role differentiation, or a consequence of sexual selection (Mueller and Meyer 1985). Ecological hypotheses describe resource partitioning and the benefits of reduced intersexual competition (Selander 1972). Sex-role differentiation hypotheses focus on the benefits of task specialization during breeding (Ydenberg and Forbes 1991), while sexual selection hypotheses often center on the intensity of sexual selection on males and the benefits of small male size for agility in display (Jehl and Murray 1984).

If selection for resource partitioning between the sexes has contributed to the evolution of reversed sexual dimorphism, then the degree of dimorphism in traits linked to resource exploitation, such as bill length, should be greater than the degree of dimorphism in other traits (Selander 1972, Durell 2000, Nebel and Thompson 2011). Bill dimorphism is more pronounced than body dimorphism in many species of shorebirds (godwits (*Limosa*), sandpipers (*Calidris*), curlews (*Numenius*), and oystercatchers (*Haematopus*); reviewed by Nebel and Thompson 2011). In Western sandpipers (*Calidris mauri*), bill length dimorphism is three times larger than size dimorphism (15% difference in culmen vs 5% in tarsus; Stein et al. 2008). Studies have demonstrated that sex-differences in bill length are linked to differences in foraging mode and diet. Mathot

and Elner (2004) found that males, with their shorter bills, employ surface feeding while females tend to probe into the sediment more. Hall et al. (2021) showed using stable isotopes that spring diet between males and female Western sandpipers differs in that females consume larger numbers of subsurface polychaetes while males consume greater proportions of epifaunal invertebrates. Further evidence for intersexual resource partitioning in this species is provided by their nonbreeding distributions where females migrate further south than males (Nebel et al. 2002, Nebel et al. 2005, Mathot et al. 2007).

All eleven extant species within the oystercatcher family (*Haematopodidae*), display reversed sexual dimorphism in bill length (Hockey and Underhill 1984, Durell et al. 1993, Lauro and Nol 1995). Bill length dimorphism can range from about 6.8% (Eurasian oystercatcher, *Haematopus ostralegus*; Hockey 1996) to as large as 19% (sooty oystercatcher *Haematopus fuliginosus*; Alpin and Cockburn 2012). Studies on several oystercatcher species have documented resource partitioning between the sexes in relation to both bill length and shape. In sooty and pied (*Haematopus longirostris*) oystercatchers in Australia, behavioral observations found that males consume more hard-shelled prey items while females tend to eat larger proportions of subsurface polychaete worms (Laura and Nol 1995; Alpin and Cockburn 2012). In the African black oystercatcher, behavioral observations suggest that males and females within a breeding pair equally feed on mussels, but males take more limpets and snails while females select more worms that are harder to reach (Hockey and Underhill 1985; but see Kohler et al. 2014). Finally, Eurasian oystercatchers with thinner, more pointed bill tips tend to be mudflat feeders and probe into the sediment while those with a “hammer-like” blunt tips hammer mussels open (Swennen et al. 1983; van de Pol 2009). Durell et al. (1993) reported that over 70% of individuals with pointed-shaped bills were females, while 90% of individuals with hammer-shaped bill tips were males.

Black oystercatchers (*Haematopus bachmani*) are a shorebird found along the west coast of North America, ranging from Baja California to Alaska (Tessler et al. 2014). This species shows a moderate dimorphism in bill length with an average difference of 9% between the sexes (Chapter 1). Black oystercatchers are also known to feed on a wide variety of marine macroinvertebrates- mussels (*Mytilus spp.*), limpets (*Lottia spp.*), chitons (family *Chitonidae*), dogwinkle snails (*Nucella spp.*), and clams (family *Veneridae*; Webster 1941, Tessler 2014, Robinson 2018, Andres and Falxa

2020), providing the opportunity for males and females to partition resources available in the rocky intertidal. Here, we test the hypothesis that bill dimorphism is linked to resource partitioning in black oystercatchers using stable isotope diet analysis. Specifically, we predict that females, with their longer bills, would be better able to access prey buried in the sediment such as clams.

3.2. Methods

Study Area

We studied black oystercatchers across British Columbia, Canada, and Alaska, USA (Figure 2.1). We captured birds at three sites across British Columbia: Salish Sea which included Gulf Islands National Park (48.77°N, -123.34°W), and the Sunshine Coast Regional District (49.44°N, -123.65°W), Pacific Rim National Park (48.94°N, -125.28°W), and Haida (53.21°N, -132.11°W). In Alaska, we captured birds across four sites in Katmai National Park (58.23°N, -154.14°W), Kachemak Bay State Park ((59.61°N, -151.23 °W), Kenai Fjords National Park (59.72 °N, -149.70°W), and Western Prince William Sound (60.19 °N, -147.91°W). We conducted fieldwork either in the spring (March-April) or summer (June-July) in British Columbia and in the summer (June-August) in Alaska. All capture and handling of birds was conducted under permits provided by Simon Fraser University animal care and local and federal permits (Canada banding permit number 10667 Y, animal use permit number 1218-2021).

Field Methods and Sampling

We captured black oystercatchers in BC and Alaska using noose mats and lines with decoys (Mad River Decoys, Bremen, ME USA) and a remote speaker playing black oystercatcher calls (Foxpro Inferno, Lewistown, PA, USA). We banded each individual bird with a stainless-steel band on the right tarsus, and two identical green plastic bands with a unique alpha-numeric on the tibia (Haggie Engraving, Millington, MD, USA). For each bird captured, we determined age based on plumage and the color of the bill and eye (Pyle 2008). We assigned sex based on the eye-fleck method (where females have a distinct black eye—fleck and males have little or no eye-fleck; Guzetti et al. 2008) in conjunction with data on the sex and size of their mate.

We recorded ten morphological measurements from each bird. We weighed them using a spring balance (Pesola Medio 1000g) and measured the wing chord, tail length, and length of the longest toe from the webbing to the tip of the toe using a 1 mm-unit ruler. We measured diagonal tarsus using 0.1 mm-unit calipers (SPI Polymid Dial 150mm). Finally, we described bill morphology with four measurements using 0.1 mm-unit calipers (SPI Polymid Dial 150mm): the length of the exposed culmen from the edge of the feathers to the tip, bill depth at the nares, bill width at the nares, and depth of the bill at the tip. From each bird, we collected the outermost greater covert feather and took a 2 mm toenail clipping for stable isotope analysis.

We chose five representative prey species of the black oystercatcher diets for stable isotope analysis. We attempted to collect the following genera and species at each site: blue mussel (*Mytilus spp.*), limpet (*Lottia spp.*), dogwinkle snail (*Nucella spp.*), black chiton (*Katharina tunicate*), and littleneck clam (*Leukoma staminea*). In sites where we could not find these specific genera or species, we collected samples of the most closely related species we could find. Within each site, we attempted to collect a minimum of four replicates from spatially distributed locations to capture any variation in stable isotope signatures within each site. Prey samples were collected from all sites during the summer season (May-July). All samples were frozen within three hours of collection and stored at -20 degrees Celsius until processed for stable isotope analysis.

Sample Preparation and Analysis

We washed the black oystercatcher feather and claw samples with a 2:1 chloroform-methanol mixture to remove surface contaminants (Paritte and Kelly 2009). The samples were covered in the solution and left to sit for 24 hours before pipetting off the liquid and dried in the fume hood. We subsampled the distal third of the feather and avoided any part of the rachis. We dissected each prey item to extract only muscle tissue and rinsed the tissue with distilled water. For larger species, we used a single individual for each sample while for smaller species we pooled 2-3 individuals from within the same sampling location to create a sufficient sample. All samples were freeze dried in a lyophilizer for up to 72 hours (Virtis SP Scientific Sentry 2.0), then ground into a powder using a mortar and pestle. We performed a lipid extraction on the powdered prey samples using a 2:1 chloroform-methanol solution following adapted protocols from Bligh and Dyer (1959). All prey, feather, and claw samples were subsampled to 0.3-0.8

mg using a microbalance and folded into tin capsules (Isomass Scientific, Calgary, AB) for analysis.

Carbon and nitrogen stable isotope analysis took place at the Alaska Stable Isotope Facility at the University of Alaska, Fairbanks. The facility uses Continuous-Flow Isotope Mass Spectrometry (CF-IRMS) with Thermo Flash EA machines (Thermo Fisher Scientific, Waltham, MA) to analyze stable carbon and nitrogen isotope ratios. Stable isotope ratios are reported in delta notation (δ) as parts per mil (‰) calculated as the deviation of the isotope ratio of the sample from known international standards (Vienna Pee Dee Belemnite for carbon and air for nitrogen). The facility performs precision checks every ten samples using known laboratory standards (peptone $\delta^{13}\text{C} = -15.8$ and $\delta^{15}\text{N} = 7.0$) and analytical precision, measured as the standard deviation of the runs from the standard, was 0.08‰ for $\delta^{13}\text{C}$ and 0.07‰ for $\delta^{15}\text{N}$. We performed our own precision checks by including replicates of randomized samples and found high repeatability between sample runs ($R=0.96 \pm 0.01$ SE for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

Statistical Analysis

We used a series of linear mixed models to test for regional differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes of the oystercatchers and prey items. The linear mixed models used either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ of each prey item or oystercatchers as the dependent variable with region as a fixed effect and site as a random term. We also included sex as a fixed effect in the models for the oystercatchers.

