Migration strategies of Black Oystercatchers (*Haematopus bachmani*) breeding in the Gulf of Alaska

by

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Abstract

Advances in tracking technology have documented an astonishing array of migratory movements and revealed that, in many species, individuals within a population can exhibit different migration strategies. Yet, the drivers responsible for variation in migration strategies remain poorly understood. In this thesis, I evaluate methods used to attach tracking devices to Black Oystercatchers (*Haematopus bachmani*), describe their migration, and test a suite of hypotheses for partial migration. I found that devices attached using a leg-loop harness had no detectable effect on whether individuals were resighted in subsequent years but that devices attached to leg bands significantly reduced resighting probability. I confirmed that Black Oystercatchers are partial migrants: some individuals remained resident in Alaska year-round while others migrated to British Columbia. I also found evidence that individual migration decisions were influenced by an individual's diet, providing support for the trophic polymorphism hypothesis for partial migration.

Keywords: tag effects; partial migration; GPS; geolocator; movement; shorebird

Acknowledgements

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Chapter 1.

Evaluating effects of tracking device attachment methods on Black Oystercatchers (*Haematopus bachmani*)

1.1. Abstract

Advances in tracking technology are greatly improving our understanding of many aspects of avian ecology. However, the diversity of tracking devices and attachment methods necessitates evaluation of how different tracking devices and attachment methods affect particular taxa. We evaluated effects of tracking devices mounted on leg bands or attached using a leg-loop harness on resighting rates of Black Oystercatchers (*Haematopus bachmani*) in Alaska and British Columbia. In Alaska, geolocators were mounted on a leg band or encased in a nylon case and attached using a leg-loop harness, and GPS devices were attached using a leg-loop harness in 2019. In British Columbia, Argos-PTT satellite transmitters were attached using a leg-loop harness in 2019 and 2020. Control birds were colour-banded but were not equipped with a tracking device. Surveys to resight birds with and without tracking devices were conducted in 2020 and 2021. Birds carrying geolocators (mass = 4 g; 1.4–2.1% of bird mass), GPS devices (mass = 7 g; 1.8–2.5% of bird mass) and Argos-PTT satellite transmitters (mass = 9.5 g; 2.2–3.0% of bird mass) attached using a leg-loop harness were as likely to be resighted as control birds. However, birds carrying geolocators mounted on leg bands (mass = 1 g; 0.07–1.1% of bird mass) were less likely to be resighted. We also used resighting data and a time-to-tag failure analysis to obtain a minimum annual survival estimate for the birds carrying an Argos-PTT satellite transmitter and compared this estimate with previous survival estimates for Black Oystercatchers in British Columbia. The minimum annual survival estimate for birds carrying Argos-PTT satellite transmitters attached using a leg-loop harness (0.81 ± 0.08 SE) did not differ from previously reported annual apparent survival estimates for Black Oystercatchers in British Columbia (0.90 ± 0.03 SE). These findings suggest that while Black Oystercatchers are able to successfully carry tracking devices weighing less than 3% of their body mass when they are attached using a leg-loop harness they are negatively affected by small tracking devices mounted directly on leg bands.

1.2. Introduction

The fields of movement ecology and population demography have benefitted enormously from attachment of markers to individual animals, including a variety of devices that electronically track the location and status of individuals (Nathan *et al*. 2008, Wilmers et al. 2015). Technological advances have reduced the size of tracking devices and increased effective battery life (Bridge *et al*. 2011, Kays *et al*. 2015), allowing attachment to a wide variety of bird species ranging in mass from the 6 g Green Hermit Hummingbird (*Phaethornis guy*) (Hadley and Betts 2009) to an 88 kg Ostrich (*Struthio camelus*) (Williams *et al*. 1993). Methods for attaching tracking devices vary depending on the species and circumstances, and may be implanted surgically (Korschgen *et al*. 1996), secured to a neck collar (Schmutz and Morse 2000), stitched/glued to feathers (Kenward 1978, Warnock and Warnock 1993), attached using a body or leg-loop harness (Rappole and Tipton 1991, Mallory and Gilbert 2008, Chan *et al*. 2016), or mounted to legs bands (Conklin and Battley 2010, Minton *et al*. 2010). With an increasing number of tracking device options and attachment techniques, biologists must decide on methods that allow appropriate scientific inference and meet ethical standards for minimizing harm to their study species.

There are a number of ways in which attached markers can have negative effects on the birds that carry them (Barron *et al*. 2010, Costantini and Møller 2013). Carrying additional weight will increase flight costs and energetic expenditure (Gessaman and Nagy 1988, Vandenabeele *et al*. 2012), which can reduce the survival of birds (Ward and Flint 1995, Dzus and Clark 1996, Paquette *et al*. 1997). A highly cited guideline is that tracking devices should weigh no more than 5% of the mass of the bird receiving them (reviewed by Casper 2009 and Fair *et al*. 2010; Bird Banding Laboratory 2018). Recently, researchers and permitting authorities have adopted a reduced threshold of no more than 3% body mass (Kenward 2001, Phillips *et al*. 2003, Bodey *et al*. 2018, Gratto-Trevor 2018, Bird Banding Laboratory 2023), yet, others argue for further reductions in weight are necessary in some cases (Weiser *et al*. 2016). However, tracking device attachment method may be more important than weight alone, no matter the threshold guideline. When tracking devices are mounted externally, controlled experiments have shown that the additional drag induced can reduce flight performance (Obrecht *et al*. 1988, Pennycuick *et al*. 2012, Vandenabeele *et al*. 2012) and have pronounced effects during migration (Steenhof *et al*. 2006). Mortalities have also been reported when birds entangle their bills in externally mounted harnesses (Chan *et al*. 2016, von der Kolk 2021) or subcutaneous anchors (Bond and Esler 2008) when attempting to remove tracking devices. Further, surgically implanted devices can both reduce survival, at least for a short period, (Mulcahy and Esler 1999) and have negative effects on reproduction (Johnson *et al*. 2010, Hooijmeijer *et al*. 2014).

Reviews of taxa specific studies can lead to more detailed recommendations regarding the use and attachment of tracking devices. Weiser *et al*. (2016) found that tracking devices with a total weight of more than 2.5% of body mass could have negative effects on return rates of some arctic-breeding shorebirds. However, tracking devices had negative effects on some small-bodied species (e.g., Semipalmated Sandpiper (*Calidris pusilla*); average mass = 26 g; 3.3-3.9% mean body mass) and not others (e.g., Western Sandpiper (*Calidris mauri*; average mass = 27 g; 3.7% mean body mass) suggesting potential for species-specific effects. Similarly, Schalter and Jones (2017) described mixed effects on return rates and chick growth between two similarly sized auklet species despite tracking devices being within 0.8-1.8% of their body mass. Species-specific effects may therefore emerge from differences in device weight, where generalized guidelines apply (5% or 3% rules), but may also be driven by variation in life histories (Barron *et al*. 2010, Schalter and Jones 2017) or device attachment method (Costantini and Møller 2013).

Tracking devices are typically deployed on shorebirds using either a leg-loop harness, wing/full body harness, internal implant, or attached directly to a leg band. Leg-loop harnesses have been used successfully on a wide range of species (Rappole and Tipton 1991, Sanzenbacher *et al*. 2000, Lislevand and Hahn 2013), but this attachment method can have negative effects on some birds, particularly those species accumulating substantial fat reserves before migration (Minton *et al*. 2010, Ruthrauff *et al*. 2019). Wing and full-body harnesses are used less frequently because studies have documented negative effects of these attachment methods (Chan *et al*. 2016, Thaxter *et al*. 2016, Gratto-Trevor 2018). Tracking devices mounted on leg bands are reported to have no negative effects on many shorebird species (Ruddy Turnstone (*Arenaria interpres):* Minton *et al*. 2010, Red Knot (*Calidris canutus*) Niles *et al*. 2010, Bar-tailed Godwit (*Limosa lapponica*): Conklin and Battley 2010, Snowy Plover (*Charadrius nivosus*): Mondain-Moval *et al*. 2020). However, Weiser *et al*. (2016) concluded that depending on the orientation of the tracking device on the leg band, the additional mass can cause leg injuries. Clearly, further assessment of tracking device mass and attachment effects on birds are required.

Oystercatchers are a family of large, conspicuous shorebirds that have been tracked to understand their ecology and assess human disturbance effects on coastal environments (Tessler *et al*. 2014, Clay *et al*. 2014, van der Kolk *et al*. 2022). However, there is some uncertainty as to how to best deploy tracking devices on this taxon. Currently, studies on Eurasian Oystercatchers (*Haematopus ostralegus*) attach tracking devices using wing harnesses (Ens *et al*. 2008, Shamoun-Baranes *et al*. 2012, van der Kolk 2022), but the use of wing harnesses is discouraged by permitting agencies in North America. In North America, surgically implanted satellite transmitters were found to reduce survival of Black Oystercatchers (Haematopus bachmanii (Johnson *et al*. 2010) and tracking devices attached using leg-loop harnesses were frequently lost (Johnson *et al*. 2010; Loring *et al*. 2017), while leg band-mounted tracking devices deployed on juvenile American Oystercatchers (*Haematopus palliatus*) have been found to cause abrasions and a range of leg injuries (Ted Simmons, Shiloh Schulte, Pamela Denmon, pers.comm).

Given uncertainties surrounding the best method for attaching tracking devices to oystercatchers, we experimentally evaluated how tracking device size and attachment method influenced the probability of resighting tagged and colour-banded Black Oystercatchers in Alaska and British Columbia over two years. Specifically, we contrasted resighting probabilities of birds with a tracking device mounted to an alpha-numeric leg band or attached using a leg-loop harness to the resighting probability of control birds that only had colour bands. We then used a combination of resighting surveys and telemetry data to estimate a minimum annual survival rate and compared our estimate to previous survival estimates for this species.

1.3. Methods

Study species, field sites and tracking device deployment

The Black Oystercatcher is a large (500-700 g) shorebird found on rocky shorelines of western North America from the Aleutian Islands, Alaska, to Baja

California, Mexico (Andres and Falxa 2020). Northern populations are partially migratory while southern populations are considered to be sedentary (Johnson *et al*. 2010, Tessler *et al*. 2014, Ware *et al*. 2023). Females and males have identical plumage but females are slightly larger and have a more distinct eye-fleck than males (Guzzetti *et al*. 2008).

We captured and marked a total of 121 Black Oystercatchers, 68 adults from four sites in Alaska (Prince William Sound, Kenai Fjords National Park, Kachemak Bay, and Katmai National Park and Preserve) in June/July 2019 and 53 adults from three sites in British Columbia (Pacific Rim National Park, Haida Gwaii, and the Salish Sea) during March 2019 and March 2020 (Fig.1.1). We located and captured territorial oystercatchers with a combination of noose-mats and mist-nets, and the aid of a visual and audio lure. We aged oystercatchers using a combination of bill and iris colour (Webster 1942) and sexed oystercatchers based on the amount of dark speckling in the iris following Guzzetti et al. (2008). We marked all individuals with a USGS stainless-steel band (size 5A and 6) on the lower leg (tarsometatarsus) and a matching pair of plastic alpha-numeric wrap-around bands (Haggie Engraving, Crumpton, Maryland, US) on the upper left and right leg (tibia).

