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Size and Retention of Breeding Territories of Yellow-billed Loons (*Gavia adamsii*) in Alaska and Canada

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Abstract.—Yellow-billed Loons (*Gavia adamsii*) breed in lakes in the treeless Arctic and are globally rare. Like their sister taxa, the well-documented Common Loon (*G. immer*) of the boreal forest, Yellow-billed Loons exhibit strong territorial behavior during the breeding season. Little is known about what size territories are required, however, or how readily territories are retained from year to year. An understanding of territory dynamics and size is needed by management agencies as most of the U.S. breeding population of Yellow-billed Loons resides in the National Petroleum Reserve-Alaska where oil and gas development is expected to increase in the next few decades. Using locational data from a set of Yellow-billed Loons marked with satellite transmitters, we quantified an index of territory radius for each of three breeding populations: two in Alaska and one in Canada. The mean territory radius was 0.42 km for Yellow-billed Loons summering on lakes within the Seward Peninsula in northwest Alaska, 0.69 km for Yellow-billed Loons within the Arctic Coastal Plain of Alaska (encompasses the National Petroleum Reserve), and 0.96 km for Yellow-billed Loons within Daring Lake in mainland Canada. In this study, the mean territory radius on the Arctic Coastal Plain was about half the distance identified in stipulations for industrial development in the National Petroleum Reserve. The range in territory size among areas corresponded to a gradient in size of lakes used by Yellow-billed Loons with territories at the two Alaska sites on lakes averaging < 200 ha while territories in Canada were generally on much larger lakes. In the year after capture, 71% of Yellow-billed Loons retained territories that were held the previous year. Most Yellow-billed Loons that lost their territories wandered over a large area within 6 km of their prior territory. No Yellow-billed Loons occupied new territories, though one reacquired its prior territory after a 1-year hiatus. Retention of a territory in a subsequent year was positively related to early arrival dates at the breeding site. For Yellow-billed Loons on the Arctic Coastal Plain, this relationship was quite strong with a week lag in arrival decreasing the probability of retaining a territory by 80%. These collective observations, in combination with theoretical studies of population regulation by floaters (non-territorial birds), suggest that lake habitat suitable for breeding Yellow-billed Loons may currently limit population size in this species. *Received 13 March 2013, accepted 10 June 2013.*

Key words.—arrival date, Common Loon, *Gavia adamsii*, *Gavia immer*, habitat limitation, Yellow-billed Loon.

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Territoriality is a common behavior in many species wherein individuals defend space from conspecifics to secure resources that will improve their relative fitness (Verner 1977). Many theoretical and empirical studies identify food density as a key attribute of territory size with greater food densities allowing for smaller territories (Hixon 1980; Schoener 1983). Other factors may also influence territory size (Adams 2001), including competition from conspecifics vying for a territory of their own. Greater competition connotes smaller territories, in part because of time and energy demands of territorial defense (Stamps 1990).

Loons (Family Gaviidae) are a group of piscivorous diving birds that exploit freshwater ecosystems in the northern hemisphere during the breeding season (Orta 1992). The most studied species, the Common Loon (*Gavia immer*), actively defends discrete summer territories (Evers *et al.* 2010). Aggressive interactions between conspecifics occur frequently, sometimes resulting in mortality. Piper *et al.* (2008) found that 16-33% of all territorial evictions in male Common Loons were fatal for the displaced owner. For species that expend significant resources defending territories, population regulation is influenced by floaters, individuals that do not currently possess territories but strive for such possession (López-Sepulcre and Kokko 2005).

The Yellow-billed Loon (*G. adamsii*), the rarest of the world's five species of loons, is a sister taxon to the Common Loon (Lindsay 2002) and shares many physical, behavioral and ecological characteristics, differing primarily in bill shape and color (Sjölander and Ågren 1976). They also differ in their choice of breeding habitat - almost entirely low-lying treeless tundra lakes for the Yellow-billed Loon vs. forested lakes for the Common Loon (North 1994; Evers *et al.* 2010). The relatively flat tundra habitat, high lake density, and clustered breeding distribution (Earnst *et al.* 2005) likely promotes the comparatively high degree of visual and vocal interchange between Yellow-billed Loons on adjacent or nearby lakes, noted by investigators experienced with both species. These observations, combined with evidence from experimental studies of other waterbirds in which habitat openness correlated with aggression and territory size (Burger 1977; Bukacinska and Bukacinska 1993), raise the question of whether breeding territories of Yellow-billed Loons are larger than their lower latitude, forest-dwelling congeners. Further, the relatively low primary productivity in high latitude ecosystems relative to more temperate latitudes (Cusens *et al.* 2012) suggests that food density may be lower for Yellow-billed Loons compared to Common Loons, thus potentially leading to larger territories for Yellow-billed Loons. Finally, given game-theoretic models that infer territory acquisition in migratory birds is linked to arrival time (Kokko 1999), one might expect an accentuation of competition for territories in long-distance Arctic migrants with temporally compressed breeding seasons, which may result in lower retention rates of territories within and between years. Some prior studies have suggested that a large proportion of Yellow-billed Loons present on breeding habitats in a given year are not breeding. For instance, based on a time series of aerial population surveys of Yellow-billed Loons, Earnst *et al.* (2005) identified that while many Yellow-billed Loons were on breeding habitats in early June, approximately 50% more Yellow-billed Loons arrived on these habitats in late June after the peak of nest initiation (J. A. Schmutz, unpubl. data). The combination of low Arctic productivity and substantial competition from non-breeders without territories suggests that, for Yellow-billed Loons, territory size and retention may be dynamic and different from conspecifics in other lower latitude ecosystems.