To quantify the diet of black oystercatchers, we used the Bayesian stable isotope mixing model MixSiar (Stock et al. 2018). Stable isotope mixing model results are sensitive to the diet-tissue discrimination factor (DTDF) used and often using a species-specific DTDF is preferred (Phillips et al. 2014). Carney (2013) estimated the DTDF for black oystercatcher whole blood to be 4.74 ± 0.71 ‰ for $\delta^{15}\text{N}$ and 1.8 ± 0.27 ‰ for $\delta^{13}\text{C}$. However, these values were obtained using a small sample of captive oystercatchers fed an unnatural diet, and are higher than expected (Post 2002, Cherel et al. 2005) and placed our oystercatcher isotope signatures outside of the source polygon (Phillips et al. 2014). Kohler et al. (2011) estimated the DTDF for African black oystercatcher whole blood to be 2.7 ± 0.4 ‰ for $\delta^{15}\text{N}$ and 0.2 ± 0.4 ‰ for $\delta^{13}\text{C}$ (Kohler et al. 2011). Diet-tissue discrimination factors can vary depending on the tissue; differences in $\delta^{13}\text{C}$ of blood and

feathers are minimal whereas $\delta^{15}\text{N}$ of blood and feathers can range from 0.7 ‰ to 1.8 ‰ (Hobson and Clark 1992, Bearhop et al. 2002, Cherel et al. 2002). We adjusted for differences in DTDF between blood and feathers and used 0.2 ± 0.4 ‰ for $\delta^{13}\text{C}$ and 3.4 ± 0.4 ‰ for $\delta^{15}\text{N}$ in our mixing models. This $\delta^{15}\text{N}$ DTDF is commonly used as an average across many taxa (Post 2002).

Stable isotope signatures of prey varied among sites (see Results), so we ran the mixing models separately for each of the seven sites. We used site-specific source samples (mean \pm SD) of the five prey items (mussel, limpet, chitons, snail, and clam) and included individual id for the oystercatchers as a fixed effect in each model. Diet studies on black oystercatchers consistently describe mussels and limpets as being consumed far more than other prey items (Webster 1942, Hartwick 1975, Hazlitt et al. 2002, Carney 2013, Robinson et al. 2018). Therefore, to increase the model's power, we used an informative prior in the model that weighted mussels and limpets twice as much as the other prey items (Moore and Semmens 2008; Figure B.1). We ran the models for a "long" run of Markov chain Monte Carlo (MCMC) sampling (chain length=300000, burn in=200000, thin=100, chains=3; Stock et al. 2018).

After running the stable isotope mixing models for each site, we extracted the mean estimated proportions of prey items for each individual oystercatcher. We used those data to test for sex differences in diet. We first ran a MANOVA to determine whether there were overall differences in the diet of males and females, controlling for any differences across sites. We then used linear mixed models to test our prediction that the diet of females would contain a greater proportion of clams than males and evaluated whether the proportion of clams in the diet of individuals varied with bill length. Individual identity was used as a random term in these models. We acknowledge that using this stepwise approach does not incorporate the error associated with the diet estimates of individuals from the stable isotope mixing model.

3.3. Results

We collected feather and claw samples from a total of 188 total black oystercatchers, 87 of which were captured in BC and 101 in Alaska. Isotope signatures in feather and claw samples were correlated and we had a larger sample size for

feathers (for $\delta^{13}\text{C}$: $r = 0.54$, $p < 0.0001$; $\delta^{15}\text{N}$: $r = 0.61$, $p < 0.0001$). Therefore, we present the results of analyses conducted using the feather samples.

Stable isotope signatures of feathers from male and female black oystercatchers did not differ (mean \pm SD; $\delta^{13}\text{C}$ male = $-16.59 \text{‰} \pm 1.17$, female = $-16.69 \text{‰} \pm 1.06$, $t = 0.63$, $p = 0.53$; $\delta^{15}\text{N}$: male = $12.76 \text{‰} \pm 0.98$, female = $12.72 \text{‰} \pm 0.90$, $t = 0.42$, $p = 0.67$). Feather stable isotope signatures from oystercatchers in Alaska also did not differ from those in British Columbia (Table 3.1). Site-specific stable isotope signatures are reported in Table B.1.

Table 3.1. Regional differences in carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope signatures of black oystercatchers and prey in Alaska and British Columbia. We report means \pm SD, sample sizes in brackets and statistical tests with significant results in bold

	Alaska	British Columbia	Region		Site	
			t	p	variance (\pm SD)	
$\delta^{13}\text{C}$	oystercatcher	-16.80 ± 1.05 (n=100)	-16.49 ± 1.65 (n=83)	0.88	0.3	0.09 ± 0.31
	chiton	-17.17 ± 1.12 (n=11)	-15.96 ± 1.96 (n=16)	1.63	0.08	0.44 ± 0.67
	clam	-17.13 ± 0.85 (n=14)	-16.47 ± 1.47 (n=18)	0.86	0.33	0.16 ± 0.40
	limpet	-15.76 ± 2.76 (n=16)	-14.95 ± 2.92 (n=19)	0.64	0.47	3.19 ± 1.79
	mussel	-17.34 ± 0.68 (n=14)	-17.18 ± 0.83 (n=20)	0.59	0.49	0.38 ± 0.62
	dogwinkle	-16.62 ± 0.67 (n=16)	-15.52 ± 0.93 (n=15)	2.00	0.04	0.39 ± 0.62
$\delta^{15}\text{N}$	oystercatcher	12.46 ± 0.65 (n=100)	13.06 ± 1.10 (n=83)	1.02	0.25	0.67 ± 0.82
	chiton	8.53 ± 0.80 (n=11)	10.86 ± 1.53 (n=16)	2.53	0.02	0.84 ± 0.92
	clam	9.69 ± 0.53 (n=14)	10.66 ± 1.59 (n=18)	1.03	0.25	0.92 ± 0.96
	limpet	8.69 ± 0.71 (n=16)	10.07 ± 1.18 (n=19)	2.15	0.03	0.71 ± 0.84
	mussel	8.75 ± 0.63 (n=14)	9.05 ± 1.35 (n=20)	0.53	0.53	0.56 ± 0.75
	dogwinkle	10.42 ± 0.41 (n=16)	11.57 ± 1.28 (n=15)	1.36	0.14	0.19 ± 0.43

We collected a total of 156 prey samples from across the seven sites. There were some regional differences in the stable isotope signatures of the five prey items (Table 3.1). $\delta^{13}\text{C}$ signatures of dogwinkle snails and $\delta^{15}\text{N}$ signatures of chitons and limpets were higher in British Columbia than Alaska (Table 3.1). There was also some variation in the prey isotope signatures across the seven sites (Table 3.1, Figure 3.1). Site-specific stable isotope signatures are reported in Table B.1. Prey isotope signatures reflected their trophic position with $\delta^{15}\text{N}$ signatures of the predatory snails (*Nucella spp.*) being enriched compared to those of limpets and mussels (Figure 3.1).

