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Seasonal Movements, Winter Range Use, and Migratory Connectivity of the Black Oystercatcher (Movimientos Inter-Estacionales, Uso de áreas de Invernada y Conectividad Migratoria en *Haematopus bachmani*)

Author(s): Matthew Johnson, Peter Clarkson, Michael I. Goldstein, Susan M. Haig, Richard B. Lanctot, David F. Tessler, Denny Zwiefelhofer

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SEASONAL MOVEMENTS, WINTER RANGE USE, AND MIGRATORY CONNECTIVITY OF THE BLACK OYSTERCATCHER

MATTHEW JOHNSON^{1,7}, PETER CLARKSON², MICHAEL I. GOLDSTEIN³, SUSAN M. HAIG¹,
RICHARD B. LANCTOT⁴, DAVID F. TESSLER⁵, AND DENNY ZWIEFELHOFER^{6,8,9}

¹U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97330

²Pacific Rim National Park Reserve of Canada, P. O. Box 280, Ucluelet, BC V0R 3A0, Canada

³USDA Forest Service, Alaska Region, P. O. Box 21628, Juneau, AK 99802

⁴U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 E. Tudor Rd. MS 201, Anchorage AK 99503

⁵Alaska Department of Fish and Game, Division of Wildlife Conservation, 333 Raspberry Road, Anchorage, AK 99518

⁶U.S. Fish and Wildlife Service, Kodiak National Wildlife Refuge, 1390 Buskin Rd., Kodiak, AK 99615

Abstract. The Black Oystercatcher (*Haematopus bachmani*) is an intertidal obligate along North America's Pacific coast and a species of high conservation concern (population size 8900–11 000 individuals). Understanding birds' movements and space use throughout the annual cycle has become paramount in the face of changing environmental conditions, and intertidal species may be particularly vulnerable to habitat change due to anticipated sea-level rise associated with climate change and increasing coastal development. Conservation of the Black Oystercatcher is hindered by a lack of information on the species' nonbreeding distribution, seasonal movements, and habitat connectivity. Using satellite ($n = 19$) and VHF ($n = 19$) radio transmitters, we tracked Black Oystercatchers from five breeding sites (Vancouver Island, British Columbia; Kodiak Island, Prince William Sound, Middleton Island, and Juneau, Alaska) through one and one half annual cycles (May 2007–Dec 2008). We documented medium- to long-distance migration (range of migration distance 130–1667 km) in three populations (Prince William Sound, Middleton Island, and Juneau) and year-round residency in two others (Kodiak and Vancouver Island). We observed variation in the timing and length of migration by study site, and individual birds demonstrated fidelity to breeding and nonbreeding sites. We did not observe strong migratory connectivity. Migratory oystercatchers distributed themselves widely along the coasts of British Columbia and southeast Alaska during winter. Results provide baseline information on the Black Oystercatcher's movements and space use throughout the annual cycle.

Key words: Alaska, Black Oystercatcher, British Columbia, *Haematopus bachmani*, migration, migratory connectivity, satellite telemetry.

Movimientos Inter-Estacionales, Uso de Áreas de Invernada y Conectividad Migratoria en *Haematopus bachmani*

Resumen. El ostrero *Haematopus bachmani* está restringido al área intermareal de la costa del Pacífico de América del Norte y es una especie que causa alta preocupación desde la perspectiva de conservación (tamaño poblacional 8900–11000 individuos). Comprender los movimientos de los individuos y su uso del espacio a lo largo del ciclo anual se ha convertido en un asunto de vital importancia porque las especies intermareales pueden ser particularmente vulnerables a los cambios en las condiciones ambientales de los hábitats debidos a los aumentos en el nivel del mar que se anticipan con el cambio climático y al aumento en el desarrollo en las zonas costeras. La conservación de *H. bachmani* se ve limitada por la falta de información sobre la distribución no reproductiva de la especie, sobre movimientos estacionales y sobre conectividad del hábitat. Empleando transmisores de satélite ($n = 19$) y de radio VHF ($n = 19$), seguimos a individuos de la especie provenientes de cinco sitios reproductivos (Vancouver Island, British Columbia; Kodiak Island, Prince William Sound, Middleton Island y Juneau, Alaska) durante un ciclo anual y medio (mayo de 2007 a diciembre de 2008). Documentamos migración a distancias medias y largas (rango de distancia de migración 130–1667 km) en tres poblaciones (Prince William Sound, Middleton Island y Juneau) y residencia a lo largo del año en otras dos (Kodiak y Vancouver Island). Observamos variación entre sitios de estudio en el momento en que tuvo lugar la migración y en su extensión, y los individuos demostraron fidelidad a los sitios reproductivos y no reproductivos. No observamos una conectividad migratoria fuerte. Los ostreros migratorios se distribuyeron ampliamente en las costas de British Columbia y del sureste de Alaska durante el invierno. Los resultados brindan información básica sobre los movimientos y el uso del espacio por parte de *H. bachmani* a lo largo de su ciclo anual.

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⁷E-mail: matthew_johnson@usgs.gov

⁸Current address: P. O. Box 2100, Kodiak, AK 99615.

⁹Co-authors are listed alphabetically.

INTRODUCTION

The importance of understanding birds' space use and movement patterns throughout the annual cycle has gained prominence over the past 20 years (Haig et al. 1997, 1998, 2002, Webster et al. 2002, Marra et al. 2006). Further development of tracking technologies such as satellite transmitters, geolocators, molecular markers, trace elements, and stable isotopes has resulted in an explosion of research aimed at understanding avian life histories in a more complete way (Gill et al. 2008, Szep et al. 2009, Carlisle et al. 2009). The Black Oystercatcher (*Haematopus bachmani*) is a relatively large (500–700 g), long-lived (15+ years) shorebird of the family Haematopodidae which occurs along North America's Pacific coast from the Aleutian Islands to Baja California (Andres and Falxa 1995, Tessler et al. 2007). As an intertidal obligate, the Black Oystercatcher is dependent year round on marine shorelines, where its invertebrate prey, including primarily bivalves and other mollusks (limpets, whelks, and chitons), are abundant (Jehl 1985). The Black Oystercatcher is a species of high conservation concern throughout its range because of its small population size (8900–11 000 individuals) and threats to the birds and their coastal habitats throughout the annual cycle (Donaldson et al. 2000, Drut and Buchanan 2000, Brown et al. 2001, Hickey et al. 2003, USSCP 2004, Tessler et al. 2007). Despite concern for this species, little information exists on locations of important wintering areas, migration pathways, or the degree of connectivity among breeding, migration, and nonbreeding sites. Determining the nonbreeding distribution and migratory connectivity between breeding and nonbreeding areas was identified as a rangewide priority in the Conservation Action Plan for the Black Oystercatcher (Tessler et al. 2007).