The principal objectives of this study were to: 1) quantify an index of territory size for Yellow-billed Loons nesting in three different regions of the Arctic; 2) evaluate how often Yellow-billed Loons retain a territory in a subsequent breeding season; and 3) ascertain whether timing of arrival on breeding areas affects their likelihood of retaining their territory from a prior year. Previous studies of this nature on Common Loons have been almost entirely conducted via visual sightings of Common Loons marked with color bands (Piper *et al.* 2000; Mitro *et al.* 2008). In contrast, our study of Yellow-billed Loons relied almost exclusively on the locational data provided by satellite transmitters (Platform Transmitter Terminals, or PTTs; Douglas *et al.* 2012). While the use of PTTs was necessitated by the remote, inaccessible nature of much of the breeding habitats for Yellow-billed Loons, it also provides a wealth of unambiguous knowledge about where individuals are located and thus high confidence in understanding spatial relationships.

METHODS

Study Area

Three geographically distinct study areas were chosen for this study (Fig. 1): two sites in Alaska (the Arctic Coastal Plain, ACP, and the Seward Peninsula, SP) and one in the Canadian Arctic (the Daring Lake area in the Northwest Territories, DL). The ACP is expansive and borders the Beaufort and Chukchi Seas. Our sampling occurred in the high density breeding area identified by Earnst *et al.* (2005) south of Barrow and mainly east of the village of Atqasuk (70' 32' N, 155° 30' W). This ecosystem is underlain by ice-rich marine sediments largely devoid of rock wherein thermokarst processes over time lead to the development of simply shaped lakes, their subsequent expansion, and ultimately their drainage (Jorgenson and Shur 2007). The SP study site (66° 18' N, 164° 43' W) is similarly characterized by thermokarst lakes although the site is farther south and warmer than

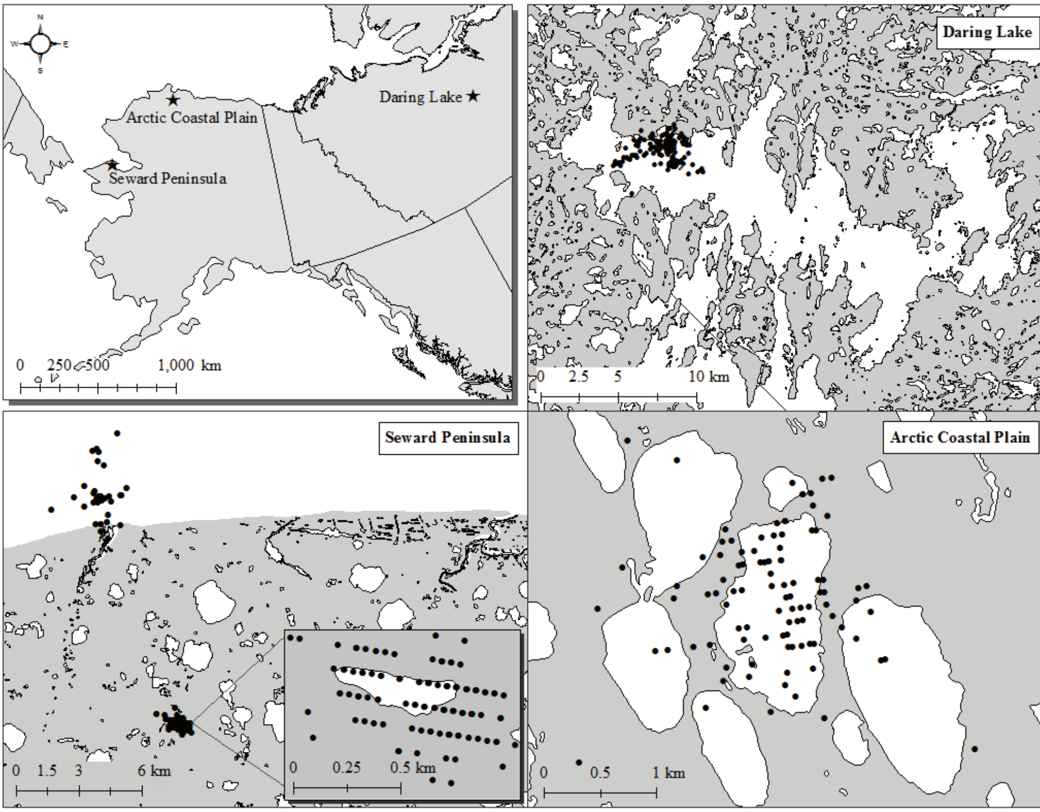

Figure 1. The three study areas where Yellow-billed Loons were captured and fitted with satellite transmitters: the Arctic Coastal Plain in northern Alaska, the Seward Peninsula in northwestern Alaska, and Daring Lake in Northwest Territories, Canada.

the ACP, which may affect the time scale of lake change (Grosse *et al.* 2013). Geographic data on lakes in the ACP and SP, including surface area, are available from the National Hydrography Dataset. Approximately 80% and 20% of the Yellow-billed Loons that breed in the United States occur in the ACP and SP, respectively (Earnst 2004). The DL site (64° 51' N, 111° 37' W) is within the Canadian Shield where shallow soils lie on top of extensive rock that was carved by subglacial flows (Gilbert and Shaw 1994), resulting in extensive lake areas with complex shorelines and deeper waters than observed in the ACP and SP. Despite recent surveys (Groves and Mallek 2012), numbers and distribution of Yellow-billed Loons in Canada are poorly quantified compared to Alaska. However, surveys by Obst (2008) identified the DL site as an area with relatively high densities of this species.

