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RESEARCH ARTICLE

Winter site fidelity and winter movements in Common Loons (*Gavia immer*) across North America

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ABSTRACT

In many avian species, breeding site fidelity has been more thoroughly investigated than winter site fidelity, yet the latter may have a greater impact on survivorship. The Common Loon (*Gavia immer*) is an example of a species whose breeding site fidelity has been well established, but whether it exhibits winter site fidelity remains unknown. Because Common Loons primarily winter in marine waters off coastal shores, winter site fidelity has been challenging to document. We investigated winter site fidelity in Common Loons across North America using satellite transmitters, recaptures, and resightings of previously color-marked individuals. Color-marked adults returned in consecutive years to the same coastal wintering locations in California, Washington, Louisiana, Maryland, and Massachusetts, USA. We estimated adult annual apparent survival as 77% (0.48–0.93) and adult winter site fidelity as 85% (0.35–0.98). This finding has important conservation implications in the aftermath of recent marine oil spills; if Common Loons return to the same contaminated wintering areas annually, decreased fitness and survivorship could result in population-level effects.

Keywords: Common Loon, *Gavia immer*, marine oil spills, satellite transmitter, winter philopatry, winter site fidelity

Fidelidad a los sitios de invernada y movimientos invernales de *Gavia immer* a través de América del Norte

RESUMEN

En muchas especies de aves, se ha investigado más a fondo la fidelidad a los sitios de reproducción que la fidelidad a los sitios de invernada, aunque lo último puede tener un mayor impacto en la supervivencia. La especie *Gavia immer* es un ejemplo de una especie cuya fidelidad a los sitios de reproducción ha sido bien establecida, pero no se sabe si presenta fidelidad a los sitios de invernada. Debido a que los individuos de *G. immer* invernan principalmente en aguas marinas frente a las costas, ha sido difícil documentar la fidelidad a los sitios de invernada. Investigamos la fidelidad a los sitios de invernada en *G. immer* a través de América del Norte usando transmisores satelitales, recapturas y avistamientos repetidos de individuos previamente marcados con colores. Los adultos marcados con colores regresaron en años consecutivos a las mismas ubicaciones costeras de invierno en California, Washington, Luisiana, Maryland y Massachusetts. La supervivencia aparente anual de los adultos fue de 77% (0.48, 0.93) y la fidelidad de los adultos a los sitios de invernada fue de 85% (0.35, 0.98). Este hallazgo tiene importantes implicancias para la conservación debido a las secuelas de los derrames marinos recientes de petróleo; si los individuos de *G. immer* regresan todos los años a las mismas áreas invernales contaminadas, podrían registrarse disminuciones en la adecuación biológica y en la supervivencia a nivel poblacional.

Palabras clave: derrames marinos de petróleo, fidelidad a los sitios de invernada, filopatría invernal, *Gavia immer*, transmisores satelitales

INTRODUCTION

Breeding philopatry is well studied in many avian species, but there have been fewer studies on winter philopatry or winter site fidelity (Robertson et al. 2000, Koronkiewicz et al. 2006, Evers et al. 2010). However, the latter may have a greater impact on survivorship, because mortality may be higher on wintering grounds than at breeding sites (Hestbeck et al. 1991, Newton 1998). To understand the demography, breeding and wintering connectivity, genetic structure, and population regulation of a migratory bird species, it is necessary to know the level of philopatry (Robertson and Cooke 1999, Guillemain et al. 2009, Petersen et al. 2012). Breeding and wintering philopatry

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are basic life-history parameters that are important for modeling population growth and also have important conservation implications (Latta and Faaborg 2001, Petersen et al. 2012). For example, if connectivity between breeding and wintering areas is strong, considerable genetic substructuring can arise (Chesser 1991), potentially leading to isolation of populations, which may also affect conservation strategies (Martin et al. 2007). Additionally, migratory species that exhibit winter site fidelity at contaminated sites, such as near a marine oil spill, may experience reduced fitness and population declines (Maki 1991).