The Black Oystercatcher is socially monogamous with biparental care of two or three eggs and young. Its rates of fidelity to a mate and breeding site are high (Andres and Falxa 1995, Hazlitt and Butler 2001, Morse et al. 2006, Spiegel 2008). Post-breeding birds generally concentrate in winter flocks ranging from a few to several hundred individuals (Andres and Falxa 1995), although in California some pairs maintain territories year round (Helbing 1977, Jehl 1985). In the southern portion of the range (Washington, Oregon, and California) some post-breeding birds are thought to make short-distance movements coincident with winter flock formation and remain relatively close to breeding areas (Nysewander 1977, Hartwick and Blaylock 1979, Falxa 1992). Likewise, the similarity of counts during summer and winter suggests that birds in Pacific Rim National Park, Vancouver Island, Canada, also are nonmigratory (P. Clarkson, unpubl. data). Among northern breeding populations in Alaska, however, the species' migratory behavior appears to be variable. Black Oystercatchers that breed in Alaska may undertake long-distance movements or be year-round residents. Formation of post-breeding flocks and subsequent departure from Prince William Sound and Glacier Bay National Park indicate that some Black Oystercatchers that

breed in Alaska abandon breeding areas in the winter (Wik and Streveler 1967, Andres and Falxa 1995, van Vliet 2005). Repeated winter surveys of Middleton Island, Alaska, found none of the approximately 700 oystercatchers present during the breeding season (Gill et al. 2004, Tessler et al. 2007). A winter survey in Prince William Sound detected only 25% of Black Oystercatchers that bred there during summer (Andres 1994). Furthermore, three Black Oystercatchers (one adult in 2004 and two chicks in 2005) banded in Alaska (Middleton Island, Glacier Bay and Kenai Fjords national parks, respectively) were resighted during winter 2006 in British Columbia, Canada (adult and unrelated young on Vancouver Island, immature on Queen Charlotte Islands; Tessler et al. 2007). Although two of these observations may represent natal dispersal and not migration, they all suggest large-scale movements. In contrast, winter and summer surveys of Kodiak Island, Alaska, each produced approximately 1700 oystercatchers, suggesting a resident population (Tessler et al. 2007).

Knowledge of migratory connectivity, the geographic linkage of individuals or populations at different stages of the annual cycle, is essential for effective monitoring and conservation of wildlife (Webster et al. 2002). Across its range, patterns of movement of migratory populations of the closely related Eurasian Oystercatcher (*H. ostralegus*) are complex. For some breeding populations, migratory connectivity is strong (most individuals from one breeding population move to the same nonbreeding site), but for others it is weak (individuals from a single breeding population migrate to different overwintering sites throughout the nonbreeding range; Dare 1970, Hulscher et al. 1996). Although approximately 65% of all Black Oystercatchers breed along the coast of southern Alaska (Andres and Falxa 1995), many of these individuals likely spend less than half the year on the breeding grounds before migrating to unknown wintering sites (Brown et al. 2001). Therefore, we need to consider how events in one stage of the annual cycle may interact with and influence subsequent events. For example, if the Black Oystercatcher's migratory connectivity is strong, then variation among breeding populations in adults' survival rates could indicate site-specific factors within or outside of the breeding season. In contrast, if survival rates at various breeding sites differ and migratory connectivity is weak, factors potentially influencing survival are more likely specific to breeding sites.

We report results from a large-scale international collaborative study designed to clarify the Black Oystercatcher's seasonal movements, its winter range, and migratory connectivity between breeding and nonbreeding sites. We used satellite and VHF telemetry to track individuals throughout the annual cycle. Use of newly available 27-g implantable satellite transmitters with percutaneous antennas in the Charadriiformes has been reported only once before (Gill et al. 2008). We tested several hypotheses by equipping and tracking oystercatchers in various portions of the range where the species was or was not thought to be migratory. First, on the

basis of observations of birds year round, we hypothesized that oystercatchers breeding on Kodiak Island, Alaska, and Vancouver Island, British Columbia, remain in the area through the winter. Second, from the absence of birds elsewhere in southern Alaska during the winter, we hypothesized that oystercatchers breeding in these areas migrate. Third, on the basis of the level of migratory connectivity (moderate to strong) reported for Eurasian Oystercatchers breeding in Europe (Dare 1970, Hulscher et al. 1996), we hypothesized that Black Oystercatchers breeding in different regions should remain segregated after migrating to their winter ranges (i.e., exhibit strong migratory connectivity). In addition to testing these hypotheses, we describe the timing of migration, migration routes, and final wintering areas of different breeding populations that migrate from Alaska.

METHODS

We studied seasonal movements of four populations of Black Oystercatchers breeding in southern Alaska (Harriman and College fjords in Prince William Sound, 61° 1' N, 148° 5' W;

Middleton Island in the Gulf of Alaska, 59° 26' N, 146° 20' W; on and near Portland Island near Juneau, 58° 20' N, 134° 44' W; Women's Bay, Kodiak Island, 57° 43' N, 152° 31' W) and one along a portion of the west coast of Vancouver Island, British Columbia, Canada (Vargas Island south to Barkley Sound, 49° 4' N, 125° 51' W; Fig. 1). We captured incubating oystercatchers on their nesting territories with noose mats, nest nooses, and walk-in traps. We marked all captured birds with U.S. Geological Survey bands and with unique UV-stable color bands. During banding, we sexed them by eye flecks and verified these assignments with molecular methods (Guzzetti et al. 2008, USGS Alaska Science Center Molecular Ecology Laboratory).

We attached 12-g VHF radio transmitters (Holohil Systems, Ltd., Carp, Ontario) equipped with mortality switches (transmitter stationary for ≥ 12 hr) to oystercatchers breeding on Kodiak and Vancouver Island with a standard backpack harness (Sanzenbacher et al. 2000) of Teflon tape (Bally Ribbon Mills, Bally, PA). We chose not to attach satellite transmitters (which would be better for documenting long-distance migration) to these populations because prior survey work indicated