Platform Transmitter Terminals (PTT) Deployment

Yellow-billed Loons were captured using bownets at nest sites or a gillnet and decoy near the nest site, with four to 24 Yellow-billed Loons captured in any given year during 2002-2003 and 2007-2010. Captured Yellow-billed Loons were taken by floatplane or helicopter to a central surgery station. All surgeries to implant PTTs were conducted by wildlife veterinarians with experience with avian abdominal implantation of transmitters. Methods for PTT implants generally followed those outlined by Korschgen *et al.* (1996). Transmitters weighed approximately 63 g, including the percutaneous antenna. PTTs were programmed with a duty cycle wherein signals were sent to satellites for an 8-hr period, followed by a quiescent period that lasted 48 to 120 hr, depending on the season and batch of PTTs. Yellow-billed Loons were taken back to their capture site for release only after they had fully recovered from anesthesia, with time from capture to release usually between 2 and 3 hr. On the ACP and SP, only one adult per nest site was captured. Of the 15 individual Yellow-billed Loons captured at DL, six pairs were in the sample (i.e., 12 individuals); time between captures of mates was about 1 day. Many PTTs emitted data up to 24 months (Range = 1-31 months; mean = 15 months), allowing us to examine the return of loons to their territory in 2 consecutive years after the capture year.

Analysis of PTT Locational Data

All PTT data were disseminated to us from Argos (Argos 2011), which assigns location quality codes to all location estimates. For this analysis of territory retention and size, we only used the two highest location quality classes (Classes 2 and 3), for which average error is estimated at 250-500 m and < 250 m, respectively (Douglas *et al.* 2012). The categorization into these location quality classes is largely a function of how many messages the PTT is able to transmit to the satellites, with more messages resulting in more accuracy in the location estimate. Because territory ownership is common and apparent during nesting and early chick-rearing (J. A. Schmutz, unpubl. data), our examination of territory retention (fidelity) and size focused on a 30-day period - the 20 days prior to and 10 days following the average hatch date per study site for which hatch date was estimated by floating eggs in nests (Rizzolo and Schmutz 2007).

The primary data for evaluating territory retention and size for each Yellow-billed Loon were the set of distances between a central location in the year of capture and each Class 2 or Class 3 location of that loon. For the ACP and SP study sites, we used the lake center as the central location as lakes were generally round, loons used much of the lake area, and nest sites were usually at or near the lake perimeter. For the DL site, nest sites were used as the central location as they were all on moderately large islands far from the mainland shore on very large lakes and, therefore, served as a natural central area of presence. These data from the three study sites are somewhat analogous to radii that imply an area of use, though we statistically analyze just the linear distance data. For an individual Yellow-billed Loon to be included in this analysis, we needed to have 10 high quality locations during the 30-day window of time in a given year. In the year of capture, territorial ownership was implied by the presence of an active nest and attendant pair. Therefore, fidelity to the territory in a subsequent year was evaluated by the similarity of locations in that year relative to the capture year.

Distance data were summarized using the median of all locations per individual within a year. We chose the median because the vast majority of distances were small, and the few large movements that occurred were sometimes reflective of Yellow-billed Loons returning to territories relatively late (and thus on their way to the previous nest site, but not quite there) or of Yellow-billed Loons departing the territory relatively early (some loons that fail to hatch eggs abandon territories and move toward the ocean). Use of the median effectively excludes influences from these large and relatively rare distance measurements that may not reflect territorial behavior. If a Yellow-billed Loon retained its breeding season territory in the first or second year after capture, then the median distance for a loon in that year should be similar to the median distance in the year of capture. More specifically, we calculated the mean median and standard deviation from the set of individuals from a given study site in the year of capture. An individual was then deemed to have returned to its breeding territory in a subsequent year if: 1) its median distance value in that year was less than two times the median for that individual in the year of capture; or 2) its median value was within two standard deviations of the study site population mean of medians in the year of capture.

To address the hypothesis that territory retention may be related to when Yellow-billed Loons first arrive at the breeding site, we used logistic regression wherein study site and arrival date were predictor variables, and the response variable was retention or loss of territory ownership. For all statistical analyses, we used an information-theoretic modeling approach and the Akaike Information Criterion statistic corrected for sample size (AIC_c; Burnham and Anderson 2002) to evaluate whether territory sizes or arrival times varied among areas. The model with the lowest change in AIC values (ΔAIC) is the best supported model among those evaluated. While models with many parameters tend to fit the data well, they are hampered by poor precision. This statistical approach is broadly useful for observational studies, including behavioral ecology questions (Burnham *et al.* 2011) wherein multiple factors are evaluated for their contribution to the response variable.

RESULTS

Nesting phenology differed among study sites with average expected hatch dates, based on egg flotation, of 10 July on the SP, 14 July on the ACP, and 25 July for DL. Correspondingly, our mean capture date was earliest on the SP (29 June), next earliest on the ACP (1 July), and latest for DL (12 July).

A total of 61 PTTs were deployed between 2002 and 2010. Most Yellow-billed Loon individuals were marked on the ACP (n = 36) with a modest number on the SP (n = 10) and at DL (n = 15). Because of mortalities, transmitter failures, or low frequencies of high precision locations, the number of PTTs emitting sufficient locational data for this analysis 1 year after marking was substantially less (ACP: n = 16; SP: n = 4; DL: n = 11). Of these, three, two, and three PTTs, respectively by study site, continued to function and again produced sufficient locational data to evaluate territory fidelity in year 2 after marking. The average number of high quality locations per Yellow-billed Loon was substantial (n = 58, 35, and 20, respectively, in the year of marking, year after marking, and 2 years after marking), providing confidence in movement patterns and identification of territories.