The Common Loon (*Gavia immer*) is a migratory species that breeds throughout Canada and across the northern United States (Evers et al. 2010). Common Loons are long lived (>25 yr), have high adult survivorship (0.91; Mitro et al. 2008), and have low fecundity (0.5 young fledged yr^{-1}; Evers et al. 2010). They winter predominantly in coastal marine environments (Kenow et al. 2002, 2009), and mortality is highest during fall migration and winter, when botulism and emaciation syndrome are prevalent (Alexander 1991, Evers 2007). They undergo a complete simultaneous wing molt in winter (Woolfenden 1967) and appear to be vulnerable to additional environmental stressors during this time (Spitzer 1995, Evers 2007). Because of their life history traits and overwintering destinations, they have been identified as a species of concern during marine oil spills (Evers 2007, Paruk et al. 2014a). Breeding site fidelity is well established in Common Loons (Evers et al. 2010), but winter site fidelity is not. Because of continued degradation of coastal ecosystems and the impending certainty of future marine oil spills (Paruk et al. 2014b), documenting and understanding the level of winter philopatry in this species is important. Our primary objective was to investigate and document winter site fidelity in the Common Loon and to provide estimates of adult and immature apparent survival. Our secondary objectives were to understand the scale of the fidelity and to provide additional data on migration patterns.

METHODS

We examined Common Loons at 4 study sites across their geographic range in the United States, using band resighting (surveys), recapture, and platform transmitter terminal (PTT) technology. In Maine we used only PTTs; in Louisiana and California we used both recapture and resighting data; and in Washington we used resighting data only. Common Loons were captured using established night-lighting techniques and playback of recordings (Evers 1993). Prior to release, each individual was uniquely color banded, and a U.S. Geological Survey aluminum band was attached. Standard body measurements and weights were taken for each individual (Gray et al. 2014). Common Loons were aged by plumage as either adult (any individual ≥20 mo of age) or immature (<20 mo of age) as described in Evers et al. (2010).

We characterized the winter home range across 2 transmittered Common Loons by generating individual utilization distributions (UDs) for each winter period using fixed kernel density methods (Worton 1989). The utilization distribution is an estimate of the relative probability of an animal occurring in an area in a given period. Several methods have been developed to estimate UDs; the kernel density estimate (KDE) is the most widely used. KDE attempts to model space use by estimating the probability of occurrence around each observed animal location, with the highest probability at the actual location and decreasing probability with distance from that point, reaching zero at a user-specified radius (bandwidth [or smoothing] parameter; Worton 1989). For the bandwidth parameter, we relied on the likelihood cross-validation method recommended by Horne and Garton (2006). Based on simulated data, this method produced estimates with better fit and less variability than least-squares cross-validation. From the KDE rasters, we generated 95% winter home-range estimates for each individual. Utilization distributions and isopleths were generated using Geospatial Modeling Environment version 0.7.3.0 (Beyer 2012).

Rangeley and Moosehead Lakes Region, Maine. To investigate the wintering sites of Common Loons that breed near the eastern seaboard, 6 PTTs were surgically implanted in individuals from 3 reservoirs in western Maine: (1) Aziscohos Lake (2,985 ha; 45.03°N, –71.03°W), (2) Flagstaff Lake (7,264 ha; 45.19°N, –70.38°W), and (3) Indian Pond (1,516 ha; 45.46°N, –69.85°W; Figure 1). These reservoirs were managed by NextEra Energy during the study period.

Barataria Bay, Louisiana. We studied Common Loons at Barataria Bay, Louisiana, to document winter site fidelity of birds utilizing the Gulf of Mexico. Barataria Bay is a large coastal estuary, about 24 km long by 19 km wide, located in southeastern Louisiana (29.39°N, –89.94°W; Figure 2). It is separated from the open gulf by 2 barrier islands, Grand Isle and Grand Terre, but connected to smaller bays and channels on the north, east, and west ends. From 2011 to 2014, 84 Common Loons (26 adults and 58 immatures) were captured and color-banded. From 2012 to 2014, surveys were carried out from shore (using a 25× spotting scope) or by boat (10× binoculars) once every 2 wk throughout January–March; each took approximately 1.5–2.5 hr to complete.

Morro Bay, California. To document site fidelity on the west coast, we monitored Common Loons at Morro Bay, California. Morro Bay is a large coastal estuary, 6.8 km long and 2.5 km wide (at mean high tide), located halfway