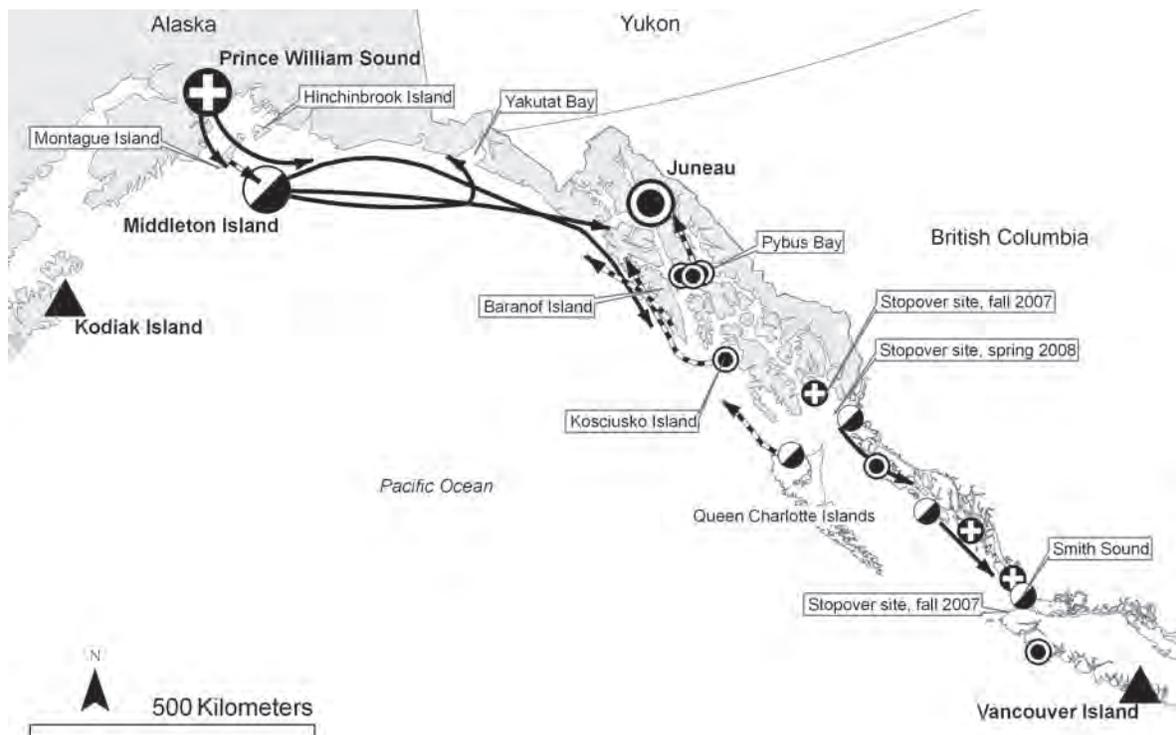


FIGURE 1. Breeding sites (large circular symbols with unique interior design), nonbreeding sites (small circular symbols with interiors that correspond with breeding sites), migration stopover sites, and migratory pathways used during fall 2007 (solid lines with arrows) and spring 2008 (dashed lines with arrows) by Black Oystercatchers implanted with satellite transmitters at three breeding sites in southern Alaska (Prince William Sound, Middleton Island, and Juneau, $n = 6$ per site). Fourteen PTTs were active (transmitting data) at the start of fall migration 2007, and eight of these transmitted location data while oystercatchers were in transit during fall migration 2007. Thirteen PTTs transmitted data sufficient for us to determine where Black Oystercatchers carrying these units spent the nonbreeding season (2007–2008), and five PTT-tagged oystercatchers transmitted location data while migrating during spring 2008. Large triangles indicate study sites where we equipped Black Oystercatchers with VHF transmitters to track movements (Kodiak and Vancouver islands).

oystercatchers likely remained in these areas year round. Radio transmitters weighed approximately 2% (range 1.8–2.2%) of the average body mass of birds used in this study (mean \pm SE body mass of Black Oystercatchers carrying a VHF transmitter 602 ± 9 g), which is well below the 5% recommended by Gaunt et al. (1997). We applied the radio transmitters on site and released birds back onto their nesting territories (~20 min handling time). When logistically possible we surveyed for VHF-tagged oystercatchers at least once every 2 weeks by land, boat, and air from June 2007 to May 2008 (search area on Kodiak Island 2000 km² by airplane, 250 km² by boat; search area on Vancouver Island 300 km² by land). During surveys, we also attempted to verify the location of radio-equipped oystercatchers via color bands and used the approximate source of VHF radio signals as the bird's location when color bands were not observable. We attempted to locate the carcass or shed transmitter as soon as we detected a mortality signal.

Using established techniques (Korschgen et al. 1996, Mulcahy and Esler 1999), a specially trained field veterinarian surgically implanted 27-g satellite platform transmitting terminals (PTT) (Microwave Telemetry, Inc., Columbia, MD) with percutaneous antennas into the coelomic cavities of oystercatchers breeding on Middleton Island, in Prince William Sound, and near Juneau, Alaska. Prior work indicated that oystercatchers in these populations did leave the area, requiring a tracking platform that could provide location data via remote means. In this study, we induced anesthesia with a 0.4- to 1.0-mL (0.7–1.9 mg kg⁻¹) bolus of propofol (Abbott Laboratories, North Chicago, IL) delivered intravenously through a 25-ga \times 1-cm butterfly catheter (Abbott Laboratories) placed in the medial metatarsal vein. Additional boluses of 1.0–2.7 mL (1.8–4.8 mg kg⁻¹) were given throughout surgery to maintain anesthesia. We provided local analgesia at the sites of the incision and the antenna's exit by subcutaneous and intramuscular infiltration of a total of 0.4–1.0 mL (0.7–1.8 mg kg⁻¹) of a 2:1 mixture (total concentration of 1 mg mL⁻¹) of bupivacaine HCl (Abbott Laboratories) and lidocaine HCl (Abbott Laboratories). Satellite transmitters were implanted into the right abdominal air sac by sterile techniques and weighed <5% (range 4.2–4.9%) of the birds' average body mass (mean \pm SE body mass of Black Oystercatchers carrying a PTT transmitter 586 ± 7 g). We released PTT-implanted birds at their nesting territories after they were fully awake and recovered from anesthesia (within 2 hr after capture in most cases). We programmed PTTs to transmit location information to satellites (duty cycle) for 6 consecutive hours every 96 hr until the end of the battery's life.

We defined fall migration as the period between when oystercatchers departed their breeding sites toward the south and when birds stopped moving consistently south from breeding sites and all locations recorded through three consecutive PTT duty cycles were ≤ 15 km apart. We defined spring migration as the period between when oystercatchers started

moving consistently north >15 km from their nonbreeding area until they returned to their breeding site. We considered all locations between termination of fall migration and initiation of spring migration to encompass a bird's nonbreeding site. During migration, we considered a site a stopover when the bird was not moving through the area in a consistent direction (south or north), all location data during a PTT's duty cycle were concentrated at a single site (e.g., cove, bay, or islet), and the bird was not at its breeding or nonbreeding site.

At our Prince William Sound study site, we assessed breeding activity of oystercatchers implanted with PTTs by revisiting nesting territories between 17 May and 26 June 2008. We surveyed nesting territories weekly and recorded the presence or absence of marked individuals and evidence of nesting.

STATISTICAL ANALYSES

CLS America, Inc. (Largo, MD), calculated and distributed PTT location data, which included an index of accuracy and data from sensors that track the bird's body temperature and the battery's voltage (Argos 1996). To track oystercatchers, we used both standard and auxiliary qualities of location class from CLS America. Standard location classes (LC 3, 2, and 1) have estimated error radii of 250, 500, and 1500 m, respectively, whereas accuracy of the auxiliary location classes (LC 0, A, B, and Z) is highly variable and not quantified by CLS America. We used a systematic filtering algorithm to remove improbable auxiliary locations (Douglas 2009), retaining auxiliary locations within 10 km of a preceding or subsequent location by virtue of their spatial redundancy. We retained the remaining auxiliary locations only if they implied movement of <70 km hr⁻¹ and the internal angles formed by preceding and subsequent movement vectors were >60°. Given the spatial scales under investigation, this filtering approach is suitable for establishing and analyzing long-distance movements and habitat use (Phillips et al. 2006, Gill et al. 2008).