In the year of capture, the mean median movement distance (analogous to territory radius) was 0.42 km (n = 9, SE = 0.06) on the SP, 0.69 km (n = 34, SE = 0.05) on the ACP, and 0.96 km (n = 14, SE = 0.18) for DL. These study area differences in mean territory size were statistically significant, as a model with mean median distances differing among study sites fit much better ($\Delta AIC_c = 0$) than a model assuming equivalence in mean median distances ($\Delta AIC_c = 10.2$). The same ordinal pattern among study sites was evident for lake size as the smallest lakes used by Yellow-billed Loons were on the SP (n = 9, $\bar{x}$ = 0.42 km^2, SE = 0.19), followed by the ACP (n = 34, $\bar{x}$ = 1.83 km^2, SE = 0.43), and then DL (n = 4). Explicit lake area metrics were not readily available for the DL area, but the lakes sampled in this study area visually appear an order of magnitude greater in size than the ACP lakes (Fig. 1).

In the first year after capture, all four Yellow-billed Loons (100%) on the SP, 12 of 16 Yellow-billed Loons (75%) on the ACP, and 6 of 11 Yellow-billed Loons (54%) at DL retained their territories. The small sample size for this analysis precludes a conclusion of site differences in territory retention as the AIC_c value for a model with site differences was 0.55 AIC_c units larger than a null model of no site differences. Across all sites, 22 of 31 (71%, SE = 8) Yellow-billed Loons retained their territory the year after marking.

The mean median distance on the SP was 4.32 km, an order of magnitude greater than in the capture year. However, most (eight of nine) Yellow-billed Loons on the SP made forays out to the ocean environment, a behavior not observed at the other study sites. We excluded these locations because the ocean environment is not likely part of the defended territory of these loons. With these ocean locations excluded, the mean median distance of SP Yellow-billed Loons was 0.36 km (n = 4, SE = 0.08), similar to the value in the capture year. Among Yellow-billed Loons that retained their territory, the mean median distance in the year after capture for the ACP was 0.62 km (n = 12, SE = 0.06) and for DL it was 1.04 (n = 6, SE = 0.19). These means are similar to those from the year of capture. Correspondingly, in this year after capture, this index of territory size appears to differ among study sites.

On the SP and ACP study sites, one and three Yellow-billed Loons, respectively, returned in the second year after capture with sufficient data for analysis. All four birds had retained their territory the previous year and again retained their territory in the second year after capture. At DL, three birds exhibited sufficient data in the second year after capture. Two of these had retained their territory in the previous year and again retained their territory in the second year after capture. The third Yellow-billed Loon had failed to retain its territory in the year after capture but, in the following year, it reacquired its territory that it held in the capture year.

In the year after capture, four birds from the ACP and five birds from DL failed to retain their territories from the previous year. Eight of these nine birds spent some time in June or July very close to their previous territory. On the ACP, two birds spent time in late June localized on an adjacent lake, possibly attempting to nest. However, in July, they then spent some time on the periphery of their previous territory on their original lake. A third Yellow-billed Loon also visited its prior territory briefly in late June, but then spent most of July moving among a few lakes that were 3-5 km from its territory in the previous year. The fourth Yellow-billed Loon from the ACP never came closer than 45 km to its territory from the capture year. It appeared to move among a small cluster of lakes in late June and then migrated back to coastal habitats away from the typical nesting areas. At DL, two of the Yellow-billed Loons that failed to retain their territories appeared to stay close by, near the periphery of their previous territory. The other three wandered broadly, staying 3-6 km away from their previous territory.

Yellow-billed Loons from the SP were excluded from the analysis of territory retention relative to arrival date as all birds retained their territories. Five models were contrasted to evaluate whether study site (ACP vs. DL), date, or the interaction of site and date affected the likelihood of territory retention. The best fitting model was the most complex one that included the interaction of site and date (Table 1). For both

Table 1. Probability of a Yellow-billed Loon not retaining its breeding territory from year *i* in relation to the timing of arrival at the breeding site in year *i* + 1. Eleven days were added to each individual from the Arctic Coastal Plain site so that sample populations from both study sites had an estimated common mean hatch date of 25 July. Relative fit of logistic regression models were evaluated with the Akaike Information Criterion adjusted for sample size (AIC_c; Burnham and Anderson 2002). The R^2 of the logistic regression model was 0.42 and max rescaled R^2 was 0.58, which provide indications of how well the best ranking model explains variation in the data (SAS Institute, Inc. 2008).

Covariates in Model	Number of Estimated Parameters	AIC_c Weight	ΔAIC_c
Day of June, Site, Day of June × Site	4	0.66	0.0
Day of June, Site	3	0.21	2.3
Day of June	2	0.11	3.6
Intercept (null)	1	0.01	8.7
Site	2	0.01	9.5

the ACP and DL, Yellow-billed Loons that arrived at the breeding site relatively late had higher probabilities of losing their territory. However, the temporal effect of date was steeper at the ACP wherein the variation in dates of first arrival were more tightly aggregated in time relative to DL (standard deviation of arrival dates at the ACP was 4.6 days, about half that for DL [9.8 days]), yet had a larger impact on territory retention (Fig. 2).