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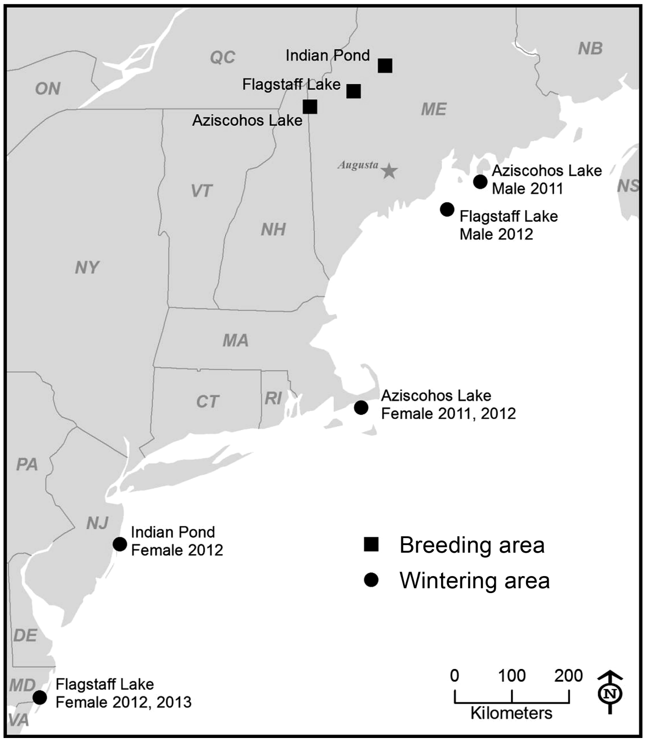

FIGURE 1. Breeding and wintering locations of Common Loons in western Maine (Rangeley and Moosehead Lakes region), USA, that received PTTs in 2011 and 2012.

between Los Angeles and San Francisco (35.32°N, –120.85°W; Figure 2). Morro Rock, a 175-m-high volcanic plug, sits at the mouth of the bay. Only relatively small watercraft are capable of passing into the harbor channel, because a large sandspit protects the harbor and bay from the Pacific Ocean. From 2004 to 2010, 80 Common Loons (14 adults and 66 juveniles) were captured and color-banded, and surveys were carried out from shore (using a 25× spotting scope) or kayak (10× binoculars) every 3–6 wk, each survey taking approximately 1.5–2.0 hr to complete. Digital photography using a Canon 7D with a 400-mm telephoto lens also aided examination of band color combinations. Imagery from land and shore was time-stamped by date and band number and archived for future reference. Morro Coast Audubon volunteers, residents, and harbor patrol opportunistically provided additional band observations or photos as encountered.

Lake Pateros, Washington. Common Loon winter surveys occurred annually at Lake Pateros (48.08°N, –119.75°W) from 2000 to 2012. Created in 1967, Lake Pateros is a freshwater reservoir on the Columbia River, approximately halfway between Seattle and Spokane, in the middle of the state (Figure 2). From October through April, surveys were conducted opportunistically from shore using binoculars (8×), a spotting scope (20×), or a digital camera (Canon 7D with 400 mm telephoto lenses) and took 1.5–2.0 hr to complete. The lack of consistent resight effort led us to exclude this site in the subsequent mark–recapture analysis. From 1995 to 2013, 101

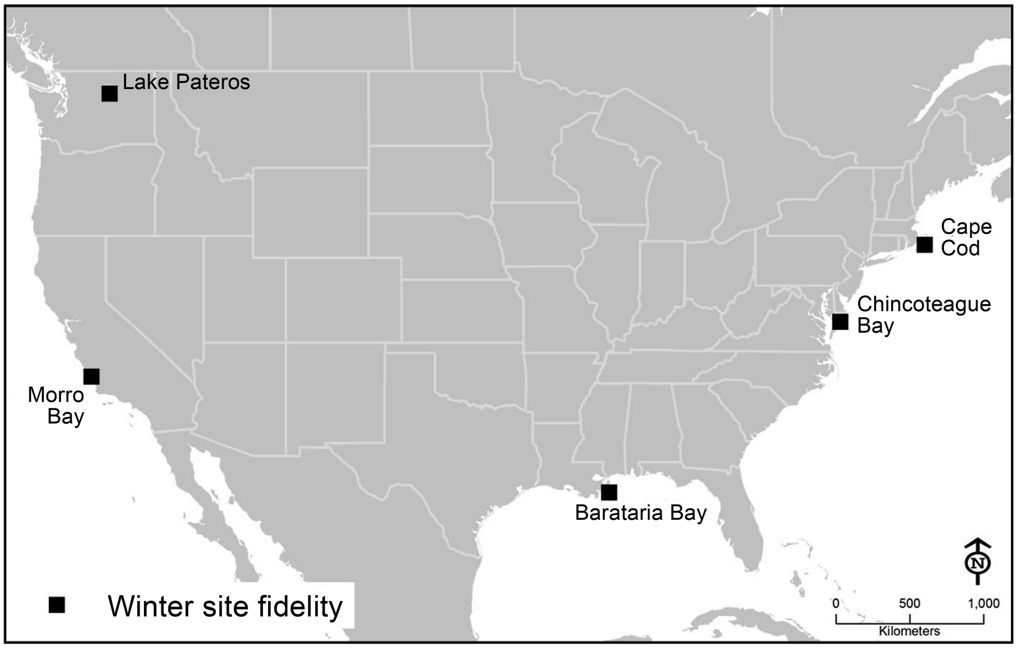

FIGURE 2. Locations across North America where Common Loons exhibited winter site fidelity: Lake Pateros, Washington; Morro Bay, California; Barataria Bay, Louisiana; Chincoteague Bay, Maryland; and Cape Cod, Massachusetts, USA.