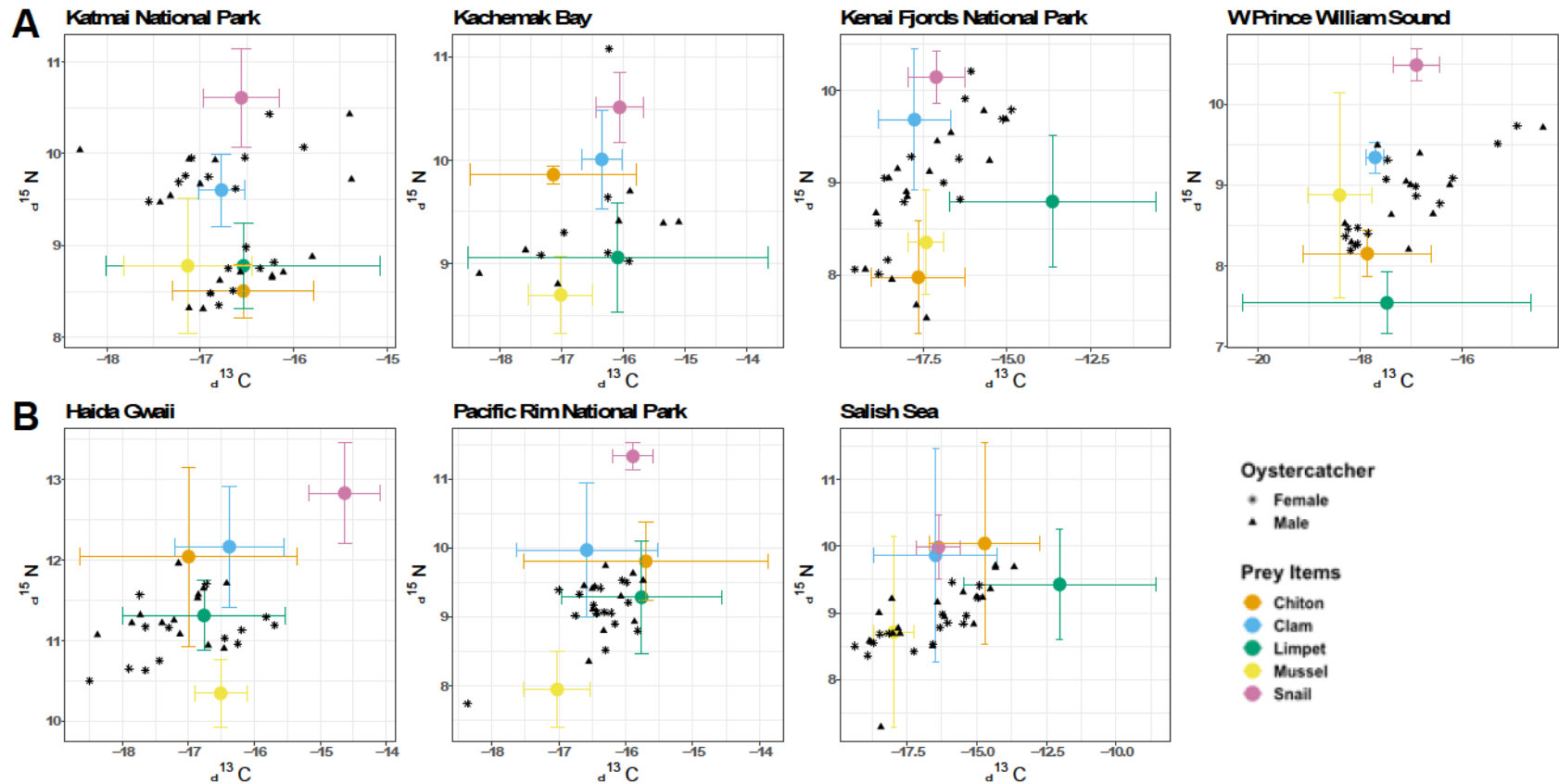


Figure 3.1. Biplots of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic values of prey items and oystercatchers within each site in (A) the four sites in Alaska and (B) the three BC sites. The colored dots and bars represent means (± 1 SD) of each of the five prey items. The raw data for black oystercatchers are shown by the black symbols with the sexes shown by different symbols. The oystercatcher isotope signatures are adjusted by a diet-tissue discrimination factor of 3.4 ‰ for $\delta^{15}\text{N}$ and 0.2 ‰ for $\delta^{13}\text{C}$.

We found no evidence of resource partitioning between sexes. Male and female diets did not differ (Figure 3.2., MANOVA controlling for site differences, sex: $F= 0.55$, $df= 5$, $p= 0.73$). Furthermore, females did not consume a greater proportion of clams than males ($t= -0.664$, $p=0.50$) and the proportion of clams consumed did not increase with bill length ($t= -0.301$, $p=0.76$).

Black oystercatcher diets varied greatly both within and among sites (Figure 3.2.; MANOVA site: $F= 16.82$, $df= 30$, $p<0.0001$). Mussels were the dominant prey item at three sites, Katmai in Alaska and Pacific Rim and Salish Sea in BC. Limpets were the dominant prey item in Haida Gwaii. Prey items were more evenly represented in the diets at two sites in Alaska, Kenai Fjords National Park, and Western Prince William Sound. There was also considerable variation in the diet of individuals with each site (Table B.3). For some individual black oystercatchers, mussels or limpets made up over 60% of the diet.

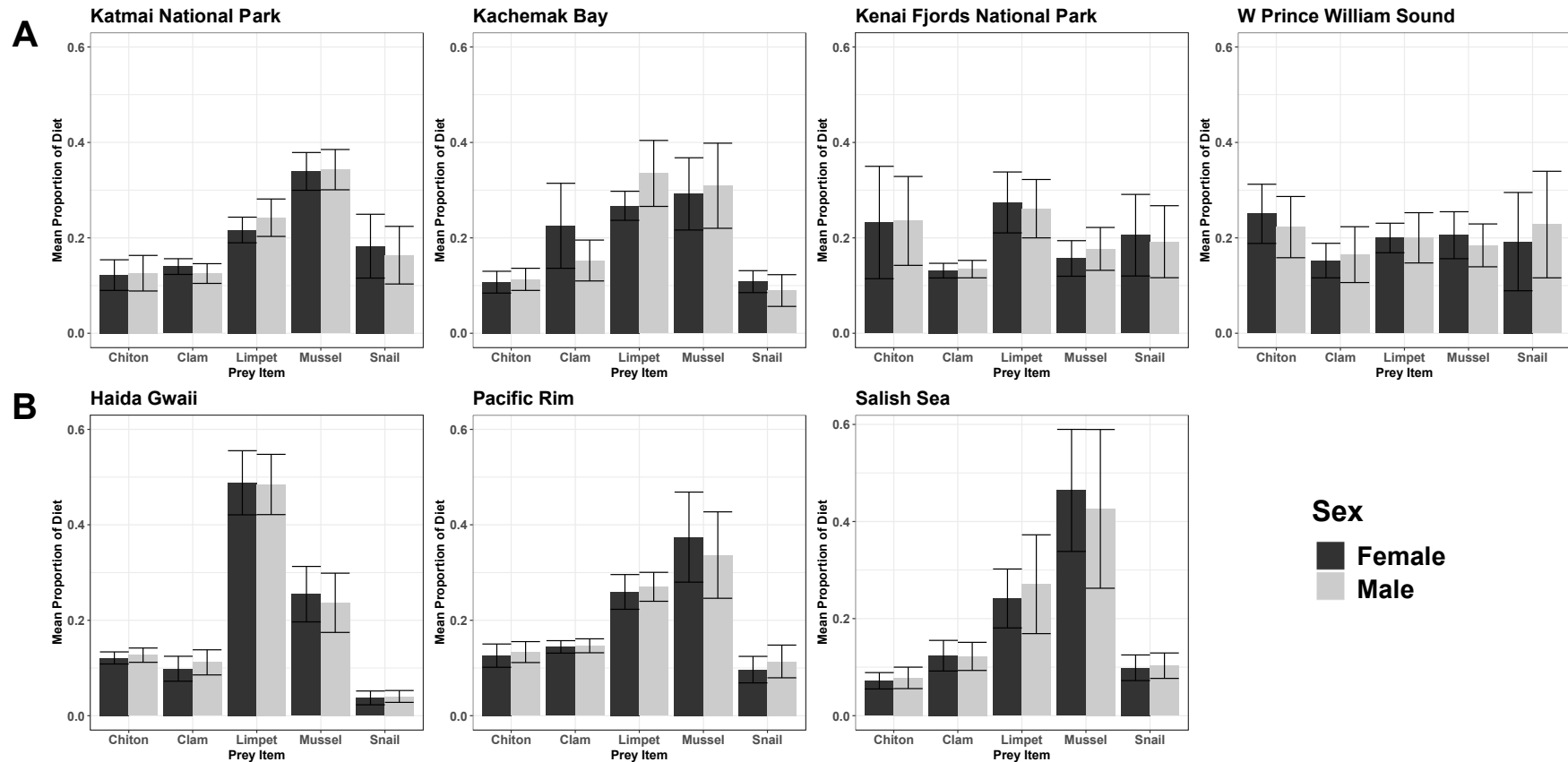


Figure 3.2. Diet proportions of black oystercatchers within each site in (A) Alaska or (B) British Columbia. The bars represent the mean (\pm SD) of the population proportion of each prey item with the sexes indicated by the colors

3.4. Discussion

Reversed sexual dimorphism can evolve as a mechanism to facilitate intersexual resource partitioning (Selander 1972, Durell 2000, Nebel and Thompson 2011). Evidence for resource partitioning comes from the observation that bill dimorphism across many shorebird families is much larger than dimorphism of other non-trophic body measurements (Nebel and Thompson 2011). Black oystercatchers are a shorebird with a large bill dimorphism between the sexes and a diverse diet. However, we found no evidence that male and female black oystercatchers partition resources available at any of the seven sites in Alaska or British Columbia. Our findings contrast with behavioral studies on other oystercatcher species that found dietary differences between males and females. For example, females of Eurasian, sooty, and pied oystercatchers tend to eat more clams and worms, which are often acquired by probing in sediment, while males consume greater proportions of hard-shelled items from the surface (Durrell 1993, Lauro and Nol 1995, Aplin and Cockburn 2012). However, our findings are consistent with a stable isotope diet study on African black oystercatchers in South Africa (Kohler et al. 2011). Kohler et al. (2011) found that despite previous behavioral observations of resource partitioning within breeding pairs (Hockey and Underhill 1983), stable isotopes revealed no difference in diet proportions between the sexes. Discrepancies in behavioral and isotope studies may arise because of seasonality of resource partitioning or differences between chick provisioning and self-feeding. The failure to detect resource partitioning in this study, however, does not preclude that resource partitioning may occur in black oystercatchers in another context or at a different time of year.

Animals are known to seasonally switch diets to adjust for changes in prey availability and abundance or competition for resources. Resource partitioning may therefore be more apparent when resources are limited or competition for resources is higher. In Western sandpipers, based on stable isotopes, male and female diet compositions only differ in the spring when resource availability changes inter- and intraspecific competition for prey increases (Hall et al. 2021). Similarly, seabird isotopic niche variation reveals greater intersexual resource partitioning during the pre-laying and breeding periods than the winter, likely when their foraging ranges are restricted, and competition is greater (Phillips et al. 2011). Our black oystercatcher feather stable

isotopes reflect the diet during their definitive pre-basic molt which takes place between June and October, but breeding adults often suspend wing molt after 1-3 primaries during breeding activity and resume molt after they finish breeding (Pyle 2008). Claws generally reflect the diet of the bird between two to five months prior to sampling (Bearhop et al. 2003). Therefore, in this study we likely captured the diet composition of black oystercatchers in the early spring with claws, and the post-breeding period with feathers, just outside of the main breeding period and the winter. Feather and claw stable isotope signatures were correlated, suggesting little change in diet between these time periods. However, black oystercatchers may demonstrate intersexual resource partitioning at other times of the year not captured in our stable isotope analysis. In the nonbreeding period, black oystercatchers often form non-territorial flocks ranging from tens to hundreds of individuals (Tessler et al. 2014). These winter flocks congregate in safer, sheltered foraging areas such as mudflats or rocky islets with mussel beds (Hartwick and Blaylock 1979, Andres and Falxa 2020). This may lead to increased intraspecific competition for more seasonally limited resources which could be alleviated by resource partitioning between the sexes. Blood and faecal samples give a more immediate picture of the diet of an individual, therefore collecting these samples during the peak nonbreeding period (November through February) would allow examination of male and female diets during this time.