We plotted and quantified location data from VHF- and PTT-tagged oystercatchers with ArcGIS software (ESRI 2007). For the PTT-tagged oystercatchers, we calculated the minimum length of migration with the standard orthodrome (great circle) formula from the nest site to the centroid of all nonbreeding locations. We recorded departure and arrival dates from breeding and nonbreeding sites if a PTT transmitted as the bird departed on or terminated migration. Otherwise, we used the date subsequent to a bird's last transmission at a site (breeding or nonbreeding) to estimate departure and the date preceding a bird's first transmission at a site (breeding or nonbreeding) to estimate arrival. Estimated departure and arrival date may vary from true departure and arrival date by 1–3 days, depending on when the bird departed or arrived during the PTT's duty cycle. We used Kruskal–Wallis and Wilcoxon–Mann–Whitney tests to compare the timing and length of migration of migratory breeding populations (Zar 1999) and report means \pm SD.

RESULTS

OYSTERCATCHERS EQUIPPED WITH VHF TRANSMITTERS

We attached VHF transmitters to eight females and two males at 10 nests on Vancouver Island between 22 May and 1 August 2007 and to five males and four females at five nests on Kodiak Island on 8 and 9 June 2007. We subsequently detected VHF-tagged Black Oystercatchers on 93 occasions on Vancouver Island and on 73 occasions on Kodiak Island between June 2007 and May 2008. Although weather hindered winter survey efforts at both sites, we tracked 12 (63%) VHF-tagged oystercatchers through October and 10 (53%) through November 2007 ($n = 19$, Fig. 2). For VHF-tagged oystercatchers not accounted for during our October ($n = 7$) and November ($n = 9$) 2007 surveys, the activation of mortality switches on the transmitters allowed us to determine that 6 (86%) and 7 (78%) of these birds, respectively, had either shed their transmitters or died. One transmitter was recovered on Vancouver Island under a perch where a Bald Eagle (*Haliaeetus leucocephalus*) fed. We could not, however, locate any Black Oystercatcher remains near the site. From inspection of recovered transmitters and subsequent observations of birds that had lost their radios, we do not suspect that any other birds died when a transmitter's mortality switch was activated. Rather, it appeared that the oystercatchers had slipped out of or cut through the material of the leg-loop harnesses.

During our final surveys in April and May 2008, we detected 14 (74%, $n = 19$) VHF-tagged oystercatchers visually by their color bands even though 16 individuals were no longer carrying the transmitters (Fig. 2). Although we surveyed for VHF-tagged Black Oystercatchers over considerably larger areas (2000 km² by airplane and 250 km² by boat on Kodiak Island; 300 km² by land on Vancouver Island), at no time did we detect VHF-tagged birds >15 km from nesting sites.

OYSTERCATCHERS EQUIPPED WITH SATELLITE (PTT) TRANSMITTERS

Between 26 May and 4 June 2007, we surgically implanted PTTs in nine female and 10 male Black Oystercatchers from 18 nests at three sites in southern Alaska (Table 1). The first individual that we implanted with a PTT, a male breeding on Middleton Island, died after the surgery before being released. We observed all but two of the remaining birds incubating within 24 hr after the procedure. Sensors indicated that three individuals implanted with a PTT died during tracking (16.6%, $n = 18$), and one PTT implanted in a female that bred in Prince William Sound never transmitted data following the bird's release; this female was not observed subsequently (fate unknown, Table 1). The three documented mortalities were at the first and second study sites where we implanted PTTs in 2007, Middleton Island and Prince William Sound, respectively (Table 1). A female breeding on Middleton Island died

41–44 days after implantation. In Prince William Sound, one male died 60 days after implantation but before it initiated fall migration, and another male completed fall migration and died on the nonbreeding grounds 173 days after implantation. For PTTs transmitting until battery failure ($n = 14$ of 18; i.e., bird carrying the unit did not die or meet with unknown fate), the transmitter's average life was 11 ± 6 months (range 2–18, Table 1), resulting in the recovery of a mean of 419 ± 211 locations per PTT. Of the 6243 total locations recovered during this study, 4329 were standard locations that were always retained, whereas 8% of 1914 auxiliary locations were removed with our filtering algorithm, leaving a total of 6094 locations for analyses.

Fall migration 2007. Fourteen PTTs were active (i.e., transmitting data) at the start of fall migration 2007 (Table 1). PTT-tagged Black Oystercatchers departed the breeding grounds between 3 August and 6 November 2007. Departure dates for fall migration 2007 differed significantly by study site ($\chi^2_2 = 9.6$, $P = 0.008$) on a latitudinal gradient, the most northern breeding birds (Prince William Sound) departing earliest and the most southern breeding birds (Juneau) departing latest (Table 2). Post-hoc comparisons revealed that departure dates for fall migration 2007 from all three study sites differed (Prince William Sound vs. Middleton Island, $z = 2.09$, $P = 0.02$, $n = 8$; Prince William Sound vs. Juneau, $z = 2.19$, $P = 0.01$, $n = 9$; Middleton Island vs. Juneau, $z = 2.1$, $P = 0.02$, $n = 11$). Eight PTT-tagged oystercatchers transmitted location data while in transit during fall migration 2007 (Fig. 1; black arrows and stopover sites, fall 2007), while the remaining six birds carrying active PTTs migrated from breeding to nonbreeding sites during the 96-hr off-duty portion of the PTT's duty cycle when it was not transmitting location data to satellites (96 out of every 102 hr). Seven PTT-tagged oystercatchers were tracked while flying south (Fig. 1, black arrows), and one PTT-tagged female that bred near Juneau transmitted location data from two stopover sites (Duke Island, Alaska, and Vancouver Island), although not while in flight, before arriving at her nonbreeding site on the west coast of Vancouver Island (Fig. 1; stopover sites, fall 2007). This PTT-tagged female transmitted location data for a single duty cycle (6 out of every 102 hr) at each of these stopover sites. Birds generally traveled a coastal route toward nonbreeding sites (Fig. 1, black arrows). Two flew over Montague Island as they departed Prince William Sound toward the east-southeast, and three birds departed Middleton Island east-southeast before heading farther south (Fig. 1). One bird departing Middleton Island initially made landfall near the mouth of Yakutat Bay, Alaska, before its PTT battery failed (Fig. 1). Latitudinal variation in the timing of fall migration also was evident in dates of arrival at nonbreeding sites. The most northern breeding birds (Prince William Sound) arrived earliest; the most southern breeding birds (Juneau) arrived latest ($\chi^2_2 = 8.4$, $P = 0.02$, Table 2). Post-hoc