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Common Loons (30 adults and 71 juveniles) were captured and color-banded in Washington.

Mark–Recapture Analysis

Surveys from Morro Bay and Barataria Bay were used to create a time-independent Cormack-Jolly-Seber mark–resight model to describe the probability of an individual returning to the wintering site in the following year (apparent survival, φ) and the probability of detecting an individual in any given year (detectability, p; Lebreton et al. 1992). Time-dependent versions of this model were explored for both φ and p, but data were too sparse to obtain estimates for each year. Resighting effort was also consistent among years, which would reduce interannual variance in p. We combined 6 yr of data from Morro Bay and 4 yr of data from Barataria Bay into one dataset. The Barataria Bay data were temporally aligned with the last 4 yr of Morro Bay monitoring. We parameterized age as the first year of life for juveniles compared with all other years (birds captured as adults would then have no juvenile year data), and site of capture (Morro Bay or Barataria Bay) was used as a simple categorical covariate. We tested 4 models and ranked them using Akaike's Information Criterion (AIC; Burnham and Anderson 2002): $\varphi_{(.)}$, $p_{(.)}$;$\varphi_{(.)}$, p_{site}; φ_{age}, $p_{(.)}$;φ_{age}, p_{site}. Apparent survival was not allowed to vary with site because we were more interested in variability in detection among sites, and detection probability was not allowed to change with age of the individual because juveniles could not be resighted again as juveniles, making this parameter impossible to estimate. Goodness-of-fit of the top models was assessed by using the median $\hat{c}$ approach estimating c (model deviance/model degrees of freedom) from the global model (φ_{age}, p_{site}) using a logistic regression from simulated data. This estimate was used to adjust the AIC of each model to account for overall lack of fit to quasi-AIC (QAIC). This new measure of model rank was used to select the top models from the candidate set; model averaging was used where multiple models were <2 QAIC from the top model (Burnham and Anderson 2002). Program Mark (White and Burnham 1999) and package RMark in the R Statistical Computing Environment (Laake 2013) were used in this analysis. Winter site fidelity was calculated by dividing our estimate of apparent survival by survival; the current best estimate of true annual survival for Common Loons is 0.91 (Mitro et al. 2008). The 95% confidence interval (CI) for F was calculated using the delta method and using the standard errors of our apparent survival and true survival estimates (Cooch and White 2006).

PTT Implantation

Rangeley and Moosehead Lakes Region, Maine. A specially trained wildlife veterinarian evaluated the condition and health of each bird before the decision was made to implant PTTs. The veterinarian surgically implanted PTTs with percutaneous antennas in the birds' coelomic cavities, following the procedure detailed by Mulcahy and Esler (1999). The surgeries were conducted under field sterile conditions and completed in <1 hr. After surgery, each bird was given a subcutaneous injection of a sterile electrolyte solution, held in a net-bottomed container for 2–3 hr, and observed to ensure full recovery. Birds were considered fully recovered when they demonstrated control of head and neck and had the ability to assume an alert posture. Birds were released at the capture site within 4–5 hr of capture.

A total of 6 PTTs, 2 in 2011 and 4 in 2012, were deployed in Common Loons from the Rangeley and Moosehead Lakes region in western Maine (Table 1). On July 20, 2011, PTTs were deployed on each member of a single breeding pair at Aziscohos Lake. In 2012, 4 PTTs were deployed: 1 each in a male and a female (members of 2 separate pairs) on Indian Pond (July 16) and 1 each in a male and a female (members of 2 separate pairs) on Flagstaff Lake (July 17).

The 2011 PTTs weighed 68 g (model PTT-100; Northstar Science and Technology, King George, Virginia, USA), and the 2012 PTTs weighed 45 g (model IMP/TAV-2640; Telonics, Mesa, Arizona, USA). Each of the PTTs was expected to receive a maximum of 2,500 hr of transmissions. Because Common Loons are more mobile during spring and fall migration (April–May and October–November) than during the summer and winter, duty cycles were programmed differently by season. During migration, transmitters were on for 6 hr and off for 30 hr, and then this cycle was repeated; during summer and winter, they were set to transmit for 6 hr once every week. Data were transferred to the Service Argos data processing center (Landover, Maryland, USA), and position estimates were acquired using ARGOS.