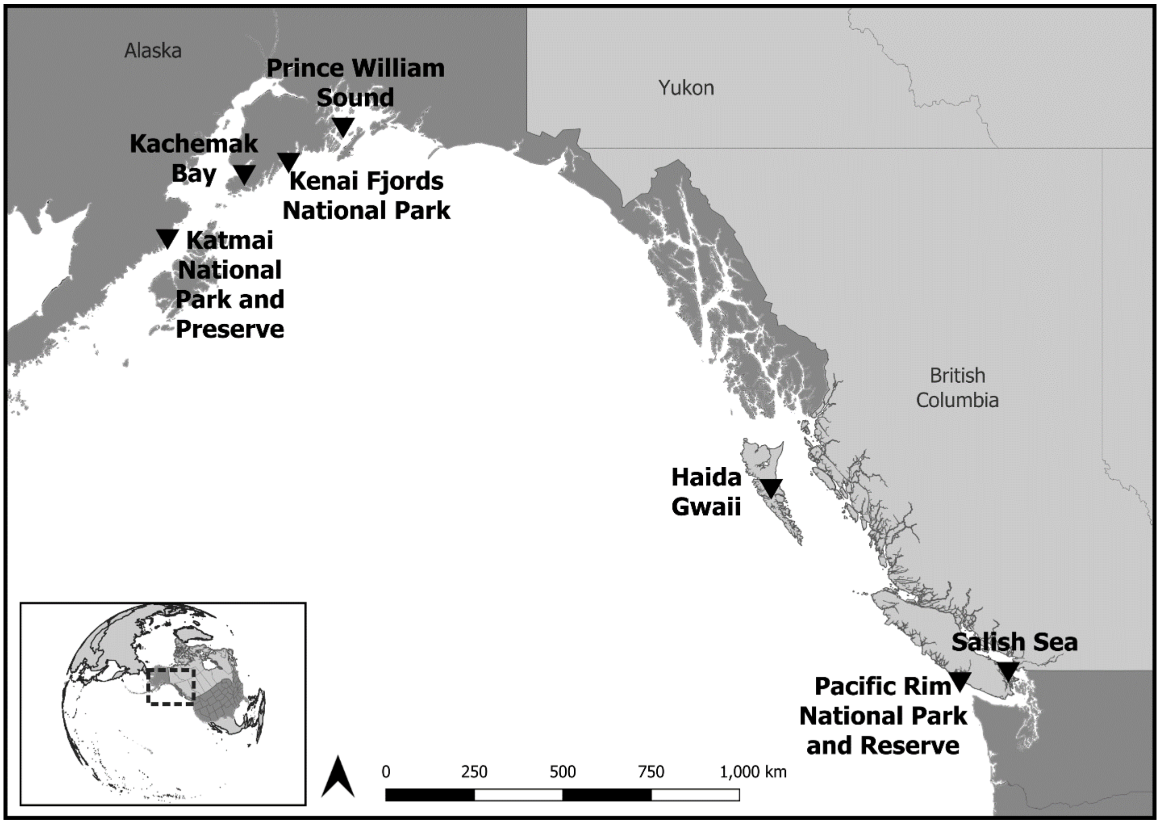

Figure 1.1. Locations of the study areas used to evaluate effects of tracking device attachment methods on resighting rates of Black Oystercatchers from 2019-2021. Dark gray represents the United States and light gray represents Canada.

In Alaska, 20 birds were equipped with light-sensor geolocators (C65-SUPER, Migrate Technology) designed to be attached to alpha-numeric coloured wrap-around leg bands. Geolocators were secured to leg bands in a vertical position using one plastic cable tie and self-amalgamating tape that went around the outside of the band and geolocator with the light sensor left exposed. Twenty birds were equipped with a geolocator encased in a nylon mount and attached using a modified leg-loop harness (Mallory and Gilbert 2008). Nylon mounts were designed with the online program Tinkercad (Autodesk 2019) and printed with a 3D printer (Ultimaker 3). An additional six birds were equipped with a solar-powered GPS logger (Sterna, Ecotone) attached using a leg-loop harness. Twenty-two birds were banded with a USGS metal band and two alphanumeric colour wrap-around bands but did not receive a tracking device (controls). In British Columbia, 26 birds were equipped with a solar-powered Argos satellite transmitter (PTT-100, Microwave Telemetry) using a leg-loop harness and 27 birds received metal and alphanumeric colour bands only (controls). Leg-loop harnesses for geolocators and GPS devices were constructed with 3/16-inch Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania; Mallory and Gilbert 2008) and reinforced with two strands of 80 lbs nylon trammel-line (Avinet) threaded through the Teflon ribbon. Harnesses with tracking devices were secured using brass crimps. Information on the number of birds captured and equipped with tracking devices or left as controls is presented in Table 1.1. Information on the dimensions and weight of the different tracking devices alone, with the harness, and with the bands is presented in Table 1.2.

Table 1.1. Distribution of tag types and attachment methods used to deploy tracking devices on Black Oystercatchers across study sites in Alaska (AK) and British Columbia (BC). Geolocator abbrevaited as "Geo".

Study Site	Geo Leg band	Geo Harness	GPS Harness	PTT Harness	Control	Total
AK West Prince William Sound	6	5	2		7	20
Kenai Fjords National Park	8	6	2		5	21
Kachemak Bay	3	3	1		3	10
Katmai National Park	3	6	1		7	17
Total in AK	20	20	6		22	68
BC Haida Gwaii				10	13	23
Pacific Rim National Park				6	8	14
Salish Sea				10	6	16
Total in BC				26	27	53

Table 1.2. Mass and dimensions of three tracking devices and mass of the devices when attached to Black Oystercatchers. We also report the total mass of the device, attachment material, and leg bands (one metal, two plastic) relative to a bird's mass (mean mass = 600 g ± 43 SD, range 510–717 g, *n* = 121). The device weight is assumed to be constant although small differences [<0.1 grams] were likely present (i.e., not all tags were weighed prior to attachment).

Device and attachment method	Device Dimensions (mm)	Device Mass (g)	Device mass + attachment mass (g)	Device mass + attachment + bands (g)	% of bird's mass
Geolocator Leg band	14 x 8 x 6	1	1.5	5.5	0.07–1.1
Geolocator in a nylon mount - Harness	26 x 18 x 14	4.5	6.5	10.5	1.4–2.1
GPS - Harness	35 x 16 x 10	7	9	13	1.8–2.5
PTT - Harness	39 x 18 x 13	9.5	11.5	15.5	2.2–3.0

Resighting effort

In 2020 and 2021, we returned to locations where birds had been fitted with tracking devices to resight and recapture birds and remove tracking devices. Travel restrictions imposed during the COVID-19 pandemic restricted our ability to revisit all seven sites in 2020. In Alaska, we conducted surveys in Prince William Sound, Kachemak Bay, and some locations in Kenai Fjords National Park in July 2020 but were unable to access parts of Kenai Fjords or conduct any surveys in Katmai National Park and Preserve. In British Columbia, we conducted surveys in the Salish Sea in March 2020 but were unable to access and conduct surveys in Pacific Rim National Park and Haida Gwaii. We revisited all 7 field sites and conducted surveys for marked birds at all capture locations in June/July 2021.

We conducted resighting surveys from small to medium watercraft with one driver and one to two observers using a combination of binoculars and spotting scopes. We were generally able to approach birds close enough to get a positive identification with binoculars and would use a spotting scope as needed. We recorded the location and alphanumeric combination of all banded birds resighted.

Statistical analysis

We used generalized linear models with a binomial distribution and logit link to evaluate whether presence of a tracking device influenced the probability a bird was resighted. We constructed separate models for Alaska and British Columbia. In Alaska, we pooled cases where geolocators and GPS tags were attached using a leg-loop harness and modelled how tracking devices and attachment method (attached to a leg band, attached using a leg loop harness, controls) influenced whether a bird was resighted, controlling for whether the site was revisited in 2020 or not. In British Columbia, we modelled whether carrying a tracking device (attached with a leg-loop harness, controls) influenced whether a bird was resighted, again, controlling for whether the site was revisited in 2020. In addition, we modelled time-to-tag failure for the 26 birds equipped with a PTT satellite transmitter tracked in British Columbia using the Kaplan-Meier estimator (Pollock *et al*. 1989). We defined the time of tag failure as the date that a bird died or the date that the last location data was uploaded to the Argos system. We estimated the minimum annual survival of oystercatchers carrying a tracking device by combining the number of individuals that were still being tracked after one year and the number of individuals where tags failed before 365 days had elapsed but were known to have survived for a year from resighting surveys. We compared this estimate with the estimated annual apparent survival of Black oystercatchers in British Columbia between 2008–2013 (0.90 ± 0.03 SE; P. Clarkson & Y. Zharikov unpubl. data, in Tessler *et al*. 2010) using Program Contrast (Hines and Sauer 1989).

1.4. Results

Tracking device attachment method effects on resighting of Black Oystercatchers

In Alaska, we resighted 3 of 20 (15%) oystercatchers for which the geolocator was attached to the leg band, 18 of 26 (69%) oystercatchers equipped with a tracking device attached using a log-loop harness, and 13 of 22 (59%) control birds on surveys conducted in 2020 and/or 2021. After controlling for whether sites were revisited in 2020, birds for which a geolocator was mounted to their alphanumeric leg band were far less likely to be resighted than control birds or birds for which a tracking device was attached using a leg-loop harness (Figure 1.2; $X^2 = 15.83$, df = 2, $P < 0.001$).

In British Columbia, we resighted 16 of 26 (62%) birds equipped with an Argos-PTT satellite tag attached with a leg-loop harness and 16 of 27 (59%) control birds during surveys of field sites in British Columbia in March 2020 and/or June/July 2021. After controlling for whether resighting surveys could be conducted in 2020, there was no difference in probability of resighting birds with an Argos-PTT transmitter attached with a leg-loop harness and control birds (Figure 1.2; $X^2 = 0.06$, df = 1, $P = 0.81$).

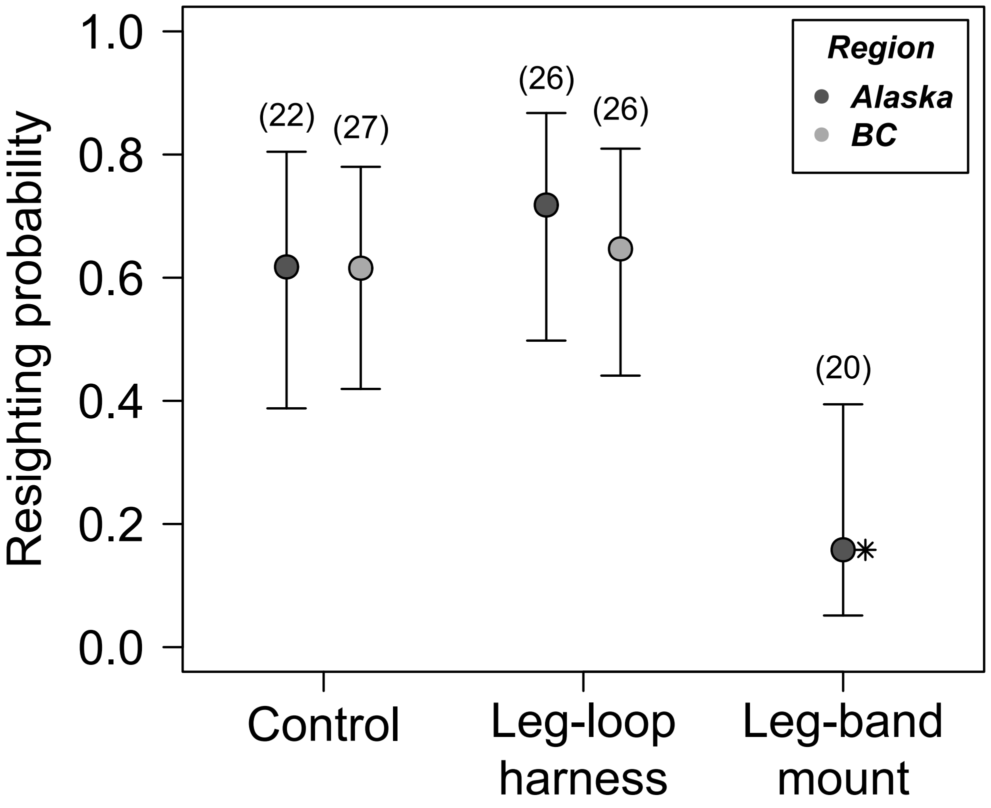

Figure 1.2. Model estimated resighting probabilities for Black Oystercatchers that received no tracking device (control), a tracking device attached with a leg-loop harness, or a tracking device mounted to a leg band. Model estimates accounted for whether resighting surveys were conducted in both 2020 and 2021. Dark gray circles are model estimates for Alaska, and light gray circles are model estimates for British Columbia. Numbers in parentheses indicate sample sizes. Asterisk denotes groups with non-overlapping 95% confidence intervals.