Proportion of marked Black Oystercatchers

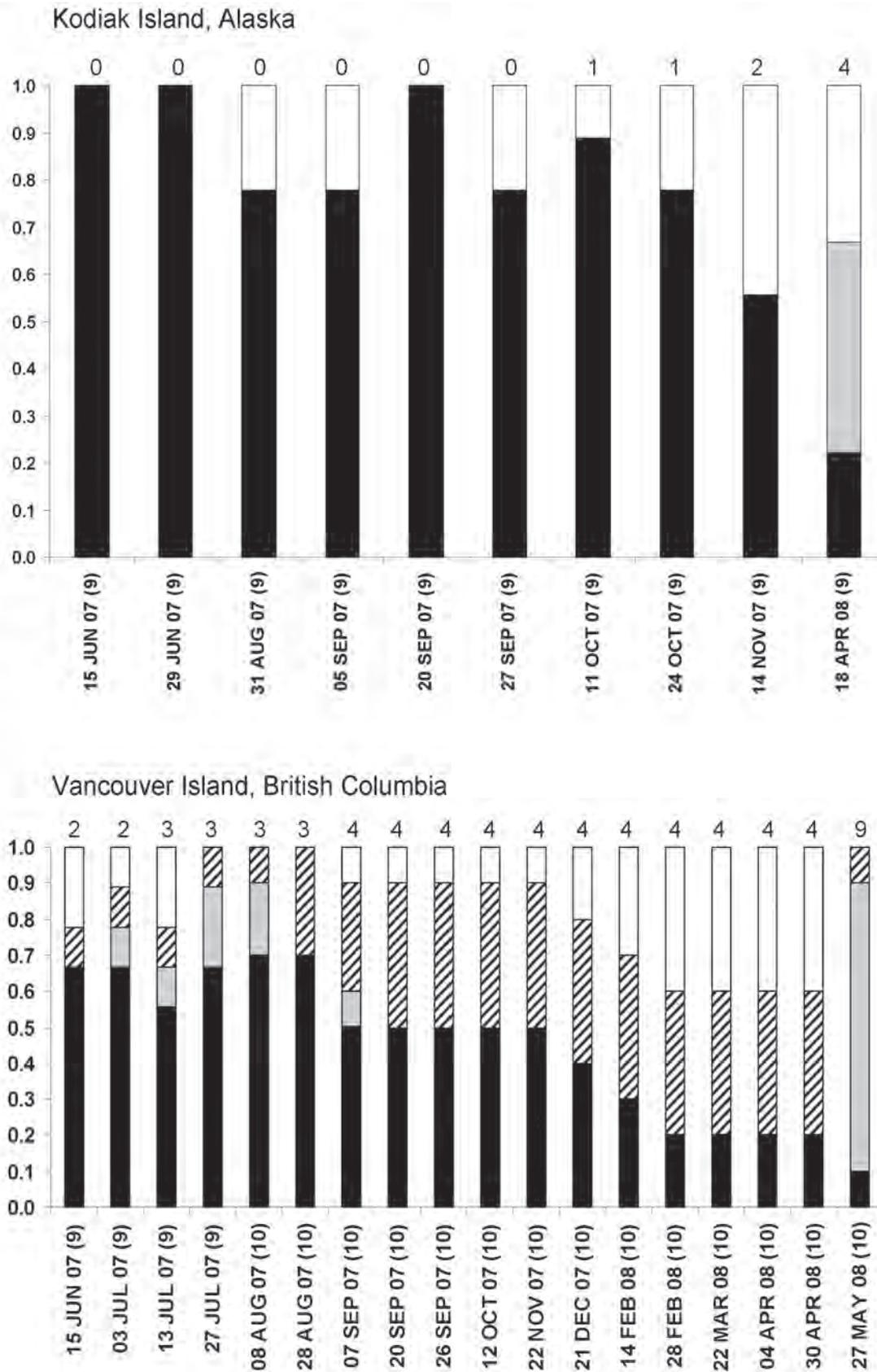


FIGURE 2. Proportion of Black Oystercatchers detected via VHF transmitters (black bars) or colored leg bands (gray bars) during surveys (15 June 2007–27 May 2008) on Kodiak Island, Alaska, and Vancouver Island, British Columbia. Hatched bars represent individuals that were not surveyed for; white bars represent individuals not detected during surveys. Numbers in parentheses after survey dates indicate total number of individuals marked with a VHF transmitter, and numbers above bars indicate the total number of individuals that shed the VHF transmitter.

TABLE 1. Transmitter and bird fates for Black Oystercatchers implanted (May–June 2007) with satellite transmitters at three breeding sites in southern Alaska. Number of Black Oystercatchers (females:males) carrying functional transmitters at the beginning of each season and year are given in parentheses.

Stage of annual cycle (year) ^a	Breeding sites (n_{females} : n_{males})		
	Prince William Sound	Middleton Island	Juneau
Breeding season (2007)	Jun–Aug (3:3)	Jun–Aug (3:3)	Jun–Nov (3:3)
Battery failure	1	0	0
Bird died	1	1 ^b	0
Unknown	1	0	0
Fall migration (2007)	Aug (2:1)	Aug–Sep (2:3)	Sep–Nov (3:3)
Battery failure	0	1	0
Nonbreeding season (2007–2008)	Aug–Dec (2:1)	Sep–Mar (1:3)	Sep–Feb (3:3)
Battery failure	2	1	1
Bird died	1	0	0
Breeding season (2008)	(0:0)	Apr–Aug (0:3)	Mar–Aug (2:3)
Battery failure	0	0	4
Nonbreeding season (2008–2009)	(0:0)	Sep–Dec (0:3)	Sep–Dec (0:1)
Battery failure	0	3	1

^aSpring and fall migration (2008) are not listed as no birds died and no batteries failed during these periods.

^bAn additional bird (male) was not released and tracked because it died immediately following completion of the implantation surgery.

comparisons revealed that arrival dates at nonbreeding sites of birds tagged at all three study sites differed (Prince William Sound vs. Middleton Island, $z = 1.94$, $P = 0.03$, $n = 7$; Prince William Sound vs. Juneau, $z = 2.19$, $P = 0.01$, $n = 9$; Middleton Island vs. Juneau, $z = 1.71$, $P = 0.04$, $n = 10$). Furthermore, the length of migration varied latitudinally ($\chi^2_2 = 8.9$, $P = 0.01$) with northern breeding Black Oystercatchers traveling greater distances than did more southern breeding birds (Table 2, Fig. 1). Post-hoc comparisons revealed that the length of migration from Juneau and that from the two more northern breeding sites differed (Prince William Sound, $z = 2.19$, $P = 0.01$, $n = 9$; Middleton Island, $z = 2.24$, $P = 0.01$,

$n = 10$) but that from Prince William Sound and Middleton Island did not ($z = 1.24$, $P = 0.11$, $n = 7$). However, the small samples from Prince William Sound and Middleton Island may not provide power sufficient to detect statistically significant differences in migration length between these more northern breeding sites. As migrants generally followed a coastal route and we calculated migration length by the standard orthodrome (great circle) formula, our estimates of migration length actually represent minimums. Despite this bias, differences among breeding populations in the true length of migration should be proportional to our estimates or exacerbated by migrants following coastal paths.

TABLE 2. Mean (\pm SD) departure and arrival dates and distance of migration (from capture site to final nonbreeding site) for Black Oystercatchers implanted with satellite transmitters at three breeding sites in southern Alaska. Sample sizes shown in parentheses.