Studies that have described resource partitioning in African black, sooty, and pied oystercatchers observed only territorial breeding pairs usually feeding chicks (Hockey and Underhill 1983, Lauro and Nol 1995, Aplin and Cockburn 2012). Similarly, most diet studies to date in black oystercatchers occur during the breeding period, often using prey remains at the nest site to determine the species' diet (Hazlitt 2002, Robinson et al. 2018). These prey remains and behavioral observations may reflect the diet that the parents are provisioning to their chicks but may not necessarily reflect what they themselves consume (Ydenberg 1994, Davoren and Burger 1998). Robinson et al. (2018) found that when estimating chick diets, using prey remains led to a bias in hard-shelled items and revealed different patterns of chick diets than stable isotope analysis. In adult black oystercatchers, the male and female could partition resources while provisioning by foraging for different prey to feed to the chicks. If adults partitioned resources in this way but in their own diets the sexes consumed prey in similar

proportions, we would see no intersexual differences in diet from stable isotope signatures as we have in this study.

Stable isotope diet studies are a valuable tool in determining the diet composition within a population or species and can use less invasive techniques for sampling from wildlife (Post 2002). Use of stable isotope mixing models in diet studies do come with limitations however, and several sources of error can lead to misinterpretation of outputs (Philips et al. 2014). Our findings of an absence of resource partitioning among the sexes in black oystercatchers are likely robust to most of these limitations as our initial analysis of the raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures did not differ between the sexes.

Stable isotope diet studies can give valuable insights into the trophic dynamics across a food web (Post 2002). Our findings suggest that clams may be a more important dietary source for black oystercatchers than previously reported. We found that clams make up between 13-19% of the diet of birds in sites across Alaska, and 11-15% of the diet of birds in British Columbia (Figure 3.2). Most previously published black oystercatcher diet studies do not describe clams as part of the diet. However, black oystercatchers frequently forage on tidal mudflats and gravel substrates during low tide probing into the mud and in the nonbreeding period in British Columbia, flocks can spend much of their time in sheltered mudflats foraging and roosting (Ware 2021, Hartwick and Blaylock 1979). Additionally, Hollenberg and Demers (2017) published evidence of black oystercatchers feeding on invasive varnish clams (*Nuttallia obscurata*) on Vancouver Island in British Columbia. Individuals foraging in mudflats often pull clams out of the sediment, open the shell, and either consume the flesh on site or carry the flesh back to the chicks (Personal Obs.). Diet studies using prey remains at the nest site or chick provisioning to determine diet which may miss clams as a more prominent diet item if they do not bring the shell back to the nest site (Robinson et al. 2018). Our findings suggest that clams should be reconsidered as an important prey item for black oystercatchers in Alaska and British Columbia.

Intraspecific diet variation can stem from adaptation to local resource availability (Garvey and Whiles 2017). A recent study on brown booby diets using stable isotopes found differences in diet among populations consistent with local prey availability and established biogeographical zonings (Jacoby et al. 2023). We found that at all, but two sites, limpets and mussels were the dominant prey items, as expected based on other

diet studies in this species (Figure 3.2). The consumption of prey items was more evenly distributed at two study sites in Alaska. Interestingly, this contrasts with previous stable isotope studies conducted in these same sites which found that mussels and limpets were the two most dominant prey items in the diets (Carney 2013 in W. Prince William Sound, Robinson et al. 2018 in Kenai Fjords). We did not test for geographic variation in prey availability at our sites, however, physical characteristics such as ocean temperature, salinity, and wave exposure can drive patterns of intertidal diversity (Lewis 1964, Zacharias and Roff 2001). Certain prey items in this study were much less abundant or completely absent from a few sampling sites (Roodenrijs personal obs.) and all sites vary in their physical characteristics, suggesting that there are different patterns of intertidal invertebrate diversity and abundance across our sites. Changes in temperature and salinity or extreme heat events can alter the intertidal diversity annually (Weitzman et al. 2021). Though black oystercatchers are generalist predators, impacts of future climate change on intertidal communities could have varying effects on the different populations due to variation in diet compositions. Collecting additional data on the patterns of local abundance of intertidal invertebrates across years and the annual cycle in our sampling locations would help understand where these population-level dietary differences stem from.

Individual diet specialization is an understudied aspect of foraging ecology that can have ecological, evolutionary, and conservation implications (Bolnick et al. 2003, Araújo et al. 2011). The niche of individuals can vary widely, and in some populations the niche breadth of an individual, on average, only reflects 47% of the overall population niche breadth (reviewed by Araújo et al. 2011). This suggests that the overall population niche breadth may not accurately reflect that of individuals due to diet specialization (Araújo et al. 2011). In this study, we found that individual black oystercatchers within a site varied in their diet composition (Table B.3). This species is known to prey on a diverse array of intertidal organisms, but our data suggests that a few individuals may be specialized in their diet. A few individuals across sites may obtain greater than 60% of their diet from a single type of prey. The extent and consequences of this individual specialization are unknown but warrant further investigation.

In conclusion, despite large intersexual bill dimorphism we found no evidence of resource partitioning in black oystercatchers. If resource partitioning during the nonbreeding and breeding periods does not provide an explanation, another mechanism

may drive reversed sexual dimorphism in black oystercatchers. Alternative hypotheses for reversed sexual dimorphism posit that larger female body size may be beneficial through increased egg size or more efficient incubation (Reynolds 1972). A decrease in male size of black oystercatchers could allow for better agility in their aerial pursuits of territorial intruders and predators (Jehl and Murray 1984, Andres and Falxa 2020). These hypotheses, however, fail to describe why bill dimorphism evolved to be much larger compared to other body dimorphisms such as tarsus and wing length. Black oystercatcher bill length also varies latitudinally with individuals in British Columbia having longer bills than those in Alaska (Chapter 1). This pattern is consistent with Allen's rule (Allen 1887) and suggests that this adaptation evolves to aid in thermoregulation (Tattersal et al. 2017). Metabolic heat production increases with body mass (Tattersall et al. 2017), therefore, if black oystercatcher bills serve a thermoregulatory function, then larger females may require a disproportionately longer bill than the smaller males to regulate their temperature.

3.5. References

- Andersson, M., & Norberg, R. Å. (1981). Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biological Journal of the Linnean Society*, 15(2), 105–130. <https://doi.org/10.1111/j.1095-8312.1981.tb00752.x>
- Andres, B. A. and G. A. Falxa (2020). Black Oystercatcher (*Haematopus bachmani*), version 1.0. In A. F. Poole and F. B. Gill (Eds.), *Birds of the World*, Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.blkoys.01>
- Allen JA (1877) The influence of Physical conditions in the genesis of species. *Radical Rev* 1: 108–140.
- Aplin, L. M., & Cockburn, A. (2012). Ecological selection and sexual dimorphism in the sooty oystercatcher, *Haematopus fuliginosus*. *Austral Ecology*, 37(2), 248–257. <https://doi.org/10.1111/j.1442-9993.2011.02263.x>
- Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation: The causes of individual specialisation. *Ecology Letters*, 14(9), 948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>
- Bearhop, S., Waldron, S., Votier, S. C., & Furness, R. W. (2002). Factors That Influence Assimilation Rates and Fractionation of Nitrogen and Carbon Stable Isotopes in Avian Blood and Feathers. *Physiological and Biochemical Zoology*, 75(5), 451–458. <https://doi.org/10.1086/342800>
- Bearhop, S., Furness, R. W., Hilton, G. M., Votier, S. C., & Waldron, S. (2003). A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. *Functional Ecology*, 17(2), 270–275. <https://doi.org/10.1046/j.1365-2435.2003.00725.x>
- Bolnick, D. I., Svanback, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The Ecology of Individuals: Incidence and Implications of Individual Specialization. *The American Naturalist*, 161(1), 1–28. doi: 10.1086/343878
- Bligh, E. G., & Dyer, W. J. (1959). A Rapid Method of Total Lipid Extraction and Purification. *Canadian Journal of Biochemistry and Physics*, 37(8), 911-917. <https://doi.org/10.1139/o59-099>
- Carney, C.B. (2013). Diet Patterns of black oystercatchers (*Haematopus bachmani*) in the northern Gulf of Alaska. [Unpublished master's thesis]. University of Alaska Anchorage.