Harness effects on annual survival of Black Oystercatchers

The 26 Black Oystercatchers equipped with an Argos-PTT transmitter in British Columbia provided location data for 456 ± 49 SE days. The time-to-event analysis estimated the probability of providing location data for at least a year to be 0.65 (95% CI 0.0.49-0.86) (Fig. 1.3); 17 of the 26 tagged birds provided location data for at least 365 days. However, four of the 9 birds where tags failed were subsequently resighted alive having dropped their tags/harnesses. The proportion known to have survived a year or more based on the Argos-PTT transmitter locations and/or resighting surveys (n = 21, 0.81 ± 0.08 SE) was not significantly different from the estimated annual survival for Black Oystercatchers in British Columbia (0.90 ± 0.03 SE; P. Clarkson & Y. Zharikov unpubl. data, in Tessler *et al*. 2014; $X^2 = 1.1$, df = 1, P =.29)(Fig. 4). This represents a minimum survival estimate as some individuals (n = 5) whose transmitters failed before one year and were not detected may have been alive.

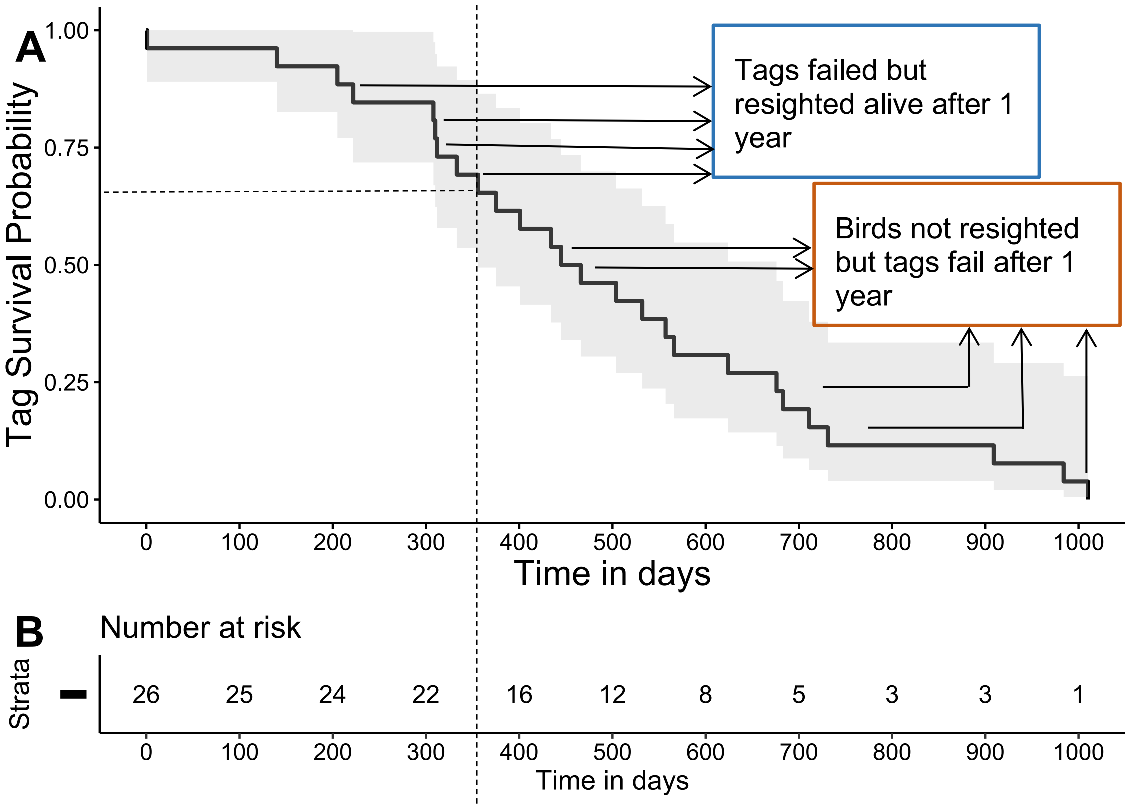

Figure 1.3. A.) Kaplan-Meier function showing the time (in days after capture) to tag failure of 26 Argos-PTT satellite transmitters attached to Black Oystercatchers in BC in 2019 and 2020. The black solid line shows the model estimated tag survival probability, and the gray shading show the 95% confidence intervals around the estimates. The black dashed line denotes the estimated tag survival probability after 365 days. The blue box highlights birds with tags that failed before one year had elapsed but that were subsequently resighted and known to be alive one year after the transmitters were deployed. The orange box highlights birds that were never resighted but that were known to be alive one year after the transmitters were deployed because the tags had not failed. B.) The number of birds transmitting location data (number at risk) at any time.

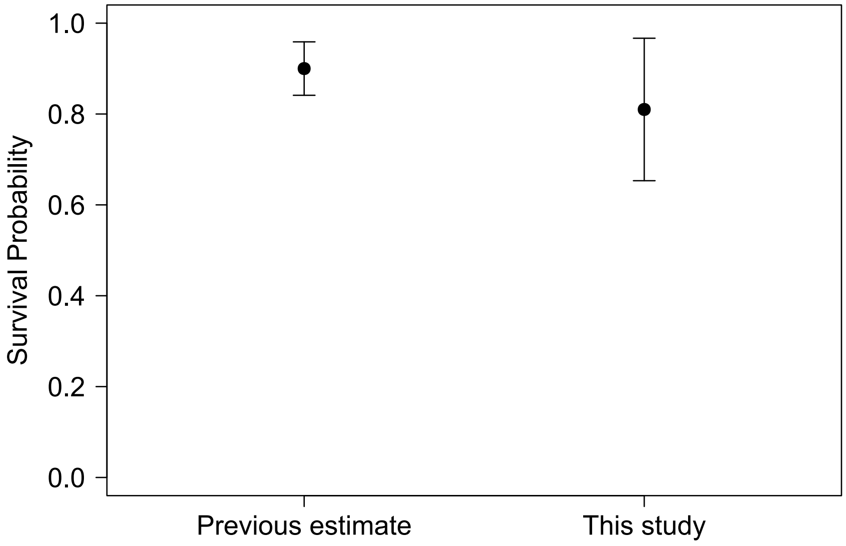

Figure 1.4. Black Oystercatcher annual apparent survival estimates in British Columbia from 2008–2013 (Clarkson & Zharikov unpubl. data, in Tessler *et al*. 2014) compared with the minimum annual survival estimates for birds carrying Argos-PTT satellite transmitters (n = 26) in this study. Bars show the 95% confidence intervals around the estimate.

1.5. Discussion

The increased use of tracking devices to study the movement and demography of birds puts the onus on avian ecologists to evaluate how their size, mass, and attachment method affects birds. We found that Black Oystercatchers can be tracked successfully with no detectable effect on survival using tracking devices attached with a leg-loop harness. However, we also found that despite their relatively large size and robust legs, even small tracking devices mounted to colour bands on the leg had significant adverse effects on the probability that Black Oystercatchers are resighted. This suggests that this method of attachment has significant impacts on their survival. We therefore recommend researchers avoid attaching devices to leg bands on Black Oystercatchers and exercise caution if considering using this method on other related species.

The general rule of thumb is that tracking devices should weigh less than 3-5% of a bird's body mass (Kenward 2001, Casper 2009, Barron *et al*. 2010, Fair 2010, Bodey *et al*. 2018) and bird banding permits under the North American Bird Banding Program now require that tracking devices with harness attachments weigh no more than 3% of the bird's body mass and no more than 2% when attached to leg bands (USGS Bird Banding Laboratory, Canadian Bird Banding Office). Consistent with recent reviews, we show that Black Oystercatchers are capable of carrying tracking devices weighing <3% of their body mass. Minimum estimates of survival of Black Oystercatchers carrying the largest tags (Argos-PTT) were similar to estimates of annual apparent survival for Black Oystercatchers in British Columbia. Similarly, resighting levels were similar between BC and Alaska and in both locations resighting rates of birds carrying tracking devices attached using a harness were no different than resighting rates of control birds. In this study tracking devices attached with a leg-loop harness were located on the sacrum (between the lower and middle back), so oystercatchers appear able to accommodate additional drag as well as the additional mass of the larger tracking devices (e.g., Argos-PTT and GPS) (Vandenbeele *et al*. 2014).

Tracking devices attached to leg bands have been used successfully on Ruddy Turnstone, Red Knot, Bar-tailed Godwit, and several species of sandpipers (Minton *et al*. 2010, Niles *et al*. 2010, Conklin 2010, Weiser *et al*. 2016, Mondain-Moval *et al*. 2020). However, attaching 1 g geolocators to Haggie colour bands (2 g) significantly reduced the probability that Black Oystercatchers were resighted. Two birds equipped with a geolocator attached to the leg band sustained leg injuries; one was reported to have died and the second had abrasions and an infection on their leg when they were recaptured. Previous studies have documented negative effects of equipping immature American Oystercatchers with 3 g tracking devices attached to leg bands. We speculate that geolocators attached to leg bands may have negative effects on Black Oystercatchers because i) the cable ties and tape used to secure the geolocator to the leg bands prevented the bands from expanding in response to small increases in the diameter of the tibia and/or ii) the off-set weight of the geolocator on one side of the leg band increased the likelihood of small abrasions occurring along the bottom edge of the band while a bird navigated the intertidal zone, resulting in infection and swelling. Regardless of the mechanism, future studies tracking Black Oystercatchers should avoid attaching tracking devices to their leg bands. Given the deleterious effects of geolocators attached to leg bands observed in this study, attention should also be given to the potential negative effects of colour banding oystercatchers above the tibiotarsus joint.

Studies of avian movement ecology have rapidly progressed with technological advancements leading to the production of smaller sized tags that can be attached using a variety of methods. This study uses a combination of data collected from Black Oystercatchers tracked using geolocators, Argos-PTT and GPS devices deployed using two different attachment methods—mounted to a leg band or secured with leg-loop harness. Although we expected that small tracking devices mounted to colour bands on the robust legs of Black Oystercatchers would have less impact than larger tags attached using a leg-loop harness, the opposite was observed. Our study highlights that tag effects can be species specific and that tag attachment methods should be considered in addition to the general guideline that a tag should weigh no more that 3-5% of the mass of a bird. We echo the call for critical assessments of tag effects in tracking studies to improve scientific rigor and increase welfare when working with free-living animals (Barron *et al*. 2010, Bodey *et al*. 2018, Geen *et al*. 2019, Ruthrauff *et al*. 2019).

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Chapter 2.