	Breeding site		
	Juneau	Middleton Island	Prince William Sound
2007 Fall migration			
Departure date	02 Oct \pm 22 (6)	08 Sep \pm 10 (5)	16 Aug \pm 11 (3)
Arrival date	09 Oct \pm 21 (6)	14 Sep \pm 9 (4)	24 Aug \pm 9 (3)
2008 Fall migration			
Departure date	16 Sep (1)	08 Sep \pm 10 (3)	—
Arrival date	19 Sep (1)	14 Sep \pm 15 (3)	—
2008 Spring migration			
Departure date	21 Mar \pm 14 (5)	01 Apr \pm 1 (3)	—
Arrival date	24 Mar \pm 13 (5)	06 Apr \pm 4 (3)	—
Migration length in 2007 (km)	383 \pm 363 (6)	1224 \pm 204 (4)	1483 \pm 234 (3)

Range use during the nonbreeding season. Thirteen PTTs transmitted data sufficient for us to determine where Black Oystercatchers carrying these units spent the nonbreeding season (Table 1). Five of these birds migrated to southeast Alaska (four birds tagged at Juneau and one that bred in Prince William Sound), and eight (two tagged in Prince William Sound, three at Middleton Island, and three at Juneau) spent the nonbreeding season in British Columbia (Fig. 1). For the five Black Oystercatchers that spent the nonbreeding season in Alaska, two males and a female that bred near Juneau spent the nonbreeding season near the mouth of Pybus Bay on the southern tip of Admiralty Island, Alaska (Fig. 1). Two of these birds were paired in 2007; however, this pair did not migrate together. Males arrived at Pybus Bay on 14 and 21 September, and the female arrived on 9 October. Of the eight Black Oystercatchers that spent the nonbreeding season in British Columbia, one bird tagged on Middleton Island spent the nonbreeding season on the Queen Charlotte Islands, another that bred near Juneau migrated to the western coast of Vancouver Island (Checleset Bay), and the remaining six birds, tagged at all three study sites, distributed themselves widely along the coast of mainland British Columbia (Fig. 1). The most northern (Pybus Bay) and southern (Checleset Bay) nonbreeding sites used by PTT-tagged Black Oystercatchers were occupied by birds that bred near Juneau (Fig. 1).

Spring migration 2008. Eight PTTs were active (transmitting data) at the start of spring migration 2008 (Table 1). Five PTT-tagged oystercatchers (Juneau, $n = 2$ males, 1 female; Middleton Island, $n = 2$ males) transmitted location data while in transit during spring 2008 (Fig. 1; dashed lines and stopover site, spring 2008), while the remaining three birds carrying active PTTs migrated while the device was not transmitting. Of the five oystercatchers that transmitted location data while flying north, one male captured near Juneau spent the nonbreeding season on Kosciusko and Heceta islands, Alaska, and returned to Juneau via the outer coast of Alaska; the other male migrated from Pybus Bay to Juneau through the Inside Passage (Fig. 1, dashed lines). One male captured at Middleton Island spent the nonbreeding season on the Queen Charlotte Islands and began migrating north on 2 April 2008 (Fig. 1). Initial data indicated that he traveled north along the outer coast of southeast Alaska (Fig. 1) before being detected on Montague Island at the mouth of Prince William Sound on 6 April 2008. He subsequently returned to his nesting territory on Middleton Island by 11 April (Fig. 1). The other male captured at Middleton Island departed his nonbreeding site near Smith Sound, British Columbia, on 31 March 2008, was next detected in flight along the outer coast of southeastern Alaska (Baranof Island) on 4 April 2008, and returned to his breeding territory on Middleton Island on 7 April 2008. A female that was captured near Juneau and wintered on the west coast of Vancouver Island transmitted location data from a stopover

site on the Dundas Island group while in transit, although not while in flight (Fig. 1; stopover site, spring 2008), before returning to Juneau. The stopover site she used during spring migration 2008 was 33 km southeast of a stopover site she used during the prior fall migration (Duke Island, Alaska). All eight oystercatchers carrying active PTTs through spring migration 2008 returned to the site where they nested and had been captured the previous year. There was no difference between sites of initial capture in departure dates on spring migration ($z = 1.2$, $P = 0.23$, $n = 8$) or arrival dates on the breeding grounds ($z = 1.8$, $P = 0.74$, $n = 8$) in 2008 (Table 2). We also failed to detect a relationship between departure dates on spring migration and latitude of the nonbreeding site, as six of eight oystercatchers carrying active PTTs initiated spring migration between 29 March and 3 April regardless of the nonbreeding site's latitude (latitudinal range of nonbreeding sites $51^{\circ} 3' \text{ N} - 57^{\circ} 3' \text{ N}$). Furthermore, the two Black Oystercatchers departing on spring migration prior to this period occupied the most northern (Pybus Bay) and southern (Checleset Bay) nonbreeding sites used by PTT-tagged oystercatchers, and both birds bred near Juneau.

Breeding season 2008. In Prince William Sound, we visited the nesting territories where Black Oystercatchers were implanted with PTTs the previous breeding season weekly from 17 May to 26 June 2008. During these surveys, we observed three oystercatchers (2 females, 1 male) previously implanted with PTTs but failed to detect the female from this site that was carrying a PTT that never transmitted data. Two of the original six oystercatchers equipped with PTTs had died by this date and so were not available to be relocated. The two females we observed were paired, and each laid an egg on 24 May. Both eggs were malformed and discolored with a thumb-sized depression near the equator (Fig. 3). The eggs had a turquoise hue and the outer surface of the shell had a flaky appearance at the depression site, although the shell was intact. By 29 May, both eggs were missing from their nests, and both scrapes were empty. We did not discover any replacement clutches laid by these two females but found additional eggshell fragments with the same turquoise hue near both nest sites on 4 June. These females behaved typically when they were last seen on their nesting territories on 26 June. The male Black Oystercatcher carrying an active PTT at this study site in 2008 also behaved typically and was observed on his territory with a mate throughout the breeding season. We did not discover any active nests in this male's territory.

Fall migration 2008. Four PTTs continued to transmit location data through fall migration 2008 (Table 1). All four birds (three males from Middleton Island, one male from Juneau) carrying these transmitters departed the breeding grounds and arrived at nonbreeding sites in 2008 within one SD of the corresponding dates for their breeding sites in 2007 (Table 2). Furthermore, all four birds returned to the same nonbreeding sites (Fig. 4).



FIGURE 3. Black Oystercatcher eggs laid on 24 May 2008 by two females that were surgically implanted with 27-g satellite transmitters into their coelomic cavity on 29 May 2007.