RESULTS

Resighting and Recapture of Banded Birds

Morro Bay, California. Nine of the 14 color-marked adults (64%) were reobserved in subsequent years. In addition, 5 of 6 color-banded immatures returned as adults and were reobserved as adults in subsequent winters, making the percentage of adults that exhibited winter site fidelity 70.0% (14/20). Banded adults returned to Morro Bay for an average 3.1 ± 0.6 winters, and 1 individual was reobserved for 6 consecutive winters. Only 5 of 66 color-marked immatures (7.7%) returned as adults; 4 were recovered as mortalities, and the great majority was never reobserved (91.9%, 57/62). An average of 42 ± 3.4 individuals survey^{-1} were observed during the winter months (December–March) across all years.

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TABLE 1. Departure dates, wintering locations, and distances traveled (km) of Common Loons breeding in western Maine, USA, that received PTTs in 2011 and 2012. [a]

Year	Sex	Lake	Departure date	Winter location	Migration distance
2011	Male	Aziscohos	November 23	Maine	230
2012	Male	Flagstaff	August 23	Maine	190*
2011	Female	Aziscohos	November 11	Massachusetts	400
2012	Female	Aziscohos	October 23	Massachusetts	400
2012	Female	Flagstaff	November 5	Maryland	890
2013	Female	Flagstaff	September 21	Maryland	890*
2012	Female	Indian Pond	November 16	New Jersey	700

[a] Does not include 7-wk northern detour, 400–500 km.

Barataria Bay, Louisiana. Five of the 26 (19.2%) color-banded adults were recaptured ($n = 4$) or reobserved ($n = 1$) in subsequent winters. All of these birds were either captured or reobserved in the same part of Barataria Bay (or the associated watercourses) where they were originally captured and marked. Only 1 of 65 immatures was recaptured (1.5%) or resighted (0%).

Lake Pateros, Washington. Five individuals banded in eastern Washington (2 adults and 3 immatures) were reobserved during the winter months (January–February) on Lake Pateros in multiple years (Figure 2). A male color-banded in 2003 from South Twin Lake was photographed in February 2008, February 2009, and January 2010; and a female banded in 1995 on Bonaparte Lake was photographed in February 2008 and 2009. A juvenile banded in 2007 on Bonaparte Lake was photographed in December 2012 and 2013. A juvenile banded in 2007 on Lost Lake was observed every February from 2011 to 2013. A juvenile banded in 2004 on Swan Lake was observed in 3 consecutive winters: February 2008, February 2009, and March 2010. The migration distance between these breeding lakes (Swan, South Twin, Bonaparte, and Lost) in eastern Washington and the wintering location (Lake Pateros) was 80–100 km.

Mark–Recapture Analysis

The top model by $\mathrm{QAIC_c}$ ($\hat{c} = 3.07$, $\mathrm{SE} = 0.43$) found that age influenced our estimate of apparent survival, and site influenced detection probability (Table 2). Our second model ($\Delta\mathrm{QAIC_c} = 1.9$) had the same effect of age on apparent survival but no effect of site on detection probability. Because the models were <2 QAIC different, we used model averaging to arrive at estimates of φ and p. Age was important in both top models. Birds in their first year had a model-averaged apparent survival of 0.11 (95% CI: 0.03–0.37), whereas birds captured as adults had a 0.77 (95% CI: 0.48–0.93) chance of returning. Detection probability varied between sites in only 1 of the 2 top models; the model-averaged chance of detecting a Common Loon at Morro Bay was 0.56 (95% CI: 0.25–0.83) in any given year, whereas the chance of detecting a Common Loon at Barataria Bay was 0.26 (95% CI: 0.06–0.68). Winter site fidelity for adults was calculated as 0.85 (95% CI: 0.35–0.98) if true survival (*S*) is 0.91 (95% CI: 0.64–0.98; Mitro et al. 2008, $F = \varphi/S$).

TABLE 2. Akaike's Information Criterion selection table for all Cormack-Jolly-Seber models considered ($\hat{c} = 3.07$); φ is a parameter for apparent annual survival, and p is detectability. Names in parentheses correspond to covariates regarding age (first-year bird or adult) and site of capture (site).