- Cherel, Y., Hobson, K. A., & Hassani, S. (2005). Isotopic Discrimination between Food and Blood and Feathers of Captive Penguins: Implications for Dietary Studies in the Wild. *Physiological and Biochemical Zoology*, 78(1), 106–115. <https://doi.org/10.1086/425202>
- Cherel, Y., Jaquemet, S., Maglio, A., & Jaeger, A. (2014). Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between feathers and blood of seabird chicks: Implications for non-invasive isotopic investigations. *Marine Biology*, 161(1), 229–237. <https://doi.org/10.1007/s00227-013-2314-5>
- Davoren, G. K., & Burger, A. E. (1999). Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Animal Behaviour*, 58(4), 853–863. <https://doi.org/10.1006/anbe.1999.1209>
- Durell, S. E. A. L. V. D., Goss-Custard, J. D., & Caldow, R. W. G. (1993). Sex-Related Differences in Diet and Feeding Method in the Oystercatcher *Haematopus ostralegus*. *The Journal of Animal Ecology*, 62(1), 205. <https://doi.org/10.2307/5495>
- Durell, S.E.A.L.V.D. (2000). Individual feeding specialisation in shorebirds: Population consequences and conservation implications. *Biological Reviews*, 75(4), 503–518. <https://doi.org/10.1111/j.1469-185X.2000.tb00053.x>
- Figuerola, J. (1999). A comparative study on the evolution of reversed size dimorphism in monogamous waders. *Biological Journal of the Linnean Society*, 67(1), 1–18. <https://doi.org/10.1111/j.1095-8312.1999.tb01926.x>
- Garvey JE, Whiles MR (2017) Trophic ecology. CRC Press, Boca Raton.
- Guzzetti, B. M., Talbot, S. L., Tessler, D. F., Gill, V. A., & Murphy, E. C. (2008). Secrets in the eyes of Black Oystercatchers: A new sexing technique. *Journal of Field Ornithology*, 79(2), 215–223. <https://doi.org/10.1111/j.1557-9263.2008.00167.x>
- Hall, L. A., De La Cruz, S. E. W., Woo, I., Kuwae, T., & Takekawa, J. Y. (2021). Age- and sex-related dietary specialization facilitate seasonal resource partitioning in a migratory shorebird. *Ecology and Evolution*, 11(4), 1866–1876. <https://doi.org/10.1002/ece3.7175>
- Hartwick, E. B. (1976). Foraging strategy of the black oyster catcher (*Haematopus bachmani* Audubon). *Canadian Journal of Zoology*, 54(2), 142–155. <https://doi.org/10.1139/z76-015>
- Hartwick, E. B., & Blaylock, W. (1979). Winter Ecology of a black oystercatcher Population. *Studies in Avian Biology*, 2, 207–215.
- Hazlitt, S. L., Ydenberg, R. C., & Lank, D. B. (2002). Territory Structure, Parental Provisioning, and Chick Growth in the American black oyster-catcher *Haematopus bachmani*. *Ardea* 90(2): 219-227.

- Hobson, K. A., & Clark, R. G. (1992). Assessing Avian Diets Using Stable Isotopes II: Factors Influencing Diet-Tissue Fractionation. *The Condor*, 94(1), 189–197. <https://doi.org/10.2307/1368808>
- Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia*, 120(3), 314–326. <https://doi.org/10.1007/s004420050865>
- Hockey, P. A. R., & Underhill, L. G. (1984). Diet of the African black oystercatcher *Haematopus Moquini* on rocky shores: Spatial, temporal, and sex-related variation. *South African Journal of Zoology*, 19(1), 1–11. <https://doi.org/10.1080/02541858.1984.11447849>
- Hockey, P.A.R. (1996). *Haematopus ostralegus* in perspective: comparison with other Oystercatchers. In: Goss-Custard, J.D. (ed). *The Oysercatcher From Individuals to Populations*, Oxford University Press, New York, NY.
- Hollenberg, E. J. R., & Demers, E. (2017). Black Oystercatcher (*Haematopus bachmani*) foraging on varnish clams (*Nuttallia obscurata*) in Nanaimo, British Columbia. *British Columbia Birds*, 27, 35-41.
- Jacoby, J., Luciano Mancini, P., Bertrand, S. L., Amorim Efe, M., Bugoni, L., & Tavares Nunes, G. (2023). Biogeographic variation on dietary aspects of a widely distributed seabird. *Marine Biology*, 170(2), 21. <https://doi.org/10.1007/s00227-022-04171-3>
- Jehl, J.R., Murray, B.G. (1986). The Evolution of Normal and Reverse Sexual Size Dimorphism in Shorebirds and other Birds. In: Johnston, R.F. (eds). *Current Ornithology*, vol 3. Springer, Boston, MA. https://doi.org/10.1007/978-1-4615-6784-4_1
- Kohler, S., Connan, M., Hill, J., Mablouké, C., Bonnevie, B., Ludynia, K., Kemper, J., Huisamen, J., Underhill, L., Cherel, Y., McQuaid, C., & Jaquemet, S. (2011). Geographic variation in the trophic ecology of an avian rocky shore predator, the African black oystercatcher, along the southern African coastline. *Marine Ecology Progress Series*, 435, 235–249. <https://doi.org/10.3354/meps09215>
- Kohler, S. A., Connan, M., Kolasinski, J., Cherel, Y., McQuaid, C. D., & Jaquemet, S. (2014). Trophic overlap between sexes in the dimorphic African black oystercatcher foraging on an alien mussel. *Austral Ecology*, 39(5), 567–578. <https://doi.org/10.1111/aec.12117>
- Lauro, B., & Nol, E. (1995). Feeding behavior, prey selection, and bill size in Pied and Sooty Oystercatchers in Australia. *The Wilson Bulletin*, 107(4), 629–640. <http://www.jstor.org/stable/4163599>
- Lindenfors, P., Szekely, T., & Reynolds, J. D. (2003). Directional changes in sexual size dimorphism in shorebirds, gulls and alcids. *Journal of Evolutionary Biology*, 16(5), 930–938. <https://doi.org/10.1046/j.1420-9101.2003.00595.x>

- Mathot, K. J., & Elner, R. W. (2004). Evidence for sexual partitioning of foraging mode in Western Sandpipers (*Calidris mauri*) during migration. *Canadian Journal of Zoology*, 82(7), 1035–1042. <https://doi.org/10.1139/z04-080>
- Mathot, K. J., Smith, B. D., & Elner, R. W. (2007). Latitudinal Clines in Food Distribution Correlate with Differential Migration in the Western Sandpiper. *Ecology*, 88(3), 781–791. <https://doi.org/10.1890/06-1225>
- Moore, J. W., & Semmens, B. X. (2008). Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters*, 11(5), 470–480. <https://doi.org/10.1111/j.1461-0248.2008.01163.x>
- Mueller, H. C. and Meyer, K. (1985). The evolution of reversed sexual dimorphism in size: a comparative analysis of the Falconiformes of the Western Palaearctic. - In: Johnston, R. F. (ed.), *Current Ornithology*, Vol. 2. Plenum Press, New York, pp. 65-101.
- Mueller, H. C. (1990). The Evolution of Reversed Sexual Dimorphism in Size in Monogamous Species of Birds. *Biological Reviews*, 65(4), 553–585. <https://doi.org/10.1111/j.1469-185X.1990.tb01238.x>
- Nebel, S. (2005). Latitudinal clines in bill length and sex ratio in a migratory shorebird: A case of resource partitioning? *Acta Oecologica*, 28(1), 33–38. <https://doi.org/10.1016/j.actao.2005.02.002>
- Nebel, S., & Thompson, G. J. (2011). The evolution of sexual bill-size dimorphism in shorebirds: A morphometric test of the resource partitioning hypothesis. *Evolutionary Ecology Research*, 13, 35-44.
- Paritte, J. M., & Kelly, J. F. (2009). Effect of Cleaning Regime on Stable-Isotope Ratios of Feathers in Japanese Quail (*Coturnix japonica*). *The Auk*, 126(1), 165–174. <https://doi.org/10.1525/auk.2009.07187>
- Phillips, R. A., McGill, R. A. R., Dawson, D. A., & Bearhop, S. (2011). Sexual segregation in distribution, diet and trophic level of seabirds: Insights from stable isotope analysis. *Marine Biology*, 158(10), 2199–2208. <https://doi.org/10.1007/s00227-011-1725-4>
- Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell A.C, Semmens X. S., & Ward E. J. (2014). Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology*. <https://doi.org/10.1139/cjz-2014-0127>
- Post, D. M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology*, 83(3), 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)

- Pyle, P. (2008). Black Oystercatcher. In *Identification Guide to North American Birds. Part II: Anatidae to Alcidae*, Slate Creek Press, Point Reyes Station, California, 535-537.
- Reynolds, R. T. (1972). Sexual Dimorphism in Accipiter Hawks: A New Hypothesis. *The Condor*, 74(2), 191–197. <https://doi.org/10.2307/1366283>
- Robinson, B. H., Coletti, H. A., Phillips, L. M., & Powell, A. N. (2018). Are prey remains an accurate indicators of chick diet? A comparison of diet quantification techniques for Black Oystercatchers. *Wader Study*, 125(1). <https://doi.org/10.18194/ws.00105>
- Selander RK. 1972. Sexual selection and dimorphism in birds. In: Campbell B. (ed.), *Sexual Selection and the descent of man 1871-1971*, Aldine Publishing Company, Chicago, pp. 180-230.
- Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, 6, e5096. <https://doi.org/10.7717/peerj.5096>
- Swennen, C., De Bruijn L.L.M., Duiven P., Leopold M.F., Marteiijn E.C.L. (1983). Differences in Bill Form of the Oystercatcher *Haematopus ostralegus*; a Dynamic Adaptation to Specific Foraging Techniques. *Netherlands Journal of Sea Research*, 17(1), 57-83. [https://doi.org/10.1016/0077-7579\(83\)90006-6](https://doi.org/10.1016/0077-7579(83)90006-6)
- Székely, T., Reynolds, J. D., & Figuerola, J. (2000). Sexual Size Dimorphism in Shorebirds, Gulls, and Alcids: The Influence of Sexual and Natural Selection. *Evolution*, 54(4), 1404–1413. <https://doi.org/10.1111/j.0014-3820.2000.tb00572.x>
- Stein, R. W., Fernández, G., de la Cueva, H., & Elner, R. W. (2008). Disproportionate bill length dimorphism and niche differentiation in wintering western sandpipers (*Calidris mauri*). *Canadian Journal of Zoology*, 86(7), 601–609. <https://doi.org/10.1139/Z08-033>
- Tattersall, G. J., Arnaout, B., & Symonds, M. R. E. (2017). The evolution of the avian bill as a thermoregulatory organ. *Biological Reviews*, 92(3), 1630–1656. <https://doi.org/10.1111/brv.12299>
- Tessler, D.F., J.A. Johnson, B.A. Andres, S. Thomas, & R.B. Lanctot. (2014). A global assessment of the conservation status of the Black Oystercatcher *Haematopus bachmani*. *International Wader Studies*, 20: 83–96.
- van de Pol, M., Ens, B. J., Oosterbeek, K., Brouwer, L., Verhulst, S., Tinbergen, J. M., Rutten, A. L., & Jong, M. D. (2009). Oystercatchers' Bill Shapes as a Proxy for Diet Specialization: More Differentiation than Meets the Eye. *Ardea*, 97(3), 335–347. <https://doi.org/10.5253/078.097.0309>