DISCUSSION

In response to our principal objectives, we quantified territory size, between-year territory retention rate, and the relationship of how the timing of arrival after spring migration affects territory retention. Variation in size of breeding territories of Yellow-billed Loons among ecosystems may largely reflect differences in geomorphology. Lakes in the SP and ACP study sites have a similar history of evolution, but with smaller lake sizes on average on the SP (Grosse *et al.* 2013). Small lake size can confer limited foraging opportunities; for Common Loons, multiple lakes are used for foraging when the nesting lake is less than 24 ha (Piper *et al.* 1997). On the SP, eight of nine Yellow-billed Loons regularly flew between the ocean (Chukchi Sea) and their nest lakes (7-53 ha; Fig. 1), thus indicating that more prey resources were required. On the ACP, where lakes are larger, there was a low frequency of lakes containing multiple Yellow-billed Loon territories (< 3% of 330 lakes; T. B. Haynes, unpubl. data). The smallest lake on the ACP with two territories was 206 ha. In contrast, the smallest lake with multiple Common Loon territories was 29 ha, and at least 22 other lakes smaller than 206 ha held multiple Common Loon territories (Evers 2001; Evers *et al.* 2010). Although territory size of Common Loons has not been explicitly evaluated with PTT locational data, these contrasts between lakes with one vs. two territories suggest that Yellow-billed Loons use larger territories than Common Loons. The basis for species differences in territory size are unknown, but may reflect differences in prey resource densities or aspects of their social behavior in tundra vs. forested environments.

The ocean movements made by most SP loons were an order of magnitude greater in distance than territorial movements (4.32 km vs. 0.36 km). Short flights for heavily wing-loaded birds such as loons (Poole 1938) is costly (Nudds and Bryant 2000), implying that foraging opportunities within SP lakes were insufficient or at least less profitable than those in the nearby marine habitats. Though such ocean forays are likely important to breeding success, we did not include them in our calculations of territory size as forage fish in oceanic systems are highly mobile and not readily defended (Fauchald 2009). Interestingly, of six Yellow-billed Loons on the ACP that nested within 10 km of the ocean (Beaufort Sea), only one of these birds made repeated use of the nearby marine waters, implying the ratio of foraging profitability of its nest lake relative to the nearby ocean was greater than that encountered at the SP.

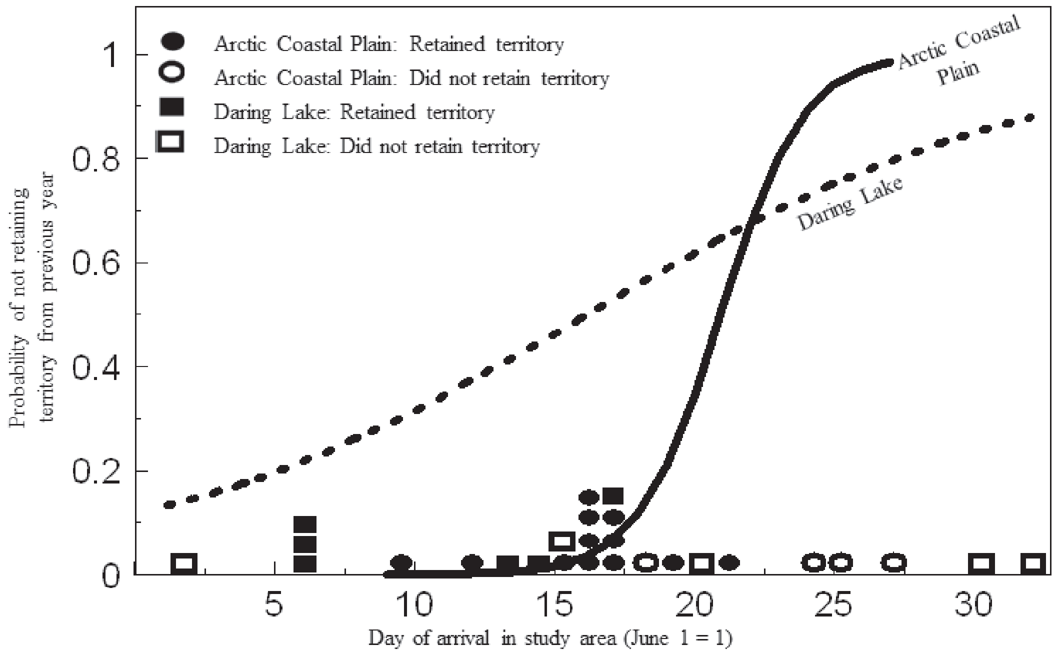

Figure 2. Probability that a Yellow-billed Loon arriving at the breeding area will not retain its territory from the previous year. The dotted and solid lines represent the date-specific probabilities of failing to retain its territory. The squares and ovals along the x-axis represent individual data points (e.g., on 6 June, three individuals arrived at the Daring Lake study area). The real arrival dates for Yellow-billed Loons at the Arctic Coastal Plain (ACP) are actually 11 days earlier than portrayed here as 11 days were added to the ACP data to achieve a common mean hatch date for the two populations. Probability of not retaining a territory = exp(-8.1512 + 0.4036 * Day – 6.1234 * Site + 0.2782 * Day * Site) / (1 + exp(-8.1512 + 0.4036 * Day – 6.1234 * Site + 0.2782 * Day * Site)), where Site = 1 for ACP and Site = -1 for DL.