Drivers of partial migration in Black Oystercatchers

2.1. Abstract

Advances in tracking technology have documented an astonishing array of migratory movements and revealed that, in many species, individuals within a population can exhibit different migration strategies. Yet, the drivers responsible for variation in migration strategies remain poorly understood. We tracked annual movements of Black Oystercatchers breeding in Alaska using geolocators and GPS devices and evaluated a suite of hypotheses commonly found in the literature to explain why some individuals migrate while others remain as residents, a phenomenon known as partial migration. We determined the migratory strategy for 23 individuals from 2019-2022. All Black Oystercatchers left their breeding territories at the end of the breeding season. However, movement distances were bimodally distributed. Some individuals remained resident in Alaska travelling 20-220 km from their breeding territory to non-breeding areas, while others migrated longer distances (930-1610 km) to non-breeding areas in British Columbia. Individuals embarking on long distance migrations from Alaska showed a leapfrog migration pattern and their wintering areas were concentrated along coastline in the Hecate Strait, near Prince Rupert, British Columbia, indicating an important non-breeding area for migrants. Variation in migration strategies was best explained by an individual's diet, providing support for the trophic polymorphism hypothesis. We found no evidence to support predictions made by the thermal tolerance, fasting endurance, dominance, or arrival time hypotheses for partial migration in oystercatchers.

Keywords

Partial migration, GPS, geolocator, diet specialization, condition, movement

2.2. Introduction

Natural philosophers, classical ornithologists and contemporary ecologists have all been fascinated by the seasonal migration of birds (Aristotle 350 BCE, Linnaeus 1757, Thomson 1926, Lack 1943, Alerstam 1990, Berthold *et al.* 2003, Newton 2008, Weidensaul 2021). Particularly puzzling is the observation that individuals within populations often vary in their migratory behavior. Individuals can migrate different distances based on sex or age leading to differential migration (Ketterson and Nolan 1976) or some may migrate while others do not, leading to partial migration (Lack 1943, Lundberg 1987, Berthold 1996, Chapman *et al*. 2011). The phenomenon of partial migration has been viewed as an intermediate step in the transition to complete migration or complete residency (Berthold 1996). Therefore, studying partial migration can lend insight to the evolution of migration in general, or test theories to explain phenotypic polymorphism. Although early studies focused on birds (Lack 1943, Ketterson and Nolan 1979, Biebach 1983), recent advances in tracking technology have revealed that partial migration is widespread in vertebrates and invertebrates (mammals: Ball *et al*. 2001, Hebblewhite and Merrill 2011; fish: Chapman *et al*. 2012; sharks: Pratt *et al*. 2018; amphibians: Grayson *et al*. 2011; reptiles: Blake *et al*. 2012; insects: Menz *et al*. 2019) Ecologists continue to marvel at the variation in migration patterns elucidated by these technologies, yet, the ultimate or proximate mechanisms driving the observed variation in migratory strategies remain poorly understood.

Migration, despite being energetically demanding (Jenni-Eiermann *et al*. 2002, Wikelski et al. 2003, Costantini *et al*. 2007, Eikenaar *et al*. 2018, Meir *et al*. 2019) and risky (Lank *et al*. 2003, Klaassen *et al*. 2014), is thought to be an adaptive response to seasonal variation in resource availability (Gauthreaux 1982, Rappole 1995, Alerstam and Hendenstrom 1998) and/or reduce competition, predation and disease (Mckinnon *et al*. 2010, Alitzer *et al*. 2011). However, not all individuals in a population are ecologically equivalent (Bolnik *et al*. 2003) and may respond differently to seasonal changes in resource availability. Within a species, individuals of certain age or sex classes have been observed to migrate different distances for the winter. Ketterson and Nolan (1976) provided a synthesis of potential hypotheses explaining differential wintering distributions of sex and age-classes (i.e., differential migration) in dark-eyed juncos (*Junco hyemnalis hyemna*). Since then, this framework has also been applied to the phenomenon of partial migration (Chapman *et al*. 2011). A key distinction between differential and partial migration is that under differential migration, all individuals are assumed to vacate breeding areas during the winter, whereas only some individuals vacate breeding areas during the winter under partial migration (Terril and Able 1987, Lundberg 1988, Cristol *et al*. 1999). Ketterson and Nolan (1976) discussed four hypotheses. The “body size hypothesis” (hereafter referred to as the “thermal tolerance hypothesis”) posits that a larger body with a lower surface-to-volume ratio provides a thermoregulatory advantage during harsh winter conditions and predicts that the largest individuals will be residents. The “fasting endurance hypothesis” argues that an individual will be better able to withstand periods of low food abundance if it has more fat reserves, therefore, the fattest birds are predicted to be year-round residents. The “dominance hypothesis” assumes an increase in intraspecific competition for resources during periods of low food abundance and predicts that subordinate individuals migrate while socially dominant individuals remain as residents. The “arrival time hypothesis” posits that individuals benefit from arriving early because they can acquire higher quality territories, therefore, individuals with the highest quality territories should remain as residents. Recently, Chapman *et al*. (2011) introduced an additional hypothesis called the “trophic polymorphism hypothesis.” This hypothesis suggests variation in feeding niches between individuals could lead to dietary specialization and predicts that individuals will be asymmetrically affected by seasonal changes in food resources with those specializing on the more limited resource more likely to migrate.

One problem with the initial four hypotheses presented above is that for many taxa each of these hypotheses generate the same or similar prediction. For example, older, larger, fatter, and more socially dominant males would be expected to migrate shorter distances or remain on breeding grounds throughout the year. Consequently, it has proven difficult to distinguish between hypotheses responsible for the observed size- or sex-structured variation in migratory behaviour. Evaluating the mechanisms underlying each hypothesis rather than just the outcome, testing novel hypotheses, and studying species with unique life histories could help disentangle circular predictions and inform the evolution and maintenance of different migration strategies within one population.

The Black Oystercatcher (*Haematopus bachmani*) is believed to be a partially migratory shorebird and has a life history that provides an opportunity to distinguish between alternative hypotheses for partial migration. Black Oystercatchers in Alaska have been reported to either remain near breeding areas or migrate to more southerly latitudes in southeast Alaska and British Columbia for the non-breeding period (Johnson *et al*. 2010, Andres and Falxa 2020). Black Oystercatchers are reverse sexually dimorphic with females having 9% larger bills and 3% longer legs than males (Webster 1941, Roodenrijs 2023). Both sexes engage in territorial displays but there is some evidence that males are more active in territorial defense than females (Purdy and Miller 1987). They feed on a collection of macro-invertebrate prey, however, a large portion of their diet consists of limpets (*Lottia spp*.) and mussels (*Mytilus spp.*) (Hartwick 1973, Falxa 1992, Robinson *et al*. 2019, Carney *et al*. 2023). In this study, we investigated the migratory strategies of Black Oystercatchers by tracking individuals breeding at four locations in Alaska to confirm that they are partial migrants, and if so, evaluate five hypotheses to explain their partial migration (Table 2.1). For this species we argue that: i) the thermal tolerance hypothesis predicts that females or the largest males are more likely to remain as residents, ii) the fasting endurance hypothesis predicts fatter birds in better condition are more likely to remain as residents, iii) the dominance hypothesis predicts males remain as residents, forcing females to migrate, iv) the arrival time hypothesis predicts individuals with the highest quality territories to remain as residents, and v) individual oystercatchers specializing on seasonally accessible limpet prey are less likely to remain at northern latitudes when conditions worsen during the winter.

Table 2.1. Summary of the hypotheses used to explain partial migration patterns along with the predictions specific to the Black Oystercatchers.

Hypothesis	Description	Predictions	Metric Tested
Thermal Tolerance (Body Size)	Large structural size with a lower surface-to-volume ratio provides a thermoregulatory advantage in harsh conditions.	Females or large males should be more likely to remain as residents.	PC1 (composite of wing, tail, tarsus, bill)
Fasting Endurance	Fuel reserves (fat) enhance the capacity to deal with seasonal reductions in food resources during the non-breeding season	Individuals with more fat reserves should be more likely to remain as residents	Time adjusted mass
Dominance	Dominant individuals are better able to compete for resources during the non-breeding season	Males outcompete females and remain as residents	Binary sex variable
Arrival Time	Competition for high quality breeding territories drives early arrival on breeding grounds	Individuals with high quality territories are more likely to remain as residents	Proportion of survey years territories have active nest
Trophic Polymorphism	Individuals may specialize on different food resources and are asymmetrically affected by seasonal reduction in food resources	Individuals selecting limpets as preferred prey are less likely to remain as residents	Proportion of limpet in diet from stable isotopes

2.3. Methods

Study area

We studied Black Oystercatchers at four areas across the Gulf of Alaska: the western portion of Prince William Sound, Kenai Fjords National Park, Kachemak Bay, and Katmai National Park and Preserve (Figure 2.2). The geography and habitat structure vary among areas (Bodkin *et al.* 2018). Prince William Sound is protected from the open Gulf of Alaska by several large islands and behind these lie many small to medium-sized islands forming a complex coastline, strongly influenced by freshwater inputs and glacial activity (Andres 1998). Kenai Fjords is dominated by deep fjords with steep shorelines and strong glacial influences at the heads of bays with an outer coastline exposed to the open Gulf of Alaska (Cook and Norris 1998). Kachemak Bay is on the leeward side of the Kenai Peninsula and is therefore somewhat sheltered from the Gulf of Alaska. The north and west portions of the bay are characterized by shallow mud flats and rolling hills, whereas the east and south shores are characterized by steep and/or shallow fjords, bays, and many islands (Carrol 1994). Katmai occurs on the Alaska Peninsula west of Kodiak Island. Katmai is characterized by a mix of broad, shallow bays and rocky coastline. We visited each area once per year between the end of May to mid-July from 2019 to 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. 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 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 using this method 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). For birds with intermediate eye fleck scores (category 2), we assigned sex first using information on the sex of their mate, and then culmen and tarsus length.

For each bird captured we recorded ten morphological measurements. 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 diagonal tarsus from the interstitial joint to the last leg scale before the toes (Pyle 1997, Gratto-Trevor 2018). 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. Additionally, we collected the outermost greater covert feather for stable isotope analysis.

After recording measurements, we attached external tracking devices to Black Oystercatchers using leg loop harnesses and leg-band mounted attachment methods (see Chapter 1). Forty birds were equipped with a light-sensor geolocator (C65-SUPER, Migrate Technology). Twenty of these devices were secured to leg bands using one cable tie and self-amalgamating tape that went around the outside of the band and geolocator with the light sensor left exposed. Twenty additional birds were equipped with a geolocator encased in a nylon mount and attached using a modified leg-loop harness (Mallory and Gilbert 2008). Thirty-three birds were instrumented with a solar-powered GPS logger (Sterna, Ecotone) attached using a leg-loop harness. Leg-loop harnesses for geolocators and GPS devices were constructed with 3/16-inch Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania) and reinforced with two strands of 80 lbs nylon trammel-line (Avinet) threaded through the Teflon ribbon. Harnesses with tracking devices were secured using two brass crimps. Tracking devices and harnesses weighed <3% of each bird's mass and generally did not affect whether a bird survived and defended a territory one year later (but see Chapter 1). See Table 1.2 for device specifications. Obtaining data from geolocator-equipped birds required us to recapture them the next year of the study. GPS birds required detecting the bird on the ground but not recapturing them.

We collected prey samples near active territories within each study area that were subsequently used to quantify proportions of prey in the diet of individuals using a stable isotope mixing model. 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 territory: limpet (*Lottia spp.*), blue mussel (*Mytilus trossulus.*), dogwinkle snail (*Nucella spp.*), black chiton (*Katharina tunicate*), and littleneck clam (*Leukoma staminea*). At territories where we could not find these specific genera or species, we collected samples of the most closely related species we could find. Within each territory, we attempted to collect a minimum of four replicates from spatially distributed locations to capture any variation in stable isotope signatures within each territory. Prey samples were collected from all study areas 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.