- Ware, L. (2021). Satellite telemetry reveals habitat selection decisions by black oystercatchers across seasonal, diel, and tidal cycles. [Master's Thesis, Simon Fraser University]. Summit Research Repository.
- Webster, J. D. (1941). Feeding Habits of the Black Oyster-Catcher. *The Condor*, 43(4), 175–180. <https://doi.org/10.2307/1364329>
- Weitzman, B., Konar, B., Iken, K., Coletti, H., Monson, D., Suryan, R., Dean, T., Hondolero, D., & Lindeberg, M. (2021). Changes in Rocky Intertidal Community Structure During a Marine Heatwave in the Northern Gulf of Alaska. *Frontiers in Marine Science*, 8, 556820. <https://doi.org/10.3389/fmars.2021.556820>
- Ydenberg, R. C., & Forbes, L. S. (1991). The Survival-Reproduction Selection Equilibrium and Reversed Size Dimorphism in Raptors. *Oikos*, 60(1), 115. <https://doi.org/10.2307/3545001>
- Ydenberg, R. C. (1994). The behavioral ecology of provisioning in birds. *Écoscience*, 1(1), 1–14. <https://www.jstor.org/stable/42902324>

Appendix A. Chapter 2 Supplementary Material

Table A.1. PCA loadings for each feather from the size-constrained components analysis of wing shape using the 9 and 7 of the outermost primaries. Feather number P10-P2 refers to primary number starting from the leading edge of the wing and counting inward with P10 being the primary at the leading edge of the wing.

Feather	9 primaries included (n= 57)		7 primaries included (n= 94)	
	C1 pointedness	C2 convexity	C1 pointedness	C2 convexity
P10	0.54619345	-0.1179157	0.58157235	-0.15874598
P9	0.41740798	-0.139449	0.37404908	-0.21991855
P8	0.32070325	-0.1032162	0.21695981	0.09541022
P7	0.06656563	0.2540931	-0.05628013	0.20565569
P6	-0.09391443	0.4995935	-0.20007959	0.45186237
P5	-0.20411592	0.3701639	-0.38110719	0.36096569
P4	-0.35535212	0.1115452	-0.53511432	-0.73522945
P3	-0.35765255	-0.2031797		
P2	-0.33983529	-0.6716351		

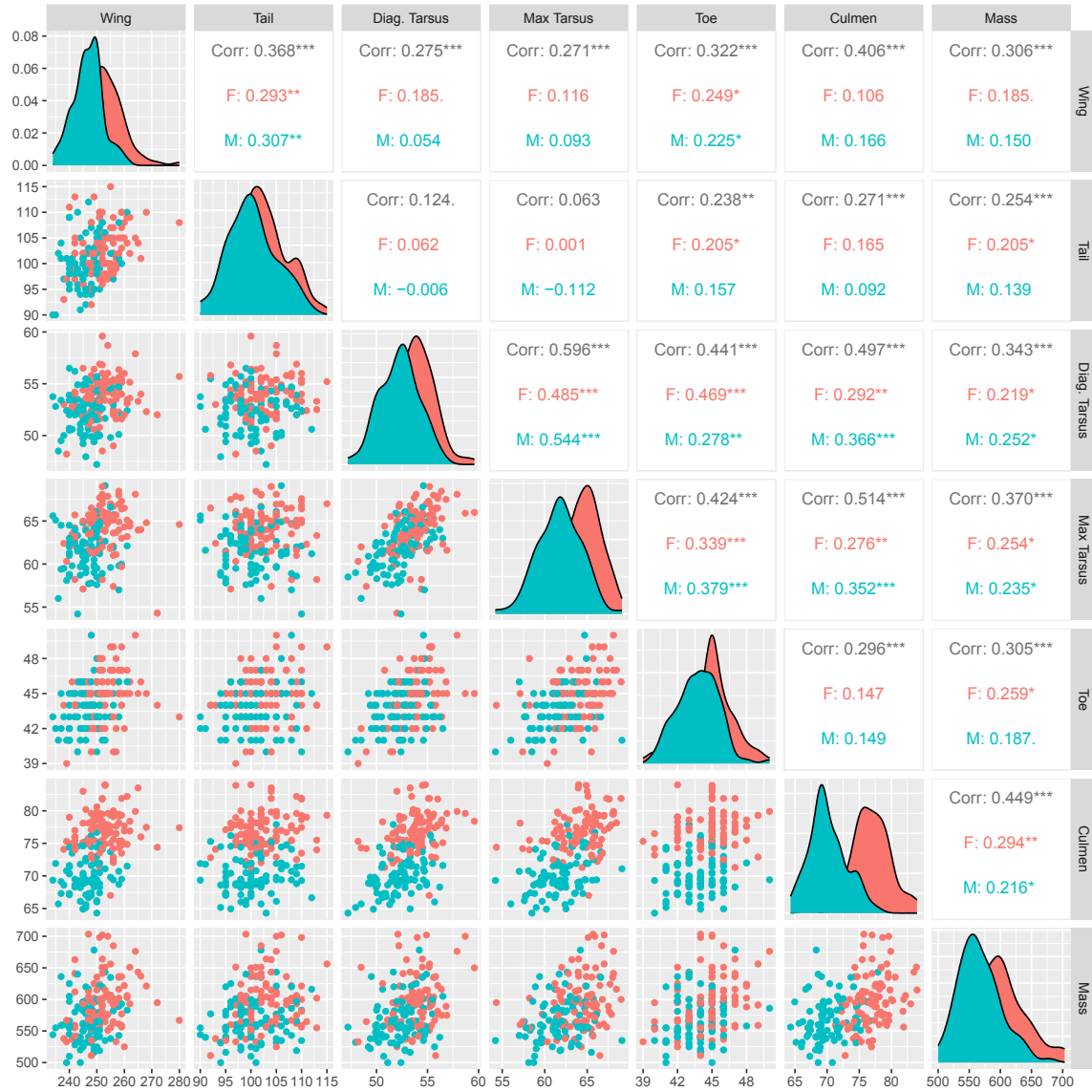


Figure A.2. Correlation metrics of the five bill measurements of overall population (black text), female (in red), and male (in blue) black oystercatchers. The diagonal panels show distribution of measurements split by sex and the lower panels show the raw data.

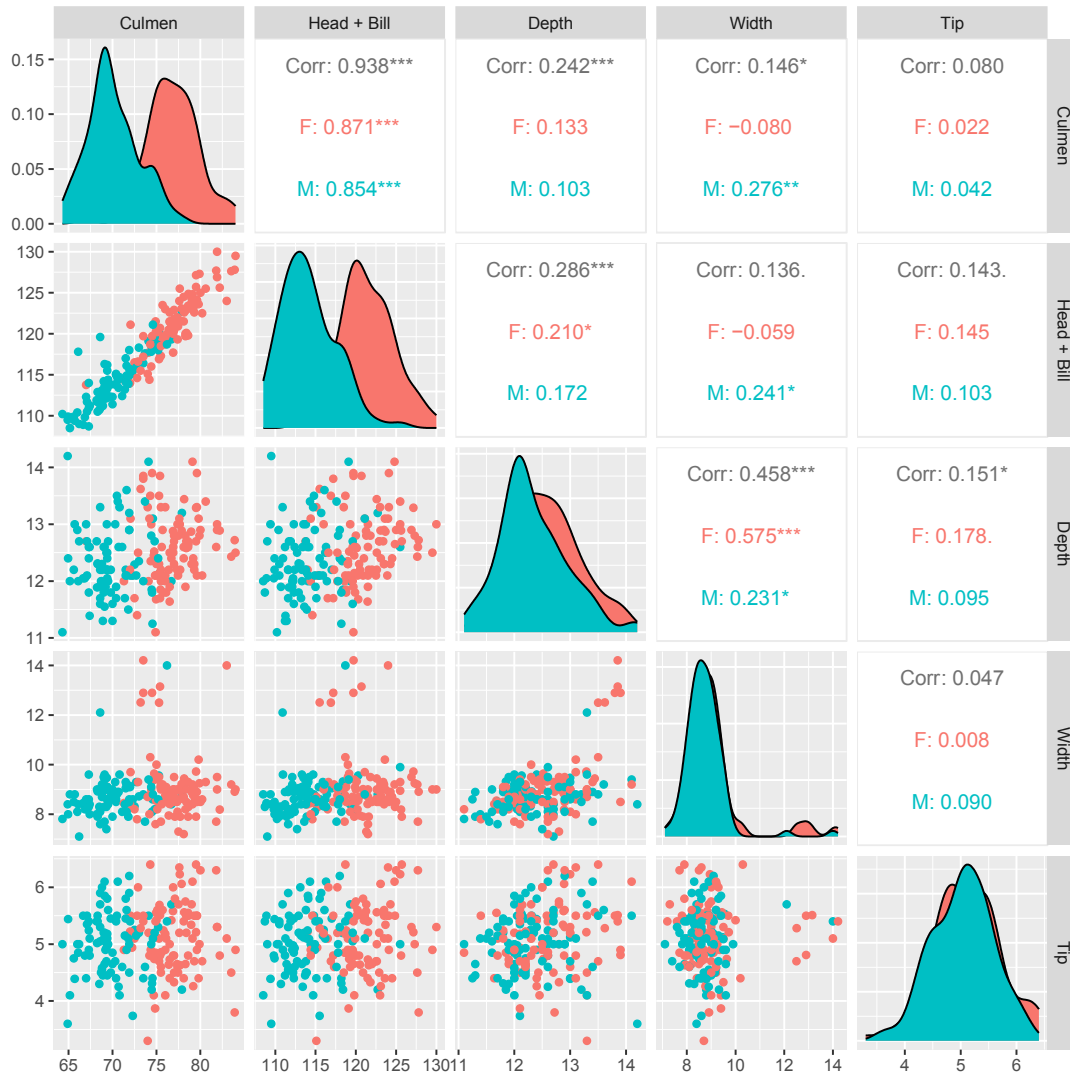


Table A.3. Correlation metrics of the five bill measurements of overall population (black text), female (in red), and male (in blue) black oystercatchers. The diagonal panels show distribution of measurements split by sex and the lower panels show the raw data.