Lakes at the DL site had complex shoreline configurations, were an order of magnitude larger than SP and ACP lakes, and geometrically resembled lakes often used by Common Loons (Evers *et al.* 2010). Though we lack data on fish communities, the larger territory sizes at this site may be partly a function of prey densities. In many ecosystems, territory size is inversely related to prey density (Hixon 1980). Our impression was that ecosystem productivity was less at DL than on the ACP and SP, a view consistent with satellite observations of spatial variation in net primary productivity among our study sites (Hicke *et al.* 2002). Potentially related to lower productivity, densities of Yellow-billed Loons in Arctic Canada appear to be about half that observed on the ACP and SP (Groves and Mallek 2012; Larned *et al.* 2012).

Indices of territory size on the ACP appear congruent with efforts to minimize impacts on Yellow-billed Loons from oil and gas development. The U.S. Department of the Interior's Bureau of Land Management, which manages the National Petroleum Reserve in Alaska where more than 75% of the U.S. population breeds, identified stipulations that any development for energy extraction must be 1.6 km or more away from Yellow-billed Loon nest sites and 500 m away from the remainder of the nesting lake shoreline (U.S. Bureau of Land Management 2013). This distance is more than twice our mean observed analog of a territory radius - the median distance of movements for 34 loons on the ACP. A median distance movement is likely an underestimate of an actual territory radius, but a true territory radius is unlikely to be more than the 1.6 km buffer (U.S. Bureau of Land Management 2013).

Our sample size was too limited to detect clear differences in territory retention among study areas. However, the low point estimate (55%) of territory retention at the DL site may be a function of the large lake sizes interacting with territorial behavior. At DL, the indefinite perimeter of a territory was usually in the middle of the open water of a large lake. Thus, other Yellow-billed Loons, both territory and non-territory holders, could more easily intrude through swimming (vs. intruding onto a smaller lake through more energetically costly flight behavior), which has significant adverse ramifications for territory retention (Evers 2001) and reproductive success (Piper *et al.* 2006). In contrast, on the ACP and SP sites with much smaller lakes, territories frequently spanned the entire lake and, thus, intruding Yellow-billed Loons were more likely dissuaded from flying into an occupied territory through territorial vocalizations, which likely results in higher territory retention and reproductive success.

Most (71%) Yellow-billed Loons retained their territory in the following year. This retention rate is similar to but somewhat less than that of Common Loon breeding populations in the Great Lakes and northeastern United States (Evers *et al.* 2010). Evers (2001) found an average between-year retention rate of 80% (n = 1,904). A lower rate of territory retention in Yellow-billed Loons might be expected, based on a higher proportion of the population composed of non-breeders. Earnst *et al.* (2005) observed that a large annual influx of Yellow-billed Loons to the ACP breeding area occurred in late June after most nests were initiated (J. A. Schmutz, unpubl. data), implying that approximately a third of the loons in the stable summering population were non-breeders. In contrast, stable Common Loon populations are observed when 20% of the population is composed of non-breeders (Evers *et al.* 2010). Higher proportions of non-breeders connote higher frequencies of territorial intrusion and likely higher rates of territorial turnover (Piper *et al.* 2006).

An alternative explanation for the lower rate of territory retention in Yellow-billed Loons could be adverse impacts from capture and implantation of satellite transmitters, which weighed 1.0-1.7% of adult mass. On the ACP, 24 Yellow-billed Loons were marked with just color bands and the annual rate of return to territory the following year was 89%, suggesting a higher rate of territory retention for Yellow-billed Loons without implanted transmitters (B. D. Uher-Koch and J. A. Schmutz, unpubl. data). In the year of capture, most Yellow-billed Loons with transmitters lost their nest, which may reduce their probability of territory retention the following year. Transmitters can impact a variety of demographic attributes (Barron *et al.* 2010), although surgical implantation minimizes those impacts compared to external devices (Hupp *et al.* 2006; White *et al.* 2013). Additionally, estimates of annual survival of the PTT-marked loons was 91% (J. A. Schmutz, unpubl. data), similar to Common Loons (Mitro *et al.* 2008). The color-band resightings occurred in different years than the transmitter work, thus annual variability in demography confounds these inferences. Because of the persistent pattern across many years of late arriving Yellow-billed Loons (Earnst *et al.* 2005), we suggest a larger floater population generally reduces territory retention in Yellow-billed Loons compared to Common Loons.

The majority of changes in territory ownership in Common Loons occur via various behavioral mechanisms shortly after arrival at the breeding site (Piper *et al.* 2000). While we do not have behavioral data to attribute directly a mechanism for territory loss in Yellow-billed Loons, the relationship between arrival date and territory retention is suggestive of passive occupation, one of the most common manners for territory change in Common Loons. Passive occupation means that a loon arrives at the breeding site and occupies a territory that is presently unoccupied but was occupied the previous year (e.g., by a PTT-marked bird). Once on site, individuals likely rapidly gain familiarity with the territory, which then confers an advantage for maintaining that territory if later challenged, such as by a late arriving PTT-marked bird (Zack and Stutchbury 1992; Sergio *et al.* 2009). Late arriving Yellow-billed Loons that failed to retain their territory wandered locally (Piper *et al.* 2000), usually 2-6 km from their prior territory. We did not document displaced Yellow-billed Loons occupying a new territory, and every Yellow-billed Loon except one at least transiently visited its territory from the prior year. Further, non-breeding Yellow-billed Loons are regularly observed on neighboring lakes and reflect the part of the population that may frequently intrude and then challenge territorial breeding pairs (Kokko 1999; Earnst *et al.* 2005; J. A. Schmutz, unpubl. data), which is a prevalent behavior for Common Loons (Piper *et al.* 2006). As has been inferred for Common Loons (Evers *et al.* 2010; Piper *et al.* 2012), Yellow-billed Loons on the breeding area are presumably 3 years old or older.