Analytical methods

Classifying migratory strategy

Black oystercatchers have been recorded moving short distances and forming flocks during winter (Johnson *et al*. 2010, Andres and Falxa 2020), therefore, we expected some movement away from territories by individuals after breeding. We classified individuals as being resident if they remained in the northern portion of the Gulf of Alaska for the entire year (within 200 km of territory), or as migratory, if they made large movements (≥900 km) to southern latitudes to spend the nonbreeding period, defined as October–March.

Movement data and processing

Geolocators estimate geographic positions based on ambient light levels recorded during the day (Lisovski *et al*. 2012) and due to their small size and relatively low cost, their application has become widespread (Stutchbury *et al*. 2009, McKinnon *et al*. 2018). However, data recovery from geolocators requires recapturing the bird to remove the device. Additional drawbacks to geolocators are the magnitude of error around location point estimates, which can be up to 200 km (Fudicker *et al*. 2012), and most methods currently employed require the user to manually set the exact point at which day becomes night and night becomes day—known as the twilight threshold. To overcome this bias, we used the 'twilight-free' method of location estimation from light sensor data implemented in the R package *TwilightFree* (Bindoff *et al*. 2017). This method models locations as hidden states in a Hidden Markov Model, which matches observed light measurements to 1° x 1° grid cells of known light levels from meteorological data, eliminating the necessity to define twilight periods subjectively. We calibrated geolocators before deployment and the twilight-free method provided one estimated location per day.

GPS tracking devices collected precise location estimates (< 10m) and data recovery required recapture or a visual line of sight. If we were unable to recapture a bird, we attempted to remotely download the data from the GPS device using a receiver and Yagi antenna. To optimize battery life and the number of days birds were tracked, we programed our tags to take a fix every four hours for a total of six fixes per day.

We used the tracking data to determine when individuals left and returned to their breeding season home ranges, and the distance travelled between their breeding territory and winter season home range. Breeding season home ranges were calculated using 95% Minimum Convex Polygons (MCP) in the R package *adehabitatHR* (Calenge 2006) from May 1 to August 1 from birds with GPS devices. Home ranges were irregularly shaped polygons, but forays from a territory center (taken to be location of capture) were no more than 20 km in any direction. Therefore, a bounding circle with a radius of 20 km was centered on each territory. GPS birds were defined as departing a territory once it left the home range bounding circle and did not return in the same day. For birds with geolocators, we estimated the date an oystercatcher departed a territory when a 1° shift in latitude was initiated, which is approximately 111 km). A non-breeding season location was estimated from the center point of the distribution of locations from October 31–March1 using the ‘centroid’ function in the R package *geosphere* (Hijmans 2022) for both GPS and geolocator birds. We calculated the great circle distance using the ‘distance’ function in *geosphere* to estimate migration distances between known breeding locations and the centered winter location for each bird. We used data from four individuals with GPS tracking devices that migrated to British Columbia to estimate the utilization distribution of space use during the winter season. We used the ‘kernelUD’ in the *adehabitatHR* to show the 95% utilization distribution to represent spatial extent of area used during the winter period.

Evaluating the thermal tolerance (body size) hypothesis

The body size hypothesis posits that large individuals are better able to thermoregulate in cold climates because with a lower surface-to-volume ratio, large individuals do not lose heat as fast as small individuals. Because the surface-to-volume relationship is a function of structural size, we generated an index of structural body size using a principal component analysis conducted with four morphological measurements (tarsus length, wing chord, tail length, and head plus bill length). Wing chord length was negatively correlated with capture date ($r_s = -0.41$, $p = 0.05$) so we controlled for capture date and used adjusted wing chord length in the principal component analysis. The first principal component explained 50.1% of the variation in the data. Males and females are known to differ in body size but there was considerable variation in the PC1 scores of the birds where migration behavior was determined and the PC1 scores did not vary with sex in this sample of birds (Welch’s t-test; $t = 1.55$, $df = 14.1$, $p = 0.14$).

Evaluating the fasting endurance hypothesis

The fasting endurance hypothesis provides a physiological explanation for partial migration, however, fasting endurance and thermal tolerance hypotheses have been used interchangeably in the literature and/or lumped into one “body size hypothesis” (Chapman *et al*. 2011). Importantly, these two hypotheses represent different mechanisms driving the response of the body to environmental conditions. A physiological explanation differs from a thermal tolerance explanation in arguing that birds with more non-structural energy reserves, in the form of fat, should be more likely to remain at northern latitudes during the winter when resources are scarce. We estimated the fat reserves, or “condition”, of a bird at capture using field measured mass. Mass and capture date were negatively correlated ($r_s = -0.22$, $p = 0.30$) so we controlled for capture date and used capture-date adjusted body mass as an index of fat reserves. Body mass also varies with body size ($r_s = 0.36$, $p = 0.09$) but we did not adjust for body size when calculating an index of fat reserves because studies suggest that body mass alone may be a better indicator of non-structural energy reserves than an unverified body condition index (Schamber *et al*. 2009, Heath *et al*. 2011, Labocha and Hayes 2012). However, using capture date and size-adjusted mass as an index of fat reserves does not alter the conclusions drawn from the AICc analysis (see Results and alternative AICc tables in Appendix A Table A.1 and A.2).

Evaluating the dominance hypothesis

The observation that different age and sex classes of some species show different migration passage timing and spend the nonbreeding period in different locations is attributed to the avoidance of unfavorable interactions with socially dominant individuals (Meyers 1981, Berthold *et al*. 2003). Although the advantage is assumed to belong to the larger sex, male oystercatchers have been observed to respond more aggressively to intruders on territories than females (Purdy and Miller 1987). To evaluate the social dominance hypothesis, we evaluated whether females were more likely to migrate than males.

Evaluating the arrival time hypothesis

Individuals defending high quality territories would be expected to benefit most from remaining on those territories year-round or remaining close to those territories and returning earlier than individuals on lower quality territories. We measured territory quality as the proportion of survey years where the territory had an active nest defined as having eggs or chicks. Territories were visited once per year but survey frequency over the last ten years varied depending on weather conditions and field logistics, so the number of surveys used to define territory quality varied (range 2-10 survey years). Nesting densities are also variable and multiple pairs can breed in close proximity. If multiple nests occurred with 20 meters of each other they were considered one territory and each nest status contributed to the number of active years for that territory.

Evaluating the trophic polymorphism hypothesis

Finally, the trophic polymorphism hypothesis is based on the idea that migratory animals track seasonal food resources (Loiselle and Blake 1991) but that individual feeding specialization (Bolnick *et al*. 2003, Arujo *et al*. 2011) will affect how individuals respond to seasonal changes in resources. Oystercatcher diets are composed primarily of limpets and mussels (Hartwick 1973, Robinson *et al*. 2018) but individual diets vary (Roodenrijs 2023). Marine invertebrates can respond to seasonal changes in the intertidal zone at high latitudes in two ways: i) behaviorally, by moving to buffered habitats, or ii) physiologically, by developing mechanisms to prevent intracellular freezing such as ice nucleating agents, antifreeze proteins or secretion of protective mucus's (Ansart and Vernon 2003). Limpets, which are mobile, have been reported to become more "cryptic" in Prince William Sound during winter months and researchers suggest a migration to the subtidal zone (Blechar and Feder 2000). Another study found limpets and other mobile invertebrates to be less abundant in January compared to May in Kachemak Bay (Patterson 2000). In contrast, sessile blue mussels have ice nucleating agents that allow them to withstand temperatures down to -10 degrees C (Aunaas, 1982a, Loomis 1991, Lundheim 1997, Patterson 2000). We quantified the proportion of limpets in the diet of Black Oystercatchers to evaluate whether migrants were selecting this seasonally variable prey.

To estimate the proportion of limpets in the diet of Black Oystercatchers we determined the carbon and nitrogen stable isotope composition of feathers and prey samples and used the Bayesian stable isotope mixing model MixSiar (Stock *et al*. 2018). Carbon and nitrogen stable isotope analysis took place at the Alaska Stable Isotope Facility at the University of Alaska, Fairbanks. Stable isotope signatures of prey varied among areas (Roodenrijs 2023), so we ran the mixing models separately for each of the four areas. We used area-specific source samples (mean ± SD) of the five prey items (mussel, limpet, chitons, snail, and clam) and included the individual identity of oystercatchers as a fixed effect in each model. We extracted and used the mean proportion of limpets in the diet of each individual in subsequent analyses. See Roodenrijs (2023) for additional details on the preparation of samples and statistical analysis of stable isotope data.

Statistical analysis

We used a Welch's t-test to compare the timing of fall departure from breeding territories (defined as a breeding home range bounding circle with a radius of 20 km or shift in 1° latitude) and spring arrival to breeding territories for migrants and residents. We used generalized linear models with a binomial distribution and logit link to examine how a PC1 body size score, adjusted mass, sex, territory quality, and proportion of limpet in the diet influenced the migratory behavior of an individual, defined as probability of migrating. Each explanatory variable was centered and standardized (Burnham and Anderson 2002). Due to limited sample size, we only constructed univariate models reflecting the five competing hypotheses (Table 2.1) and compared them using an information-theoretic framework and the Akiake's information criteria corrected for small sample sizes (AICc) (Burnham and Anderson 2002). Diet data (% limpets) were not available for two birds so we constructed two candidate model sets: i) a candidate set that excluded the 'trophic polymorphism' model (5 models, $n = 23$ individuals), and ii) a candidate set evaluating all five hypotheses (6 models, $n = 21$ individuals). An alternative approach to missing data is to use multiple imputation to predict the missing values based on other variables in the data. We performed multiple imputation using R package *mi* (Gelman *et al*. 2011) and reanalyzed the full set of univariate candidate models using the imputed dataset. Results from model selection using the imputed dataset did not differ from treating candidate model sets independently and is therefore not further discussed. We compared the support for models in each candidate set using the R package *AICcmodavg* (Mazerolle 2023) Following model comparison we assessed model goodness-of-fit using Nagelkerke's pseudo R^2 index (Nagelkerke 1991, Veall and Zimmerman 1994, Smith and McKenna 2013, Murray and Sandercock 2020). All statistical analyses were performed in program R (R Development Core Team 2023).

2.4. Results

Movement and migration patterns

We retrieved data on migration movements from 14 of 40 geolocators and nine of 33 GPS devices. Five geolocators contained movement data for multiple years. Geolocators provided 365 daily locations per year and GPS devices provided, on average 771 (range = 403-1449) locations on 128 days (range = 67-241) per year.

All the oystercatchers tracked moved away from their breeding territory at the end of the breeding season, but individuals differed in the distance that they travelled, the time of departure from their breeding territory and the time that they returned to their breeding territory the following year. Migration distances were bimodally distributed with some individuals travelling 20–220 km and others 930–1610 km (Fig. 2.1). We defined individuals travelling short distances (20–220 km) as residents and individuals travelling long distances (930–1610 km) as migrants. Of the 23 individuals tracked, 13 were classified as residents (3 females, 10 males) and 10 were classified as migrants (4 females, 6 males). The five birds tracked for more than one year were assigned the same strategy in each year (resident n = 5, migrant n = 0).

Resident and migratory individuals were documented at three of the four areas (Table 2.1). Residents remained at northern latitudes throughout the year with those from Prince William Sound remaining in the Sound for the winter, those from Kenai Fjords moving northeast to Prince William Sound and southwest to Afognak Island, those from Kachemak Bay remained in the Bay, and those from Katmai remaining close to the Katmai coast, moving east to Kodiak Island or north to Kachemak Bay (Fig. 2.2) Migrants moved to southern latitudes concentrated between 53 ° and 55 ° latitude. Migrants with breeding territories from Prince William Sound, Kenai Fjords, and Kachemak Bay migrated to islands and islets within the Hecate Strait off the coast of mainland British Columbia, Canada, near Prince Rupert (Fig. 2.2). Migratory birds tracked using GPS tags indicate birds follow the coast along the southeast panhandle of Alaska and British Columbia but can and do cross open water between Montague and Middleton Islands (Fig. 2.2).