Model name	$\Delta\mathrm{QAIC_c}$ [a]	QAIC weight	*K*	QDeviance
$\varphi_{\mathrm{age}}, p_{\mathrm{site}}$	0	0.72	4	30.3
$\varphi_{\mathrm{age}}, p_{(.)}$	1.9	0.28	3	34.3
$\varphi_{(.)}, p_{\mathrm{site}}$	12.2	0.02	3	44.6
$\varphi_{(.)}, p_{(.)}$	13.2	<0.01	2	47.7

[a] Lowest $\mathrm{QAIC_c} = 72.45$.

PTT Data

Rangeley and Moosehead Lakes Region, Maine. We were able to use data from 5 of the 6 deployed PTTs; the PTT in the male from Indian Pond stopped transmitting on October 10, 2012 (~3 mo after deployment), at which time he was presumed dead. Several patterns emerged: (1) Males left their breeding lakes sooner than females; (2) males migrated shorter distances than females; (3) pair members overwintered in different locations; (4) individuals did not depart or migrate at the same time each year, but did arrive on the wintering grounds within 2 wk of their arrival date in the previous year; and (5) winter use areas were consistent for the same individuals between years.

Transmittered males from our study site left their breeding lake sooner than females. Males from Aziscohos and Flagstaff lakes left on October 23 and August 23, whereas females from those two lakes and Indian Pond left on November 11, 5, and 16, respectively. The males departed from Aziscohos and Flagstaff lakes when the chicks were 8 and 17 wk old, whereas females from Aziscohos Lake, Flagstaff Lake, and Indian Pond departed when their chicks were approximately 18, 20, and 20 wk old, respectively.

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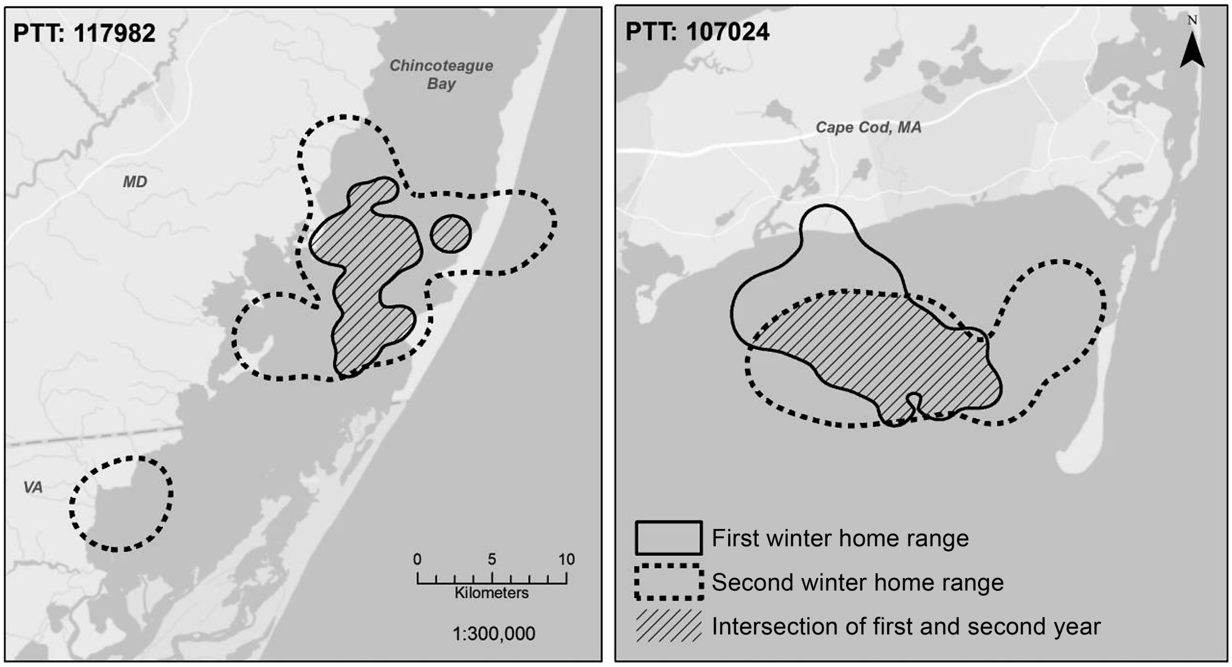

FIGURE 3. Comparison of consecutive winter use areas of 2 female Common Loons implanted with platform terminal transmitters (PTTs) in Chincoteague Bay, Maryland, and Cape Cod, Massachusetts, USA, 2011 and 2012.