Table A.2. Site-specific morphological traits of female and male black oystercatchers in Alaska and British Columbia. Data are presented as means \pm SD. Statistical tests are reported below each trait with significant results in bold.

Alaska								
Sex	Site	Wing	Tail	Toe	Tarsus	Culmen	Bill Depth	Mass
Female	Katmai (n= 16)	252.4 \pm 10.6	105.7 \pm 4.8	44.3 \pm 2.0	53.5 \pm 1.9	77.3 \pm 2.0	12.7 \pm 0.5	584.4 \pm 30.7
	Katchemak Bay (n= 7)	252.4 \pm 10.6	105.6 \pm 4.4	46.8 \pm 1.5	53.4 \pm 1.7	76.5 \pm 3.1	12.6 \pm 0.8	580 \pm 20.6
	Kenai Fjords (n= 21)	253.0 \pm 7.6	103.2 \pm 3.7	44.9 \pm 2.3	52.2 \pm 1.9	75.7 \pm 2.6	12.8 \pm 0.9	600.7 \pm 40.2
	W Prince William Sound (n= 15)	248.2 \pm 7.8	102.0 \pm 4.2	44.7 \pm 1.2	53.9 \pm 1.3	75.6 \pm 1.4	12.6 \pm 0.9	598.8 \pm 52.2
Male	Katmai (n= 19)	244.9 \pm 5.1	102.4 \pm 4.5	43.3 \pm 2.5	52.0 \pm 2.0	69.8 \pm 3.2	12.6 \pm 0.7	544.4 \pm 24.3
	Katchemak Bay (n= 8)	247.8 \pm 2.1	101.0 \pm 5.5	44.7 \pm 0.8	51.4 \pm 2.4	70.1 \pm 3.1	12.3 \pm 0.7	554.0 \pm 31.6
	Kenai Fjords (n= 18)	247.2 \pm 6.2	102.5 \pm 3.7	44.3 \pm 2.0	51.9 \pm 1.6	69.0 \pm 1.7	12.5 \pm 0.8	560.9 \pm 24.9
	W Prince William Sound (n= 11)	250.2 \pm 6.0	100.3 \pm 4.3	44.3 \pm 1.8	52.0 \pm 1.7	69.7 \pm 2.8	12.3 \pm 0.7	570.7 \pm 22.4
anova	Site	F=0.40, p=0.75	F=1.50, p=0.22	F=2.43, p=0.07	F=1.53, p=0.20	F=0.18, p=0.91	F=2.35, p=0.08	F=2.55, p=0.06
	Sex	F= 8.79, p=0.004	F=5.26, p=0.02	F=2.38, p=0.13	F=11.17, p=0.001	F=205.8, p<0.00001	F=6.19, p=0.01	F=26.1, p< 0.00001
	Sex*Site	F= 1.76, p=0.16	F=0.70, p=0.55	F=0.94, p=0.42	F=1.09, p=0.36	F=1.06, p=0.37	F=0.30, p=0.82	F= 0.26, p= 0.86
British Columbia								
Female	Haida Gwaii (n= 17)	255.5 \pm 6.8	101.8 \pm 4.9	44.9 \pm 2.3	54.3 \pm 1.6	78.4 \pm 3.2	12.4 \pm 0.3	619.2 \pm 48.7
	Pacific Rim (n= 16)	253.5 \pm 3.6	101 \pm 3.6	45.1 \pm 1.6	54.6 \pm 2.1	77.9 \pm 2.4	13.0 \pm 0.4	612.6 \pm 38.5
	Salish Sea (n= 16)	251.8 \pm 3.5	102.6 \pm 5.3	45.5 \pm 2.0	55.1 \pm 1.5	76.9 \pm 4.1	12.5 \pm 0.6	608.1 \pm 44.4
Male	Haida Gwaii (n= 17)	248.1 \pm 4.6	100.1 \pm 5.4	43.8 \pm 1.9	51.5 \pm 2.0	69.8 \pm 3.2	12.1 \pm 0.8	591.0 \pm 45.8
	Pacific Rim (n= 11)	245.5 \pm 5.8	97.8 \pm 5.2	43.4 \pm 1.3	53.2 \pm 1.9	72.6 \pm 2.8	12.5 \pm 0.5	568.1 \pm 21.5
	Salish Sea (n= 19)	245.4 \pm 4.6	98.3 \pm 4.0	43.8 \pm 1.9	53.1 \pm 1.5	70.8 \pm 3.1	12.6 \pm 0.4	584.9 \pm 38.7
anova	Site	F=4.32, p=0.01	F=0.53, p=0.59	F=0.01, p=0.99	F=4.80, p=0.01	F=3.71, p=0.028	F=5.89, p=0.004	F=0.64, p= 0.53
	Sex	F=50.21, p<0.0001	F=9.54, p=0.002	F=16.43, p=0.0001	F=33.52, p<0.0001	F=104.5, p<0.0001	F=3.20, p=0.08	F= 12.54, p= 0.0006
	Sex*Site	F=0.19, p=0.83	F=0.62, p=0.54	F=0.31, p=0.73	F=1.10, p=0.33	F=2.09, p=0.13	F=1.94, p=0.15	F= 0.54, p= 0.59

Appendix B. Chapter 3 Supplementary Material

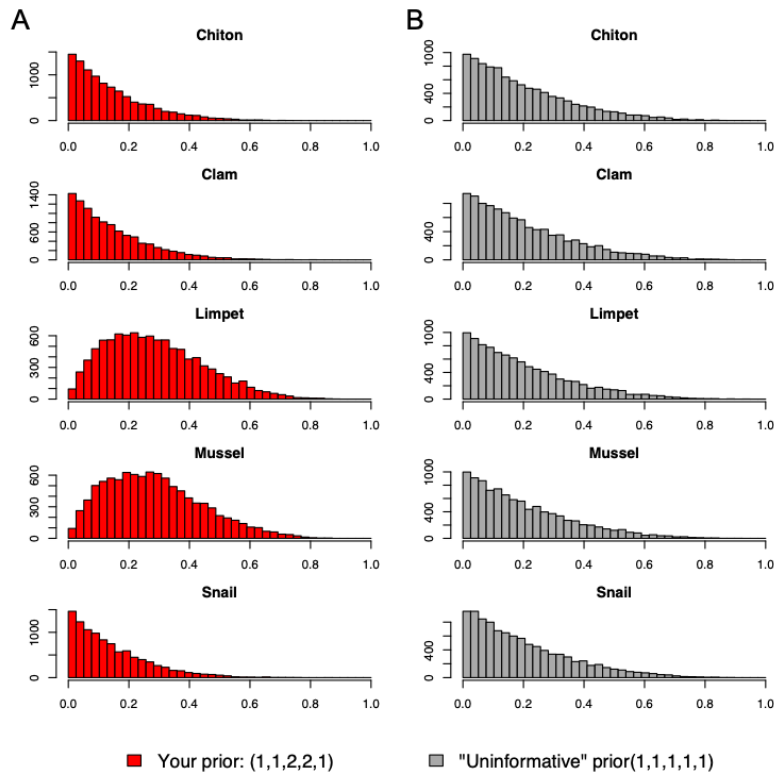


Figure B.1. A graphical representation of (A) the informative prior used the stable isotope mixing model compared to (B) an “uninformative” prior. The informative prior weights limpet and mussel prey items twice as heavily as the other three prey items. The standard uninformative prior weights all prey items equally.

Table B.1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of black oystercatchers split by site, and sex. Values represented as means (± 1 SD) for isotope values and bill length by group.