Residents, individuals that remained in Alaska year-round, left their breeding season home ranges later than migrants. Residents also returned to their breeding season home ranges earlier than migrants. On average, migrants departed breeding home ranges 20 days before residents moved away from breeding home ranges (t = 3.02, df = 16.13, p = 0.008) and arrived back to breeding home ranges on average 10 days later than residents (t = -3.11, df = 18.03, p = 0.006) (Table 2.3).

Table 2.2. Total number of tracked Black Oystercatchers classified as migrants and residents from 2019-2022.

Site	Migrant	Resident	Total
Prince William Sound	1	3	4
Kenai Fjords National Park	6	4	10
Kachemak Bay	3	1	4
Katmai National Park and Preserve	0	5	5
Total	10	13	23

Table 2.3. Mean departure and arrival dates with 95% confidence intervals for each migratory strategy.

Strategy	Mean Departure Date (95% CI)	Mean Arrival Date (95% CI)
Migrant (n=10)	August 28 (Aug 22 – Sep. 3)	April 7 (Apr 3 – Apr 11)
Resident (n=13)	September 17 (Sep 3 – Sep 30)	March 28 (Mar 21 – Apr 3)

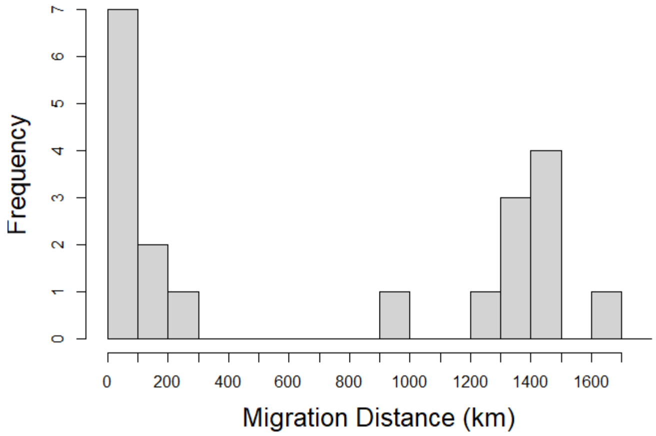

Figure 2.1. Distribution of estimated distances moved for 23 individual Black Oystercatchers carrying either a geolocator or GPS tracking device between the breeding (Apr-Sep) and nonbreeding periods (Oct-Mar) from 2019–2022.

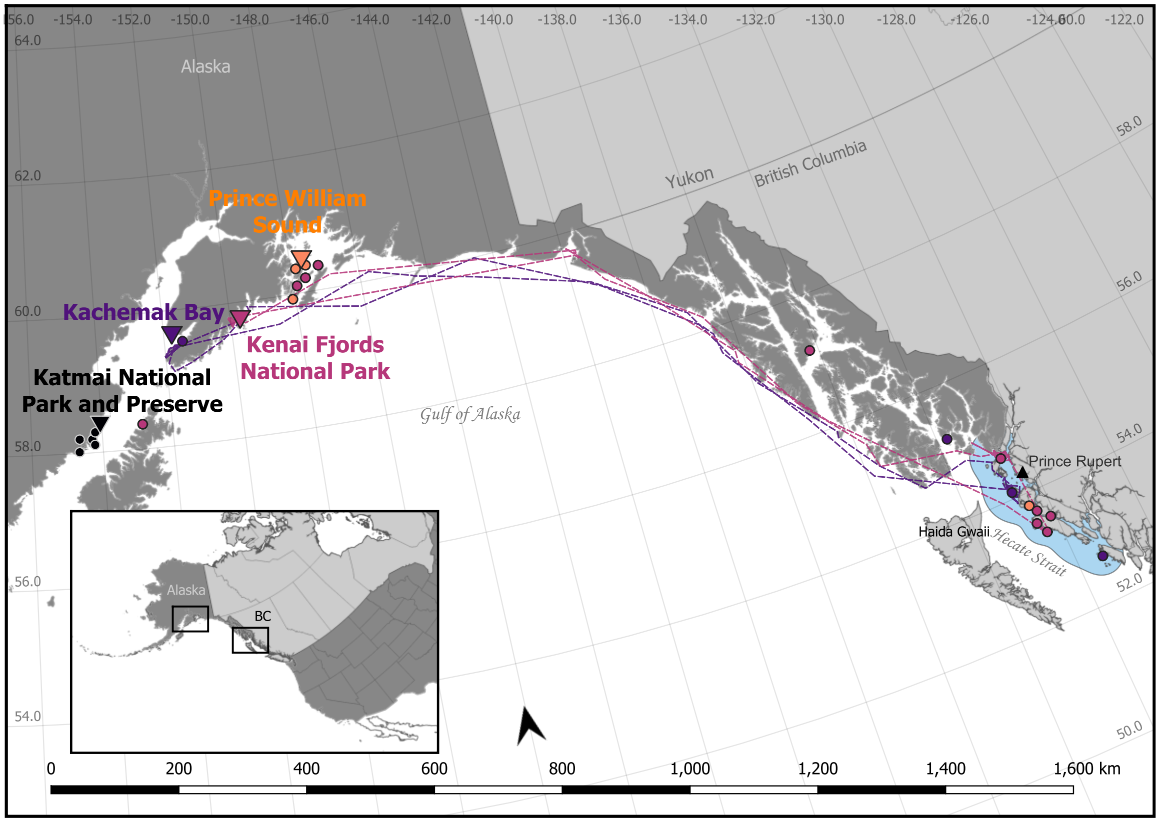

Figure 2.2. **Summary of movement patterns from 23 Black Oystercatchers captured across four study areas (triangles) from 2019-2022 (this study). Movements have been simplified for visual interpretation. Triangles represent general breeding locations (April-September) and our study areas (*n* = 4), and circles represent the centered location of movements during the non-breeding period (October-March) for each bird (*n* = 23). Colors connect breeding and non-breeding locations according to study area (Western Prince William Sound = orange, Kenai Fjords National Park = magenta, Kachemak Bay = purple, Katmai National Park and Preserve = black). Dotted lines indicate migration routes from two birds with GPS devices and are shown as examples. The blue polygon represents a non-breeding 95% kernel utilization distribution for GPS birds (*n* = 4) that migrated to British Columbia. The black triangle marks the location of Prince Rupert, British Columbia.**

Evaluating hypotheses for partial migration of Black Oystercatchers

Partial migration of Black Oystercatchers was best explained by the trophic polymorphism hypothesis. We found no evidence to support the thermal tolerance, fasting endurance, dominance, or arrival time hypotheses for partial migration. In the first candidate set, the best supported model included the condition term but, counter to the fasting endurance hypothesis, this model suggested that the probability of migration increased, not decreased, with adjusted body mass (Fig 2.3; Table 2.3; standardized β=0.04 (95% CI 0.0002-0.07)). The remaining models received less support than the null model. In the second candidate set, the best supported model included the diet term. This model, consistent with the trophic polymorphism hypothesis, suggested that the probability of migration increased as the proportion of limpets in an individual's diet increased (Fig 2.4; Table 2.3; (standardized β=1.2 (95% CI 0.09-2.95). This model received a similar level of support as the model that included the condition term and accounted for more variation in the data. Support for the two models was only partially explained by the relationship between diet and capture date-adjusted mass (r_s = 0.41, p = 0.07; Fig A.2). The remaining models received less support than the null model.

Table 2.4. Model selection results from two candidate sets assessing the influence of condition (total mass adjusted for capture date), sex, body size, territory quality, and diet (representing five hypotheses for partial migration) on migratory decisions of Black Oystercatchers. Candidate set 1 excludes a diet covariate representing the trophic polymorphism hypothesis because two birds lack diet data (*n* = 23). Candidate set 2 considers a smaller dataset and includes a diet covariate (*n* = 21). Bold models represent models with strong support (Δ_i < 2). Pseudo R^2 is Nagelkerke's approximation of percentage of variance accounted for.

Hypothesis	Model	K	AICc	Δ_i	w_i	Log-Likelihood	Pseudo-R^2
Candidate Set 1 (n = 23)							
Fasting Endurance	**condition**	**2**	**32.20**	**0.00**	**0.50**	**-13.80**	**0.21**
Null	**constant**	**1**	**33.68**	**1.48**	**0.24**	**-15.75**	**0.00**
Dominance	sex	2	35.33	3.13	0.10	-15.37	0.04
Thermal Tolerance	size	2	35.79	3.59	0.08	-15.60	0.02
Arrival Time	territory	2	35.99	3.79	0.08	-15.70	0.01
Candidate Set 2 (n = 21)							
Trophic Polymorphism	**diet**	**2**	**28.71**	**0.00**	**0.43**	**-12.02**	**0.27**
Fasting Endurance	**condition**	**2**	**29.48**	**0.77**	**0.29**	**-12.41**	**0.23**
Null	constant	1	30.89	2.18	0.14	-14.34	0.00
Dominance	sex	2	33.17	4.46	0.05	-14.25	0.01
Arrival Time	territory	2	33.28	4.57	0.04	-14.30	0.00
Thermal Tolerance	size	2	33.34	4.63	0.04	-14.34	0.00

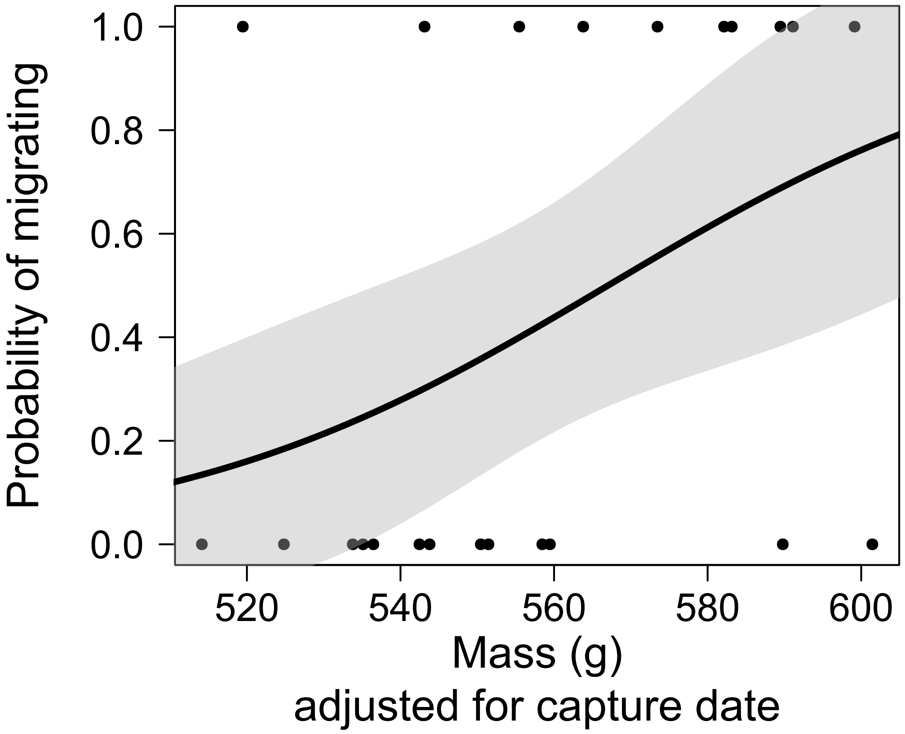

Figure 2.3. **The relationship between mass adjusted for capture date and the probability of migrating. The black circles represent field-measured mass of individual Black Oystrcatchers after controlling for capture date (*n* = 23) and the black solid line shows model predicted values with 95% confidence intervals (gray). Shown are values on the original scale of the variable, however, models were compared using scaled variables.**