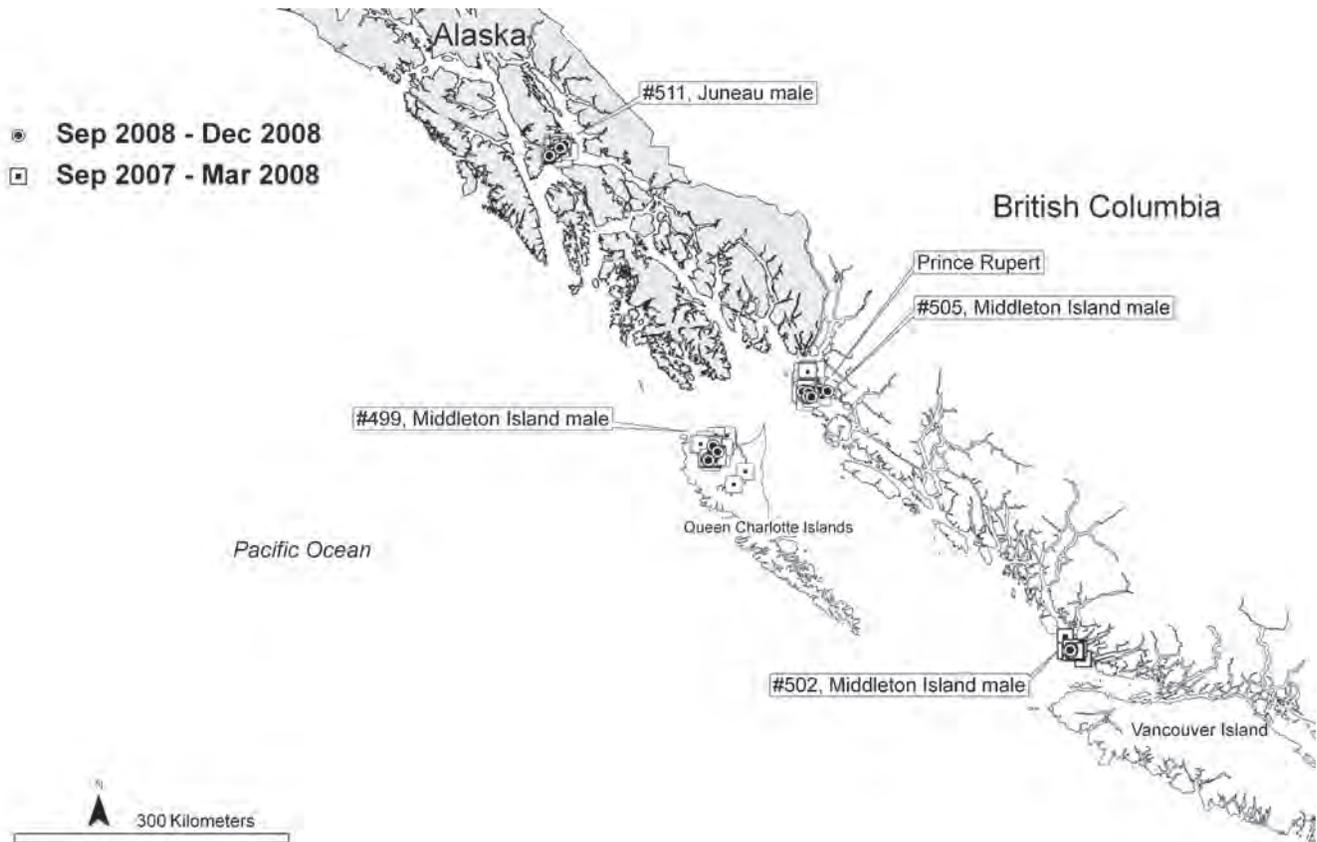


FIGURE 4. Winter locations (squares, September 2007–March 2008; circles, September–December 2008) of four Black Oystercatchers that were implanted with satellite transmitters at two breeding sites in southern Alaska (Middleton Island, May 2007; Juneau, June 2007).

DISCUSSION

Black Oystercatcher populations varied in the timing and length of migration. Birds followed a latitudinal gradient of northern breeding oystercatchers departing the breeding grounds sooner and arriving at nonbreeding sites earlier; northern breeding birds also migrated farther than did those breeding farther south. All Black Oystercatchers with functioning PTTs migrated to distinct nonbreeding sites during this study. Migratory birds traveled a coastal route between breeding and nonbreeding sites during spring and fall migration. Results indicate the coasts of British Columbia and southeastern Alaska provide important winter habitat for Black Oystercatchers breeding in south-central and southeastern Alaska. It is unclear whether Black Oystercatchers breeding in other southern Alaska locales (e.g., Aleutian Islands, Alaska Peninsula, Kenai Fjord, and Glacier Bay) are predominantly migratory and, if so, where they spend the nonbreeding season. Our results may not have captured the full range of migratory behavior in the Black Oystercatcher, as our study was limited to three breeding sites in southern Alaska ($n = 19$ individuals implanted with PTTs). Given the limited number of birds tracked from each region, the observed migration patterns are also likely conservative; they are, however, almost certainly genuine because of the consistency of the patterns detected by conservative analyses.

MIGRATORY CONNECTIVITY

Previous studies of the Black Oystercatcher have revealed high rates of fidelity to breeding sites and mates (Andres and Falxa 1995, Hazlitt and Butler 2001, Morse et al. 2006, Spiegel 2008). Our results support these findings but also show that migratory Black Oystercatchers have strong fidelity to nonbreeding sites. Similar high rates of fidelity to nonbreeding sites have been documented in the Eurasian Oystercatcher (Goss-Custard et al. 1982) and many other shorebirds (Pienkowski and Evans 1985). However, in contrast to Eurasian Oystercatchers that breed in Europe, for which migratory connectivity is moderate to strong (most individuals from one breeding population move to the same nonbreeding site; Dare 1970, Hulscher et al. 1996), we observed weak connectivity between the Black Oystercatcher's breeding and nonbreeding sites, as migratory oystercatchers from all three breeding populations studied were widely distributed during the nonbreeding season. Three Black Oystercatchers from Juneau did winter together in Pybus Bay, Alaska (breeding pair and additional male); however, the other three oystercatchers tagged near Juneau spent the nonbreeding season 165–900 km farther south in southeastern Alaska and British Columbia. Furthermore, the most northern and southern nonbreeding sites that we identified were occupied by birds that bred near Juneau.

In terms of latitude, the nonbreeding distribution of migratory Black Oystercatchers is generally consistent with that of most Eurasian Oystercatchers of subspecies *H. o. ostralegus*

that breed in Europe. The winter range of these oystercatchers is vast (64–12° N; Hulscher et al. 1996), yet roughly 98% of birds winter in Europe, generally at the same latitude (58–51° N; Smit and Piersma 1989, Hulscher et al. 1996) as migratory Black Oystercatchers (57–49° N). The other two races of the Eurasian Oystercatcher that breed in the Northern Hemisphere (*H. o. longipes* and *osculans*) undertake seasonal movements and generally spend the nonbreeding season at lower latitudes (<43° N); however, *H. o. osculans* occasionally winters as far north as the Anadyr estuary (64° N) in eastern Asia (Hockey 1996).

We found that most of the Black Oystercatchers tracked during this study on Kodiak and Vancouver islands were resident. Although several birds shed their VHF transmitters, we were able to track most individuals and confirm residency (<15 km away from nesting territories) after migratory Black Oystercatchers had settled at nonbreeding sites. We can not rule out the possibility that some individuals breeding on Kodiak and Vancouver islands undertook short-distance migration coincident with winter flock formation and/or in response to harsh weather, as has been reported in more southern portions of the species' range (Nysewander 1977, Hartwick and Blaylock 1979, Falxa 1992). However, it does not appear that movement out of these areas is common, as we found that most individuals remained relatively close to their nesting territories throughout the annual cycle and prior surveys reported comparable counts of birds during summer and winter.