The difference among study areas in the magnitude of the date effect on territory retention connotes that there is greater competition for territories at the ACP compared to DL (Kokko 1999). We mentioned earlier the high numbers of floaters on the ACP based on aerial survey data and timing of nesting. In our limited studies at DL, the densities of Yellow-billed Loons appeared low, similar to the relatively low densities documented in the Arctic islands of Canada (Groves and Mallek 2012), and, therefore, there was potentially less competition for territories at DL. However, the floaters that do occur at DL may be more effective at displacing territory owners because of the aforementioned ability to intrude across the large lake surface.

Yellow-billed Loons exhibit territorial behavior and patterns of territory retention generally similar to Common Loons. By tracking known individuals, we documented a strong pattern of returning to territories occupied in a previous year. Those that failed to retain their territory did not attain territories elsewhere, but remained on neighboring lakes. These collective patterns suggest that breeding territories of high quality are limited. What defines high quality habitat is presently unclear; models of physical characteristics of lakes do not have strong explanatory power (Stehn *et al.* 2005; Earnst *et al.* 2006). Recent studies of Common Loons suggest that conspecifics may simply use the presence of successful breeding pairs as an indication of habitat quality in a local area (Piper *et al.* 2006; Hammond *et al.* 2012). Ongoing studies of Yellow-billed Loons on the ACP are evaluating the role of fish communities and lake characteristics in explaining the distribution and breeding success of loons (Haynes *et al.* 2013), as well as examining patterns of territory establishment across the landscape.

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LITERATURE CITED

Adams, E. S. 2001. Approaches to the study of territory size and shape. Annual Review of Ecology and Systematics 32: 277-303.

Argos. 2011. Argos User's Manual. Argos Service, Toulouse, France. http://www.argos-system.org, accessed 5 January 2013.

Barron, D. G., J. D. Brawn and P. J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behavior and ecology. Methods in Ecology and Evolution 1: 180-187.

Bukacinska, M. and D. Bukacinski. 1993. The effect of habitat structure and density of nests on territory size and territorial behavior in the black-headed gull (*Larus ridibundus*). Ethology 94: 306-316.

Burger, J. 1977. Role of visibility in nesting behavior of *Larus* gulls. Journal of Comparative and Physiological Psychology 91: 1347-1358.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York, New York.

Burnham, K. P., D. R. Anderson and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65: 23-35.

Cusens, J., S. D. Wright, P. D. McBride and L. N. Gillman. 2012. What is the form of the productivity-animal-species-richness relationship? A critical review and meta-analysis. Ecology 93: 2241-2252.

Douglas, D. C., R. Weinzierl, S. C. Davidson, R. Kays, M. Wikelski and G. Bohrer. 2012. Moderating Argos location errors in animal tracking data. Methods in Ecology and Evolution 3: 999-1007.

Earnst, S. L. 2004. Status assessment and conservation plan for the Yellow-billed Loon (*Gavia adamsii*). Scientific Investigations Report 2004-5258, U.S. Department of the Interior, Geological Survey, Reston, Virginia.

Earnst, S. L., R. Platte and L. Bond. 2006. A landscape-scale model of Yellow-billed Loon (*Gavia adamsii*) habitat preferences in northern Alaska. Hydrobiologia 567: 227-236.

Earnst, S. L., R. A. Stehn, R. M. Platte, W. W. Larned and E. J. Mallek. 2005. Population size and trend of Yellow-billed Loons in northern Alaska. Condor 107: 289-304.

Evers, D. C. 2001. Common Loon population studies: continental mercury patterns and breeding territory philopatry. Ph.D. Dissertation, University of Minnesota, St. Paul.

Evers, D. C., J. D. Paruk, J. W. McIntyre and J. F. Barr. 2010. Common Loon (*Gavia immer*). No. 313 *in* The Birds of North America Online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. http://bna.birds.cornell.edu/bna/species/313, accessed 13 March 2013.

Fauchald, P. 2009. Spatial interaction between seabirds and prey: review and synthesis. Marine Ecology Progress Series 391: 139-151.

Gilbert, R. and J. Shaw. 1994. Inferred subglacial meltwater origin of lakes on the southern border of the Canadian Shield. Canadian Journal of Earth Sciences 31: 1630-1637.

Grosse, G., B. Jones and C. Arp. 2013. Thermokarst lakes, drainage, and drained basins. Pages 323-353 *in* Treatise in Geomorphology (J. Shroder, Ed.). Academic Press, San Diego, California.

Groves, D. J. and E. J. Mallek. 2012. Migratory bird survey in the western and central Canadian Arctic 2011. Unpublished report, U.S. Department of the Interior, Fish and Wildlife Service, Juneau, Alaska.

Hammond, C. A. M., M. S. Mitchell and G. N. Bissell. 2012. Territory occupancy by Common Loons in response to disturbance, habitat, and intraspecific relationships. Journal of Wildlife Management 76: 645-651.

Haynes, T. B., A. E. Rosenberger, M. S. Lindberg, M. Whitman and J. A. Schmutz. 2013. Method- and species-specific detection of Arctic fishes in lakes on the North Slope, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 70: 1055-1062.

Hicke, J. A., G. P. Asner, J. T. Randerson, C. Tucker, S. Los, R. Birdsey, J. C. Jenkins and C. Field. 2002. Trends in North American net primary productivity derived from satellite observations, 1982-1998. Global Biogeochemical Cycles 16: 2-1–2-14.

Hixon, M. A. 1980. Food production and competitor density as the determinants of feeding territory size. American Naturalist 115: 510-530.