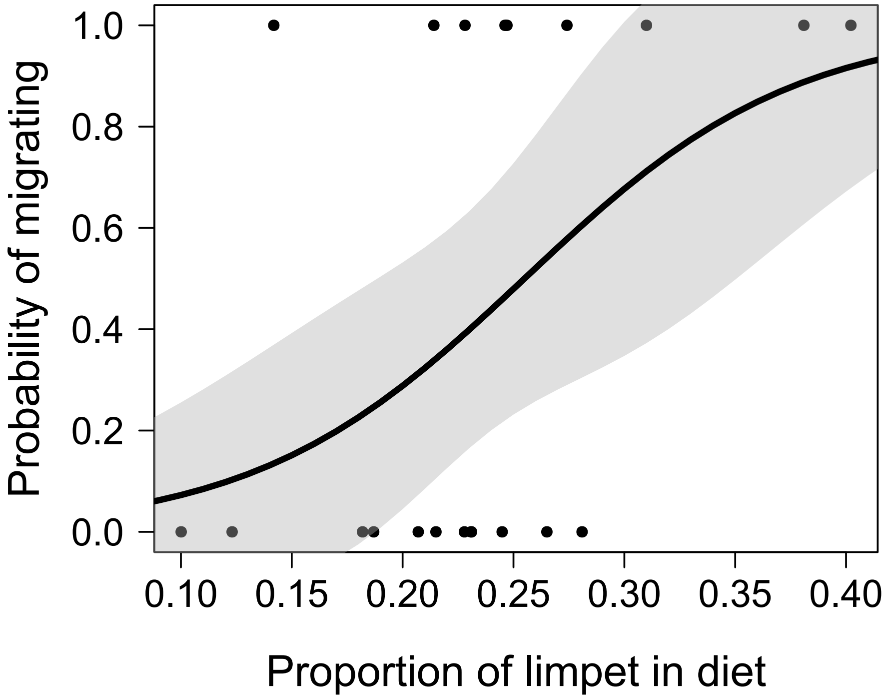

Figure 2.4. The relationship between the proportion of limpet in diet estimated from prey stable isotope data and the probability of migrating. Black circles represent mean values of limpet in the diet of each Black Oystercatcher (*n* = 21) and the black solid line shows model predicted values with 95% confidence intervals (gray). Shown are values on the original scale of the variable, however, models were compared using scaled variables.

2.5. Discussion

Black Oystercatchers exhibited a diversity of migratory strategies. Here we show that Black Oystercatchers breeding in the Gulf of Alaska either leave their breeding territories and migrate very short distances or embark on longer migrations up to 1600 km to British Columbia. Previous studies have demonstrated that Black Oystercatchers breeding on Kodiak Island, Alaska tracked using VHF-radio telemetry remain at or near their breeding territories year-round while Black Oystercatchers from Prince William Sound tracked using satellite transmitters migrated south to British Columbia (Johnson *et al*. 2010). Meanwhile, Black Oystercatchers breeding in Haida Gwaii, Pacific Rim and the Salish Sea, British Columbia tracked using Argos-PTT satellite tags maintain a small home range year-round (Ware *et al*. 2023). Here we show that variation in the migratory behaviour of Black Oystercatchers is dependent on their diet providing some of the first support for the trophic polymorphism hypothesis. Black Oystercatchers that consume more limpets, a prey species that are mobile and become less available in the winter, are more likely to migrate south and spend the non-breeding season in British Columbia.

The majority of the world's Black Oystercatchers are found in Alaska and British Columbia and studies have now tracked birds across a vast region of the Gulf of Alaska (southwest: Katmai National Park and Kodiak Island, southcentral: Kachemak Bay and Kenai Fjords National Park, northeast: western and eastern Prince William Sound, Middleton Island, and southeast: Juneau, AK) and the BC coast (central: Haida Gwaii, southern: Pacific Rim and the Salish Sea) (Fig 2.5). Johnson *et al*. (2010) provided the first detailed movements of Black Oystercatchers in the Gulf of Alaska using radio transmitters.

Tracking data from this study confirmed suspected patterns of oystercatcher movements and elucidates others. We confirm that Black Oystercatchers breeding in Alaska are partially migratory. Our data confirm that there are resident individuals in the southern portion of Prince William Sound (Johnson *et al*. 2010, Tessler *et al*. 2014) consisting of breeding individuals and short distance migrants from Kenai Fjords National Park. Our data also support a leapfrog migration pattern (Johnson *et al*. 2010). Migrants from Kachemak Bay (*n* = 2), one of our western most sites, but not the most northern, migrated the farthest, moving beyond residents in Prince William Sound and other migrants originating from Kenai Fjords and Prince William Sound (Fig 2.2). Fall and spring migration routes followed the coastline in the eastern Gulf of Alaska (e.g., southeast Alaska, northern British Columbia). However, some migration routes in the northern Gulf suggest offshore flights (Fig 2.2). One bird was recorded 77 km from mainland Alaska and 22 km from Middleton Island. Johnson *et al*. also documented offshore flights from Prince William Sound to Middleton Island, and Middleton Island to the shores of the northeast Gulf. These data, along with the rapid colonization of Middleton Island by Black Oystercatchers following Middleton Island's seismic uplift in 1964 (Gill *et al*. 2004), suggest offshore flights by oystercatchers are more common than previously appreciated. Johnson *et al*. demonstrate that migrants from Alaska distribute them themselves widely along the coast of British Columbia for the non-breeding season. Our data generally agree but we suggest that coastline between 53º–55º N within the Hecate Strait and near Prince Rupert, British Columbia is a particularly important non-breeding area for migrating oystercatchers (Fig. 2.5).

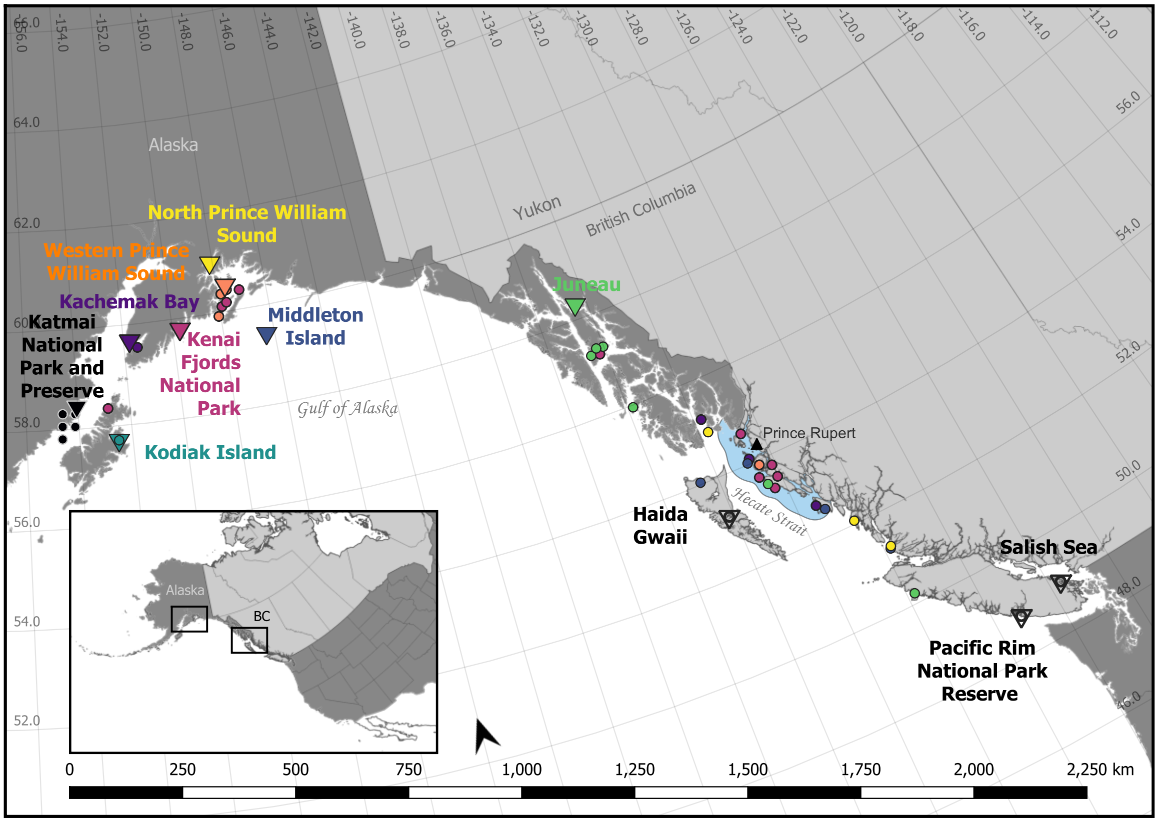

Figure 2.5. Summary of the movement patterns of Black Oystercatchers from this study (see Fig 2.2) and previous tracking studies (Johnson *et al*. 2010, Ware *et al*. 2023). Movements have been simplified for visual interpretation. Triangles represent general breeding locations and circles represent individuals at their centered movement locations during the non-breeding period. Additional study areas include North Prince William Sound (yellow), Middleton Island (blue), Kodiak Island (blue-green), and Juneau, AK (light green) (Johnson *et al*. 2010), and Haida Gwaii, Vancouver Island and Salish Sea (figures with black outline) (Ware *et al*. 2023). Circles inside or near triangles represent short movements.

Migratory strategies of individuals may depend on the degree to which individuals specialize on particular food resources and seasonal change in availability of those resources (i.e., the trophic polymorphism hypothesis). Comparative studies provide some support for this hypothesis (Boyle *et al*. 2011, Macpherson *et al*. 2023), but the hypothesis has rarely been evaluated when examining drivers of intra-specific variation in migratory behavior (Chapman *et al*. 2011). Aparicio (2000) recognized that seasonal variation in prey resource availability may influence migratory decisions in a population of partially migratory Eurasian Kestrels (*Falco tinnunculus*). The study quantified diet differences between migrants and residents, however, it did not test against, nor rule out, other factors influencing migratory decisions such as reproductive benefits from remaining on territories year-round (i.e., arrival time hypothesis). Here, we show that, as predicted by the trophic polymorphism hypothesis, Black Oystercatchers with more limpets in their diet at the end of the breeding season are more likely to migrate. Eurasian Oystercatchers are also partially migratory (Mendez *et al*. 2018), have a diverse diet (Dare 1966, Hulscher 1996) and can specialize on different prey types (Sutherland *et al*. 1996). However, the influence of diet on migration has not been evaluated in this species. In a recent study, partial migration of Eurasian Oystercatchers was not related to traits associated with sex or body size (Mendez *et al*. 2018). Instead, migratory status varied by geographic location within breeding areas in Iceland and young were likely to adopt their migratory strategy from their parents. Black Oystercatchers, and perhaps Eurasian Oystercatchers, may learn a feeding strategy at a young age, such as feeding on limpets, prefer that strategy into adulthood, and use seasonal changes in prey availability as a cue to migrate.