Black Oystercatchers followed a leapfrog migration pattern, as birds breeding at Prince William Sound and Middleton Island migrated beyond those breeding farther south (Kodiak Island). The Rock Sandpiper (*Calidris ptilocnemis*) is the only other North American shorebird species known to migrate in a leapfrog pattern (Boland 1990). A prior study in Prince William Sound estimated the size of the winter population of the Black Oystercatcher to be about 25% that of the summer population, indicating that some individuals may be resident (Andres 1994), in contrast with our results that all the oystercatchers tagged there migrated. We suspect these differences are due to where we captured birds within Prince William Sound. The estimates of the winter population in Prince William Sound were derived from a single survey (February) near the sound's southern entrance on and around Montague, Green, and Hinchinbrook islands (Andres 1994). The migratory oystercatchers that we studied bred in Harriman and College fjords, in the northwest portion of Prince William Sound. Seasonal variation in rates of circulation and nutrient input within the inner sound and consistent nutrient exchange near Montague and Hinchinbrook islands at the sound's entrance likely result in greater replenishment of resources near the mouth of Prince William Sound throughout the year and more productive intertidal communities (Niebauer et al. 1994, Wang et al. 1999, 2001, Eslinger et al. 2001, Jin and Wang 2004, Spies and Springer 2007). Although we were unable to locate data that allowed specific comparison of intertidal

productivity between inner and outer Prince William Sound during winter, variation in food availability is probably the most significant predictor of the winter distribution of oystercatchers elsewhere (Goss-Custard et al. 1996). Concomitantly, intermittent shore-fast ice and winter snow may limit oystercatchers' access to foraging and roost sites in Harriman and College fjords during winter. These factors might lead to a portion of the Prince William Sound oystercatcher population, most likely the southern portion, remaining in the sound and not migrating. This possibility requires further study.

Like oystercatchers near the entrance to Prince William Sound, resident Black Oystercatchers at our Kodiak Island study site are apparently able to sustain themselves on a rich and abundant intertidal habitat that results from consistent exchange of oceanic nutrients (Kvitek et al. 1992, Ben-David 1998, Dean et al. 2002). Kodiak Island has a climate mild in comparison to areas of similar latitude because the archipelago lies between the Alaska and Alaska Coastal currents (Favorite 1976, Royer 1981, Stabeno et al. 1995, 2004). As a result, Kodiak's nutrient-rich waters support numerous species of birds and mammals year round (Barnes and Smith 1998, Gould and Forsell 1981, Ferguson and McLoughlin 2000, Zwiefelhofer 2007). During winter, flocks of >600 Black Oystercatchers are regularly observed at our Kodiak Island study site (the greater Chiniak Bay area), and a flock of >1100 individuals was observed during this study (Zwiefelhofer, pers. obs.). We suspect these birds are likely local breeders and short-distance migrants from the Kodiak Archipelago. Alternately, Black Oystercatchers using Chiniak Bay during winter may be migrants from breeding sites elsewhere in southwestern Alaska (e.g., Aleutian Islands) or even south-central Alaska (e.g., Prince William Sound). The latter seems unlikely given the similarity of the population size estimated for the archipelago during summer and winter and because none of the PTT-tagged birds from Prince William Sound and Middleton Island were detected in this region. Furthermore, an oystercatcher marked on the breeding grounds in Kenai Fjords National Park (west of Prince William Sound) was resighted during winter in British Columbia (Tessler et al. 2007).

Historic records indicate that Black Oystercatchers have nested along >80% of British Columbia's shoreline (Campbell et al. 1997). Known areas of abundance are the Queen Charlotte Islands, north and west coasts of Vancouver Island (Barkley Sound to Queen Charlotte Strait), the southern Gulf Islands, and the outer areas of the north/central coast. Data from winter surveys are scarce; however, evidence suggests that most of these areas are generally occupied by Black Oystercatchers throughout the nonbreeding period (Hartwick and Blaylock 1979; T. Golumbia, pers. comm.). Our results indicate that Black Oystercatchers wintering along British Columbia's shoreline migrate from a geographically broad breeding area. This lack of migratory connectivity suggests that site-specific alteration, or loss, of nonbreeding habitat will likely not affect an entire segment of the breeding population.

SATELLITE TRANSMITTERS IN CONNECTIVITY STUDIES

This study is the second to document migration patterns of a large shorebird with implantable satellite transmitters, following the first of the Bar-tailed Godwit (*Limosa lapponica baueri*) on its nonstop migration from nesting grounds in Alaska to nonbreeding sites in New Zealand (Gill et al. 2008). Both studies provide unprecedented information on the migration pattern of each species. However, unlike the godwit study, we observed a relatively high overwinter mortality rate after implantation (17%). This rate was not anticipated and was higher than that previously reported in Alaska for individually marked Black Oystercatchers not equipped with PTTs (7%; Tessler et al. 2007). Mortality rates associated with implanted transmitters seem to vary by species, with some species (e.g., murre) having upward of 40% mortality (Hatch et al. 2000). This variation in mortality is difficult to explain and seems most likely due to differences in how species can cope with invasive devices inside the body cavity, particularly because in all three studies the same veterinary team implanted the transmitters (D. Mulcahy, pers. comm.). In female Black Oystercatchers implantation of the transmitter we used may have consequences for residual productivity, as two females laid similarly malformed eggs and may not have produced any offspring during the first breeding season subsequent to implantation. Future studies should consider these data before these particular transmitters are implanted in Black Oystercatchers.

Despite these setbacks, we think the migratory behavior that we documented was not significantly biased from the use of implantable PTTs. We say this for three reasons. First, all birds that survived the nesting period immediately following transmitter implantation completed their initial migratory flight in fall 2007, and several migrated successfully again in 2008. Second, Black Oystercatchers carrying PTTs maintained fidelity to breeding and nonbreeding sites during subsequent migrations and departed on and completed these migrations within one SD of prior departure and arrival dates. Third, the individuals that we were able to track during the subsequent breeding season paired up and in the case of two females laid eggs (although deformed). These factors suggest that the migration data we obtained are likely representative of the species as a whole, although equipping more birds in more locations would likely yield additional information. Broad-scale satellite-telemetry studies offer a different perspective on how individuals and populations use habitats both in space and time. Such knowledge is paramount given that changes in climatic conditions and continuing human development are likely to influence species negatively. Intertidal species such as the Black Oystercatcher may be particularly vulnerable to projected sea level rise as their prey base may be altered or inaccessible and/or nesting areas may become inundated. Baseline information on the temporal and spatial variation in the use of habitats by the Black Oystercatcher throughout its annual cycle presented here will help biologists ascertain the

relative importance of different coastal areas and how adaptable this species is to projected changes.

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