Additionally, males ($n = 2$) migrated shorter distances than females ($n = 3$; males, 210 ± 28.3 km; females, 645 ± 346.5 km; Table 1). For example, males from Aziscohos and Flagstaff lakes wintered off Mt. Desert Island, Maine (230 km), and Matinicus Island, Maine (190 km; Figure 1), whereas females on Aziscohos and Flagstaff lakes and Indian Pond wintered just south of Cape Cod, Massachusetts (400 km); Chincoteague Bay, Maryland (890 km); and the New Jersey coast (700 km), respectively.

We had 1 pair of breeding birds from Aziscohos Lake in which both the male and the female were equipped with PTTs. The members of this pair did not migrate together or winter in the same location. The male wintered off the coast of Maine, and the female wintered south of Cape Cod (Figure 1). We found consistency in the pair's arrival dates at the wintering area and variability in their departure dates from the breeding lakes. Each individual left their breeding lake at a different date each year but arrived at the wintering area within 2 wk of the previous year. For example, the female left in mid-November of 2011, and left several weeks earlier in 2012 (September 23–October 23; exact date unknown), but arrived at Cape Cod each year within 12 days of November 20. Similarly, the Flagstaff female departed in early November and late August in 2012 and 2013, respectively, but arrived at Chincoteague Bay each year within 6 days of November 17.

The female from Aziscohos Lake and the female from Flagstaff Lake occupied the same local wintering area in successive years (2011 and 2012; Figures 1 and 3). From November 17, 2011, to January 12, 2012, the Aziscohos female used the same area just south of Cape Cod. In 2011, the area of use consisted of 7,556 ha (75.6 km^2); in 2012, it consisted of 9,642 ha (96.4 km^2), with a 100% overlap between years (Figure 3). From November 23 to February 3, the Flagstaff female used the same local area in Chincoteague Bay of 3,705 ha (37.1 km^2) in 2011 and 14,179 ha (141.8 km^2) in 2012, with a 64% overlap between years (Figure 3).

DISCUSSION

Previously, it was unclear whether Common Loons returned to the same winter locations annually. Our data on banded and tagged birds indicate that adults exhibit strong winter site fidelity (0.85), much as they exhibit breeding site fidelity (0.93; Evers 2001), across North America. Site fidelity is difficult to estimate for winter juveniles because of the lack of an estimate of apparent or true survival in this or previous studies, but a value much lower than that of adults seems likely. Our results show that adults revisit the same wintering areas annually in the Pacific Ocean (Morro Bay, California), the Gulf of Mexico (Barataria Bay, Louisiana), the Atlantic Ocean (Massachusetts and Maryland), and a freshwater reservoir (Lake Pateros, Washington). Three of the 4 marine wintering locations were protected bays (Morro Bay, Barataria Bay, and Chincoteague Bay), and 1 was in open water (south of Cape Cod). Although many wintering individuals remain

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near shore, in coastal bays and coves, many are also found ≤100 km offshore (Powers and Cherry 1983, Haney 1990, Jodice 1993). On a broad scale, factors that may influence their winter distribution and abundance include availability of protected bays, zones of high primary productivity, prey availability, water clarity, and tidal regime (McIntyre 1978, Daub 1989, Thompson and Price 2006, Winiarski et al. 2013). One of our study areas, Lake Pateros, was a freshwater reservoir, which indicates that as long as suitable prey are available, some Common Loons will use these water bodies to overwinter (Kenow et al. 2002). With these considerations, site fidelity may be a product of individuals choosing wintering areas that exhibit suitable characteristics, and of certain wintering areas consistently exhibiting preferred characteristics.

On a local scale, our data suggest that Common Loons return to precise wintering locations, usually within 2 km of previous wintering locations. Adults returned to the Morro Bay area for several years, and one of the first adults we captured in 2004 returned every year for 6 consecutive winters, through 2010. Five individuals recaptured in Barataria Bay were all found within 1 km of the initial capture location years later, and the 2 females with PTTs from Maine returned to sites within 1 km of the previous year. We suspect that winter site fidelity developed in Common Loons, in part, because individuals that returned to the same area annually gained local knowledge (e.g., about prey resources and predator refugia) that increased their survival and fitness (Robertson et al. 2000). Given this, we expect that many adult Common Loons may overwinter in one location throughout their life.