Migration allows individuals to escape the harsh conditions at high latitudes but imposes a cost as long-distance migration to low latitudes is energetically costly and is known to be a period of high mortality for some species (Adriaensn and Dhont 1990, Wikelski *et al*. 2003, Klassen *et al*. 2014, Lok *et al.* 2015). The thermal tolerance and fasting endurance hypothesis posit that structural size and fat resources, respectively, would allow larger and/or fatter individuals to better cope with harsh environmental conditions and remain on their breeding grounds and not pay a cost of migration. In contrast to early work on House Finches (*Haemorhous mexicanus*; Belthoff and Gauthreaux 1991) and recent work studying White-ruffed Manakins (*Corapipo altera*; Boyle 2008), Skylarks (*Alauda arvensis*; Hegemann *et al*. 2015) Yellow-eyed Juncos (*Junco phaeonotus*; Lundblad and Conway 2020), and Willow Ptarmigan (*Lagopus lagopus*; Arnekleiv et al. 2022), which support the prediction that larger birds remain as residents, we found that the thermal tolerance prediction in our system had little to no support (Table 2.3). Further, our results do not support the fasting endurance prediction where fatter–not larger–birds should remain as residents (e.g., White-ruffed Manakins: (Boyle 2008); kingbirds: (Jahn *et al*. 2011); Northern Flickers (*Colaptes auratus*): (Gow and Wiebe 2014); and Brown Pelicans (*Pelacanus occidentalis*): (Wilkinson and Jodice 2023). In fact, in stark contrast, we show that Black Oystercatchers with less fat reserves are more likely to remain in Alaska near breeding grounds year-round. This result could be in part because individuals with more limpets in their diet, which have a high energy density (Robinson *et al*. 2019), have more fat reserves. However, fat reserves may also be associated with the probability of migrating because migration is condition dependent. Condition dependent migration has been described in fish (Brodesrson *et al*. 2008) ungulates (Berg *et al*. 2019) and birds (Hegemann *et al*. 2015). In the present study, we did not have sufficient data to evaluate models combining multiple drivers of migration, but diet and condition may interact to contribute to the migration strategy of an oystercatcher. Factors that might affect condition during the breeding season with carry-over effects that influence migratory strategies include parental care (Goss-Costard 1996, Hegemann *et al.* 2013, Gow and Wiebe 2014) and/or pathogen pressure (Hegemann *et al*. 2015. Hegemann *et al*. 2019).

Seasonal changes in resource availability are also central to the dominance hypothesis which posits that only dominant individuals remain on their breeding grounds because the decline in food resources increases competition with conspecifics. Several studies have found evidence consistent with the dominance hypothesis (e.g. Blue Tit (*Parus caeruleus*): Smith and Nilsson 1987; European Blackbirds (*Turdus merula*): Lundberg 1985; Redstarts (*Phoenicurus phoenicurus*): Marra 2000; European Robins (*Erithacus rubecula*): Catry 2004). However, the evidence that males, that are dominant to and larger than females in these species, are less likely to migrate is also consistent with the thermal tolerance hypothesis and the arrival time hypothesis. Few studies, including ours, measure dominance directly or examine intraspecific competition for resources in the winter (but see Rogers et al. 1989; Cristol and Evers 1992, and Marra 2000). We found no evidence that male Black Oystercatchers that are thought to be more aggressive on territories, despite being smaller than females, are less likely to migrate. We also found no evidence that structurally large Black Oystercatchers that might be expected to have an advantage in intraspecific competition for resources in the winter are less likely to migrate. Although we were not able to track the movements of young individuals, the proportion of migrant and resident adults was approximately equal (Table 2.2), which suggests that migration is not determined by age. Although the dominance hypothesis was one of the first explanations for variation in migration strategies (Ketterson and Nolan 1976, Gauthreaux 1982), and causality supporting the prediction has been difficult to demonstrate in field, three lines of evidence in this study (e.g., sex, size, and age) suggest dominance does not influence migration.

The arrival time hypothesis was developed to explain the differential migration of male and female juncos and posited that males were expected to benefit from an early return to their breeding territory so they should not migrate as far as females (Ketterson and Nolan 1976). Several studies have now demonstrated that males do not migrate as far, males do return to their breeding territories before females, and males that return early obtain a fitness benefit (Myers 1981, Aebischer et al. 1996, Fudickar et al. 2013). We posited that individuals with high quality territories (i.e., those most likely to support breeding and have active nests) were more likely to remain as residents. This was a mechanistic prediction rather than a pattern confounded with sex or dominance effects. We found no support for this prediction. However, we found that residents departed later and arrived earlier than migrants (Table 2.3), which is consistent with the arrival time hypothesis, but it is not clear whether residents who return sooner obtain a fitness benefit. If individuals with the highest quality territories are not staying, perhaps individuals with intermediate territories are. One hypothesis proposed by Lundblad and Conway (2020) posits that the individuals of intermediate competitive ability gain the most by remaining on or near territories during the winter (competitive asymmetry hypothesis). The argument rests upon ‘prior residency’ effects (Cristol et al. 1990, Sandell and Smith 1991, Kokko 2006) where intermediate individuals are more competitive for a high quality territory the closer and longer they are around that territory. According to the competitive asymmetry hypothesis the most competitive individuals have the highest quality territories, can overcome prior residency effects, and can still migrate to avoid the cost of remaining resident in a harsh climate. If that high quality territory holder dies or is weak, the next bird with prior residency may take over. Indeed, only Eurasian Oystercatchers holding intermediate territories directly adjacent to high quality territories were successful at acquiring high quality territories (Ens *et al*. 1996). Additionally, nest success is negatively correlated with laying date in Eurasian Oystercatchers (Harris 1974) so there is an advantage to arrive early. Birds that hold an intermediate territory may benefit most from arriving early, or not leaving, by increasing their chance of acquiring a high-quality territory and/or starting nesting early to maximize reproductive benefits. However, an alternative explanation for this result is that those who specialize on limpets time their arrival with the accessibility of this resource in the intertidal. The potential cost of migrating and late arrival would then be compensated for with high quality food. Additional years of resighting and survey data from our marked population and a rapid habitat classification system applied to each territory may help resolve this.

This is one of the first studies to explicitly test and provide evidence in support of the trophic polymorphism hypothesis proposed to explain partial migration. Our results suggest that a migratory decision within a partially migratory population of Black Oystercatchers breeding in the Gulf of Alaska is partly driven by individual specialization on predation of limpets. Further, we did not find support for four other predictions made from common hypotheses in partial migration literature. Instead, we found support counter to the prediction posited by the fasting endurance hypothesis and found that the decision to migrate is condition dependent and those with less fat are more likely to forgo migration. The importance of diet and condition as drivers of migration raises interesting questions of whether dietary preferences are inherited from parents or reflect local prey availability, the phenotypic plasticity in the diet of individuals, and how diet and condition combine to determine migratory behaviour of Black Oystercatchers. We suggest three avenues for future work: (1) quantify Black Oystercatcher daily foraging activity, diversity of diet and prey availability during the non-breeding season to better understand the relationship between oystercatchers and limpets, (2) examine relationships between mass variation and migration strategy in terms of which is cause-and-effect, and (3) determine how migratory behaviour influences survival and reproductive success to evaluate whether migration is a conditional strategy where migrants are able to have the best of both worlds and residents are making the 'best at a bad job', or whether migration is an evolutionary stable strategy (ESS) with equal fitness payoffs (Lundberg 1987, 1988, Adriaensen and Dhont 1900, Kaitala *et al.* 1993, Gillis et al. 2008, Chapman *et al.* 2011). Insights from each avenue will aid in understanding the fitness balancing between each strategy and their role in the evolution and maintenance of migration in this system as well as others.

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Appendix. Chapter 2 Supplementary Material

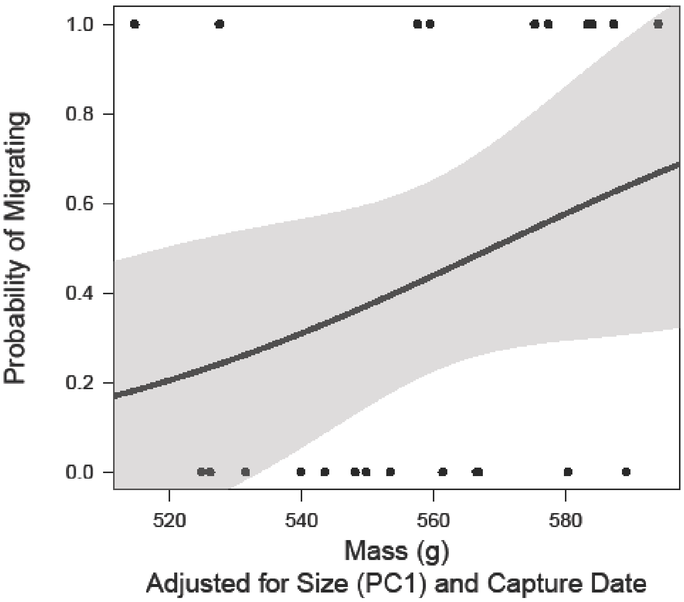

Figure A.1. The influence of mass taken in the field, adjusted for capture date and body size (PC1) on the probability of migrating. Black circles represent individuals and are the estimated residuals from mass on capture date and PC1 regression, and added to original mass values a from mean values of limpet for each oystercatcher (*n* = 21) and the black solid line shows model predicted values with 95% confidence intervals (gray). Figure depict variable son the original scale, however models were compared using scaled variables.

Table A.1. Model selection results from an analysis of condition (mass adjusted for capture date and body size (PC1)), sex, body size, and territory quality (representing four hypotheses for partial migration) influences on migratory decisions of black oystercatchers (*n* = 23).

Modnames	K	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt	R2
null	**1**	**33.68**	**0.00**	**1.00**	**0.34**	**-15.75**	**0.34**	**0.00**
condition	**2**	**34.02**	**0.34**	**0.85**	**0.29**	**-14.71**	**0.63**	**0.12**
sex	2	35.33	1.65	0.44	0.15	-15.37	0.77	0.04
size	2	35.79	2.11	0.35	0.12	-15.60	0.89	0.02
territory	2	35.99	2.31	0.32	0.11	-15.70	1.00	0.01

Table A.2. Model selection results from an analysis of diet, condition (mass adjusted for capture date and body size (PC1), sex, body size, and territory quality (representing five hypotheses for partial migration) influences on migratory decisions of black oystercatchers (*n* = 21).

Modnames	K	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt	R2
diet	**2**	**28.71**	**0.00**	**1.00**	**0.49**	**-12.02**	**0.49**	**0.27**
condition	**2**	**30.48**	**1.77**	**0.41**	**0.20**	**-12.91**	**0.69**	**0.17**
null	1	30.89	2.18	0.34	0.16	-14.34	0.85	0.00
sex	2	33.17	4.46	0.11	0.05	-14.25	0.90	0.01
territory	2	33.28	4.57	0.10	0.05	-14.30	0.95	0.00
size	2	33.34	4.63	0.10	0.05	-14.34	1.00	0.00

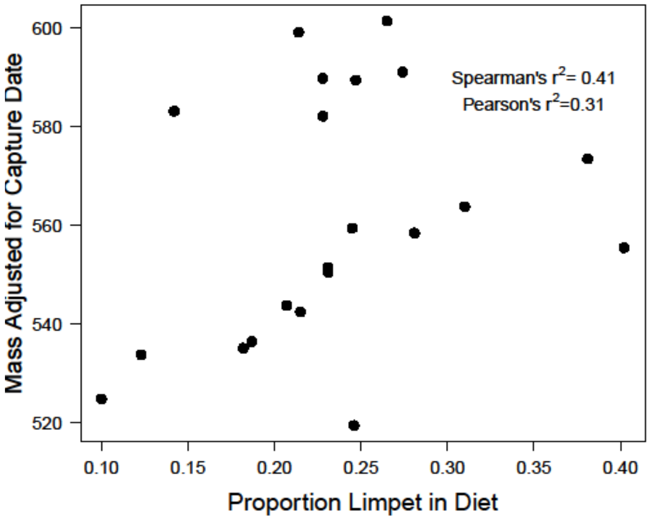

Figure A.2. The relationship between the amount of limpet in Black Oystercatcher diet and condtion measure as the mass taken in the field adjusted for capture date (May-July).