Hupp, J. W., J. M. Pearce, D. M. Mulcahy and D. A. Miller. 2006. Effects of abdominally implanted radiotransmitters with percutaneous antennas on migration, reproduction, and survival of Canada geese. Journal of Wildlife Management 70: 812-822.

Jorgenson, M. T. and Y. Shur. 2007. Evolution of lakes and basins in northern Alaska and discussion of the thaw lake cycle. Journal of Geophysical Research 112: 1-12.

Kokko, H. 1999. Competition for early arrival in migratory birds. Journal of Animal Ecology 68: 940-950.

Korschgen, D. E., K. P. Kenow, A. Gendron-Fitzpatrick, W. L. Green and F. J. Dein. 1996. Implanting intra-abdominal radiotransmitters with external whip antennas in ducks. Journal of Wildlife Management 60: 132-137.

Larned, W., R. Stehn and R. Platte. 2012. Waterfowl breeding population survey, Arctic Coastal Plain, Alaska 2011. Unpublished report, U.S. Department of the Interior, Fish and Wildlife Service, Anchorage, Alaska.

Lindsay, A. R. 2002. Molecular and vocal evolution in loons (Aves: Gaviformes). Ph.D. Dissertation, University of Michigan, Ann Arbor.

López-Sepulcre, A. and H. Kokko. 2005. Territorial defense, territory size, and population regulation. American Naturalist 166: 317-325.

Mitro, M. G., D. C. Evers, M. W. Meyer and W. H. Piper. 2008. Common Loon survival and mercury in New England and Wisconsin. Journal of Wildlife Management 72: 665-673.

North, M. R. 1994. Yellow-billed Loon (*Gavia adamsii*). No. 121 *in* The Birds of North America Online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca,

New York. http://bna.birds.cornell.edu/bna/species/121, accessed 4 February 2013.
Nudds, R. L. and D. M. Bryant. 2000. The energetic costs of short flights in birds. Journal of Experimental Biology 203: 1561-1572.
Obst, J. 2008. Field report on the Yellow-billed Loon *Gavia adamsii* survey at Daring Lake, Northwest Territories, in 2008. Unpublished report, Department of Environment and Natural Resources, Yellowknife, Northwest Territories, Canada.
Orta, J. 1992. Family Phaethontidae. Pages 280-289 *in* Handbook of the Birds of the World, vol. I: Ostrich to Ducks (J. del Hoyo, A. Elliot and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.
Piper, W. H., K. B. Tischler and M. Klich. 2000. Territory acquisition in loons: the importance of take-over. Animal Behaviour 59: 385-394.
Piper, W. H., J. S. Grear and M. W. Meyer. 2012. Juvenile survival in Common Loons *Gavia immer*: effects of natal lake size and pH. Journal of Avian Biology 43: 280-288.
Piper, W. H., C. Walcott, J. N. Mager and F. J. Spilker. 2008. Fatal battles in common loons: a preliminary analysis. Animal Behaviour 75: 1109-1115.
Piper, W. H., J. D. Paruk, D. C. Evers, M. W. Meyer, K. B. Tischler, M. Klich and J. J. Hartigan. 1997. Local movements of color-marked Common Loons. Journal of Wildlife Management 61: 1253-1261.
Piper, W. H., C. Walcott, J. N. Mager, M. Perala, K. B. Tischler, E. Harrington, A. J. Turcotte, M. Schwabenlander and N. Banfield. 2006. Prospecting in a solitary breeder: chick production elicits territorial intrusions in Common Loons. Behavioral Ecology 17: 881-888.
Poole, E. L. 1938. Weights and wing areas in North American birds. Auk 55: 511-517.
Rizzolo, D. J. and J. A. Schmutz. 2007. Egg flotation estimates nest age for Pacific and Red-throated loons. Waterbirds 30: 207-213.
SAS Institute, Inc. 2008. SAS/STAT 9.2 user's guide. SAS Institute, Inc., Cary, North Carolina.
Schoener, T. W. 1983. Simple models of optimal feeding-territory size: a reconciliation. American Naturalist 121: 608-629.
Sergio, F., J. Blas and F. Hiraldo. 2009. Predictors of floater status in a long-lived bird: a cross-sectional and longitudinal test of hypotheses. Journal of Animal Ecology 78: 109-118.
Sjölander, S. and G. Ågren. 1976. Reproductive behavior of the Yellow-billed Loon, *Gavia adamsii*. Condor 78: 454-463.
Stamps, J. A. 1990. The effect of contender pressure on territory size and overlap in seasonally territorial species. American Naturalist 135: 614-632.
Stehn, R. A., R. M. Platte, W. W. Larned, E. J. Mallek, T. K. Mills and D. K. Marks. 2005. Habitat associations of Yellow-billed Loons on the Arctic Coastal Plain of Alaska. Unpublished report, U.S. Department of the Interior, Fish and Wildlife Service, Anchorage, Alaska.
U.S. Bureau of Land Management. 2013. Record of decision, National Petroleum Reserve-Alaska, Integrated Activity Plan. Unpublished report, U.S. Department of the Interior, Bureau of Land Management, Anchorage, Alaska.
Verner, J. 1977. On the adaptive significance of territoriality. American Naturalist 111: 769-775.
White, C. R., P. Cassey, N. G. Schimpf, L. G. Halsey, J. A. Green and S. J. Portugal. 2013. Implantation reduces the negative effects of bio-logging devices on birds. Journal of Experimental Biology 216: 537-542.
Zack, S. and B. J. Stutchbury. 1992. Delayed breeding in avian social systems: the role of territory quality and floater tactics. Behaviour 123: 194-219.