Region	Site	Sex	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Bill Length	n
BC	Haida Gwaii	Female	-16.82 \pm 0.89	14.46 \pm 0.36	78 \pm 2.9	13
		Male	-16.95 \pm 0.57	14.74 \pm 0.32	70.6 \pm 2.9	14
	Pacific Rim	Female	-16.26 \pm 0.59	12.45 \pm 0.44	77.7 \pm 2.4	16
		Male	-16.06 \pm 0.31	12.64 \pm 0.41	72.6 \pm 2.8	11
	Salish Sea	Female	-16.65 \pm 1.52	12.22 \pm 0.34	76.9 \pm 4.1	16
		Male	-16.25 \pm 1.77	12.37 \pm 0.56	70.8 \pm 3.1	19
Alaska	Katmai	Female	-16.29 \pm 0.54	12.94 \pm 0.79	76.9 \pm 2.4	7
		Male	-16.28 \pm 1.20	12.65 \pm 0.32	69.7 \pm 3.4	8
	Kachemak Bay	Female	-16.51 \pm 0.43	12.73 \pm 0.66	76.5 \pm 3.1	16
		Male	-16.48 \pm 0.75	12.58 \pm 0.69	69.5 \pm 3.2	18
	Kenai Fjords	Female	-17.11 \pm 1.48	12.44 \pm 0.70	75.5 \pm 2.5	21
		Male	-17.25 \pm 1.26	12.24 \pm 0.73	69.1 \pm 1.6	18
	W. Prince William Sound	Female	-17.01 \pm 1.09	12.18 \pm 0.49	74.7 \pm 3.2	15
		Male	-16.77 \pm 1.06	12.30 \pm 0.49	69.7 \pm 2.7	11

Table B.2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values and sample size of each prey item by site represented as the group mean (± 1 SD).

Common Name	Scientific Name	Region	Site	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
Chiton	<i>Mopalia spp.</i>	BC	Haida Gwaii	-17.00 \pm 1.65	12.04 \pm 1.11	7
Chiton	<i>Katarina tunicata</i>	BC	Pacific Rim	-15.7 \pm 1.82	9.81 \pm 0.56	4
Chiton	<i>Mopalia spp.</i>	BC	Salish Sea	-14.72 \pm 1.97	10.04 \pm 1.52	5
Chiton	<i>Katarina tunicata</i>	Alaska	Katmai	-16.54 \pm 0.76	8.51 \pm 0.29	4
Chiton	<i>Katarina tunicata</i>	Alaska	Kachemak Bay	-17.13 \pm 1.34	9.86 \pm 0.08	2
Chiton	<i>Katarina tunicata</i>	Alaska	Kenai Fjords	-17.78 \pm 1.70	7.73 \pm 0.47	3
Chiton	<i>Katarina tunicata</i>	Alaska	W. Prince William Sound	-17.85 \pm 1.27	8.15 \pm 0.28	2
Clam	<i>Leukoma stamina</i>	BC	Haida Gwaii	-16.38 \pm 0.82	12.17 \pm 0.75	6
Clam	<i>Leukoma stamina</i>	BC	Pacific Rim	-16.58 \pm 1.05	9.97 \pm 0.98	5
Clam	<i>Leukoma stamina</i>	BC	Salish Sea	-16.48 \pm 2.20	9.86 \pm 1.61	7
Clam	<i>Leukoma stamina</i>	Alaska	Katmai	-16.77 \pm 0.25	9.60 \pm 0.39	3
Clam	<i>Leukoma stamina</i>	Alaska	Kachemak Bay	-16.35 \pm 0.33	10.01 \pm 0.48	4
Clam	<i>Leukoma stamina</i>	Alaska	Kenai Fjords	-18.05 \pm 1.12	9.42 \pm 0.67	3
Clam	<i>Leukoma stamina</i>	Alaska	W. Prince William Sound	-17.70 \pm 0.18	9.34 \pm 0.19	3
Limpet	<i>Lottia spp.</i>	BC	Haida Gwaii	-16.77 \pm 1.23	11.31 \pm 0.44	7
Limpet	<i>Lottia spp.</i>	BC	Pacific Rim	-15.76 \pm 1.19	9.29 \pm 0.82	6
Limpet	<i>Lottia spp.</i>	BC	Salish Sea	-12.03 \pm 3.44	9.43 \pm 0.82	6
Limpet	<i>Lottia spp.</i>	Alaska	Katmai	-16.54 \pm 1.47	8.78 \pm 0.46	5
Limpet	<i>Lottia spp.</i>	Alaska	Kachemak Bay	-16.09 \pm 2.43	9.06 \pm 0.53	4
Limpet	<i>Lottia spp.</i>	Alaska	Kenai Fjords	-15.22 \pm 3.05	8.47 \pm 0.71	3
Limpet	<i>Lottia spp.</i>	Alaska	W. Prince William Sound	-17.47 \pm 2.83	7.54 \pm 0.38	3
Mussel	<i>Mytilus spp.</i>	BC	Haida Gwaii	-16.51 \pm 0.40	10.34 \pm 0.42	7
Mussel	<i>Mytilus spp.</i>	BC	Pacific Rim	-17.02 \pm 0.49	7.95 \pm 0.55	6
Mussel	<i>Mytilus spp.</i>	BC	Salish Sea	-17.98 \pm 0.73	8.71 \pm 1.43	7
Mussel	<i>Mytilus spp.</i>	Alaska	Katmai	-17.14 \pm 0.68	8.78 \pm 0.74	4
Mussel	<i>Mytilus spp.</i>	Alaska	Kachemak Bay	-17.01 \pm 0.52	8.70 \pm 0.38	4
Mussel	<i>Mytilus spp.</i>	Alaska	Kenai Fjords	-17.68 \pm 0.09	8.35 \pm 0.70	3
Mussel	<i>Mytilus spp.</i>	Alaska	W. Prince William Sound	-18.39 \pm 0.63	8.87 \pm 1.27	3
Dogwinkle	<i>Nucella spp.</i>	BC	Haida Gwaii	-14.63 \pm 0.54	12.83 \pm 0.63	6
Dogwinkle	<i>Nucella spp.</i>	BC	Pacific Rim	-15.89 \pm 0.31	11.33 \pm 0.20	5
Dogwinkle	<i>Nucella spp.</i>	BC	Salish Sea	-16.38 \pm 0.80	9.98 \pm 0.48	4
Dogwinkle	<i>Nucella spp.</i>	Alaska	Katmai	-16.56 \pm 0.41	10.61 \pm 0.53	5
Dogwinkle	<i>Nucella spp.</i>	Alaska	Kachemak Bay	-16.06 \pm 0.39	10.51 \pm 0.34	4
Dogwinkle	<i>Nucella spp.</i>	Alaska	Kenai Fjords	-17.24 \pm 0.97	10.26 \pm 0.30	3
Dogwinkle	<i>Nucella spp.</i>	Alaska	W. Prince William Sound	-16.89 \pm 0.45	10.48 \pm 0.20	3

Table B.3. Metrics of individual variation within each site. Data presented include the mean (\pm SD) consumption of each prey item across all individuals within the site, as well as Quartiles one and three, and the range of the diet proportions of each prey item.

Region	Site	Prey Item	Mean (\pmSD)	Q1	Q3	Range
Alaska	Katmai	Chiton	0.12 \pm 0.03	0.10	0.16	0.06-0.17
		Clam	0.13 \pm 0.02	0.12	0.16	0.09-0.17
		Limpet	0.23 \pm 0.04	0.20	0.25	0.17-0.33
		Mussel	0.34 \pm 0.04	0.32	0.37	0.26-0.42
		Snail	0.17 \pm 0.06	0.12	0.21	0.10-0.32
	Kachemak Bay	Chiton	0.11 \pm 0.02	0.1	0.13	0.7-0.14
		Clam	0.19 \pm 0.07	0.15	0.2	0.10-0.38
		Limpet	0.30 \pm 0.06	0.25	0.33	0.24-0.42
		Mussel	0.30 \pm 0.08	0.24	0.35	0.16-0.44
		Snail	0.10 \pm 0.03	0.08	0.13	0.06-0.15
	Kenai Fjords	Chiton	0.23 \pm 0.11	0.14	0.31	0.10-0.44
		Clam	0.13 \pm 0.02	0.12	0.15	0.10-0.16
		Limpet	0.27 \pm 0.06	0.22	0.31	0.19-0.40
		Mussel	0.17 \pm 0.04	0.13	0.20	0.10-0.25
		Snail	0.20 \pm 0.08	0.13	0.27	0.08-0.34
	W Prince William Sound	Chiton	0.24 \pm 0.06	0.20	0.29	0.11-0.32
Clam		0.16 \pm 0.05	0.13	0.18	0.08-0.29	
Limpet		0.20 \pm 0.04	0.18	0.22	0.10-0.27	
Mussel		0.20 \pm 0.05	0.16	0.25	0.10-0.26	
		Snail	0.21 \pm 0.11	0.11	0.27	0.10-0.47
British Columbia	Haida Gwaii	Chiton	0.12 \pm 0.01	0.11	0.13	0.10-0.16
		Clam	0.11 \pm 0.03	0.09	0.12	0.05-0.15
		Limpet	0.49 \pm 0.06	0.44	0.53	0.40-0.60
		Mussel	0.25 \pm 0.06	0.21	0.29	0.15-0.35
		Snail	0.04 \pm 0.01	0.03	0.05	0.02-0.07
	Pacific Rim	Chiton	0.13 \pm 0.02	0.12	0.14	0.05-0.17
		Clam	0.15 \pm 0.01	0.14	0.16	0.11-0.16
		Limpet	0.26 \pm 0.03	0.26	0.28	0.14-0.32
		Mussel	0.36 \pm 0.09	0.31	0.38	0.3-0.67
	Salish Sea	Snail	0.10 \pm 0.03	0.09	0.13	0.03-0.17
		Chiton	0.07 \pm 0.02	0.06	0.09	0.04-0.11
		Clam	0.13 \pm 0.03	0.11	0.14	0.06-0.18
		Limpet	0.26 \pm 0.09	0.19	0.33	0.10-0.46
		Mussel	0.44 \pm 0.15	0.31	0.56	0.21-0.76
		Snail	0.10 \pm 0.03	0.08	0.12	0.04-0.15