It also appears that Common Loons consistently use one area (about 10–20 km^2) for the duration of the winter (Figure 3). One reason for this may be that adults undergo a simultaneous wing molt in midwinter that renders them flightless for several weeks (Woolfenden 1967). Their most common reaction to danger is to dive; collectively, we have observed these birds in midwinter (January–February) for more than 20 yr and have never observed an adult in flight (J. D. Paruk et al. personal observation). So, unless they swim a great distance, either on the surface or under water, their winter use area is highly restricted. Immatures do not molt during their first winter; thus, although capable of flight, they are rarely observed flying. However, this possibly allows juveniles greater mobility during winter, which could increase the size of their winter use areas. If so, this may help explain the fewer juvenile resightings in some of our study areas.

Our top model found that age influenced our estimate of apparent survival and that site influenced detection probability. Apparent survival for adults was 77%, compared with 11% for immatures. The low winter survival rates for immatures compared with adults is likely due to the former experiencing greater mortality (Piper et al. 2012); this is not surprising, given that many long-lived seabirds exhibit high juvenile mortality (Orians 1969, Nisbet and Spendelow 1999). Still, the possibility exists that some immatures survived but did not return to their banding location because they switched wintering areas. The high apparent survival of adults is jointly due to high annual survival and high winter site fidelity.

Detection probability differed by site; individuals at Morro Bay were >3 times more likely to be detected than those at Barataria Bay. We were not surprised by this result, for a couple of reasons. First, Morro Bay is an enclosed area that can be easily surveyed from shore at just a few vantage points, whereas Barataria Bay and its associated inlets and watercourses need to be surveyed largely by boat because there are few vantage points from shore. Second, water clarity is very different between the 2 sites (0.5 vs. 3.5 m Secchi disk; Paruk et al. 2014b). For example, an observer on a boat in Barataria Bay could be looking directly down on a Common Loon in the water; and, if the color band were below the waterline, the observer might not be able to detect it; yet, in Morro Bay, an observer from shore with a spotting scope would be able to determine whether a Common Loon were banded from 100 m away. These differences in water clarity have implications for Common Loons other than observer detectability. Loons are visual predators, and their foraging success is directly linked to water clarity (Barr 1973). As such, Common Loons in Barataria Bay likely face greater challenges in foraging than those in Morro Bay. To our knowledge, no studies of Common Loon winter diets have been published, and more research in this area may help establish why they choose and return to particular wintering areas.

Movements

Because both winter and breeding site fidelity are high in Common Loons, understanding the level of connectivity between breeding and wintering grounds would improve our knowledge of the species' population dynamics. Preliminary investigations on Common Loon migration suggest that connectivity may be weak between breeding and wintering areas (Kenow et al. 2002, 2009, Paruk et al. 2014a). This information would be useful, especially given that the Common Loon is listed as a species of concern or as threatened in several U.S. states (Evers 2007). Similarly, more studies on Common Loon genetic variation and substructure across North America may prove useful for understanding the level of connectivity between breeding and wintering areas (McMillan et al. 2004).

Preliminary data from Common Loons with PTTs revealed differences in migration timing and distance between the sexes. Males left the breeding area sooner in the fall (or late summer) and migrated a shorter distance to their wintering location than females from the same water

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body. Because immatures are independent of the adults by 10–12 wk (Evers et al. 2010), both parents would be freed of chick-rearing responsibilities and should be equally likely to depart around the same time. This topic warrants further consideration. Females may have migrated farther south than males because the latter may be selected to remain closer to their breeding lakes, ensuring that they return to their breeding lake before rival conspecifics. Males are also 25% heavier than females, and migration distance in Common Loons has been shown to be strongly correlated with body mass (Gray et al. 2014), so the shorter flight distance may reduce energetic costs. More data on differences in winter site selection between pair members, and between intrasexual members on the same water bodies, are needed to better understand the ecological and evolutionary forces shaping these patterns.

Implications

Our finding that Common Loons exhibit winter site fidelity has important implications for assessing damages that occur after a marine oil spill (Natural Resource Damage Assessment [NRDA], administered by the USFWS). Two fairly recent NRDA studies investigating the impacts of marine oil spills on Common Loons in New England (North Cape in 1996, Buzzards Bay in 2002) would have benefited from knowing whether Common Loons exhibited winter site fidelity. Models based on the population dynamics of color-marked individuals indicate that ~3,900 Common Loon–years were lost in the North Cape event, but the numbers might have been higher if winter site fidelity were known (Sperduto et al. 2003). Thus, in light of recent marine oil spills (e.g., *Deepwater Horizon*, 2010; Paruk et al. 2014b), and given the high probability of another oiling event, our data on wintering site fidelity in Common Loons will increase the accuracy of predictive models during NRDA investigations.

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