

Post-Breeding Densities, Population sizes and Lake Size Partitioning of Loon Species in Western Chukotka, Russia¹

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Received March 14, 2017; in final form, April 20, 2017

Abstract—Loons (family Gaviidae) breed in small ponds and lakes across Arctic landscapes and are high level predators in the lake ecosystems. As such, they may serve as sentinel species, warning humans of alterations in habitat and ecosystem integrity in a region that is undergoing vast change due to climate warming. Here, we characterized the abundance and habitat use of four arctic breeding species of loons in the plains and surrounding mountains of western Chukotka, Russia. Loon surveys were conducted on foot and by boat from 2009–2015. Loon species differed in their use of the four lacustrine habitat types within the study area. In yedoma habitat, the yellow-billed loon (*Gavia adamsii*) was the most abundant (0.593 birds/km²); on fluvial plain habitat, Pacific loons (*G. pacifica*) outnumbered other loons (0.701 birds/km²); mountain valleys were inhabited similarly by *pacifica* (0.354 birds/km²) and red-throated loons (*G. stellata*; 0.307); and maritime tundra was used only by *pacifica* (1.13) and Arctic loons (*G. arctica*; 0.553). *G. adamsii* was not observed in mountain valleys or maritime tundra. Mountainous portions of rivers were predominantly occupied by *stellata* and *pacifica*, and lowland rivers by *stellata*, *pacifica* and *arctica*. There was a significant difference in the size of lakes occupied by the four congeners. The largest loon, *adamsii*, occupied the largest lakes (0.69 km²), 80% larger than lakes utilized by *pacifica* (0.39 km²) and *arctica* (0.38 km²), and 35 times larger than *stellata* (0.02 km²). Most lakes were occupied by a single loon species (125/162, 77.2%).

Keywords: Arctic loon, diver, *Gavia arctica*, Pacific loon, *Gavia pacifica*, red-throated loon, *Gavia stellata*, yellow-billed loon, *Gavia adamsii*, Chukotka, Russia

DOI: 10.1134/S1995425517060130

INTRODUCTION

Few avian ecological studies have been undertaken in remote regions of Western Chukotka, Russia (Lebedev and Filin, 1959; Stishov, 1990; Krechmar et al., 1991; Hodges and Eldridge, 2001; Solovyeva, 2012). Information about the distribution and density of species in the region could be important for management, especially with respect to protected species, such as the yellow-billed loon. Loons (known as divers in Europe) are considered an indicator of ecosystem health (Evers, 2006), but little is known about the abundance and habitat preferences of the four loon species in Russia (Il'ichev and Flint, 1982; Solov'ev, 1991, 1992). With the threat of increasing oil exploration and development in the arctic (Earnst, 2004), the need to identify key breeding areas in Russia is a critical component of any global conservation plan.

Gaviiformes is a monophyletic order consisting of five species worldwide that exhibit high adult survivorship, delayed maturity and low reproductive success (Paruk et al., 2014). In addition, they are piscivorous, migratory, and aggressive to both conspecifics and congeners (Barr et al., 2000; Russell, 2002; Piper et al., 2008). The five species vary greatly in size: red-throated loons (*G. stellata*) body mass 1.0–2.2 kg; Pacific loons (*G. pacifica*) body mass 1.2–3.0 kg; Arctic loons or black-throated divers (*G. arctica*), body mass 3.0–4 kg; Common loons or great northern divers (*G. immer*) body mass 3.5–7.0 kg; and yellow-billed loons or white-billed divers body mass 3.7–7.0 kg. The common loon breeds at lower latitudes than the other four species, which breed principally in the arctic (Evers et al., 2010). The red-throated loon is circumpolar, breeding across Eurasia and North America. The Pacific loon breeds in a narrow strip of land in Northeastern Siberia, from the Yana River

¹ The article is published in the original.

delta to Chukotka, and across northern Alaska and northern Canada to the Hudson Bay (Il'ichev and Flint, 1982; Russell, 2002). The Arctic loon breeds across northern Eurasia, from the N. British Isles and Scandinavia eastward across arctic Russia to the Bering Strait. In the United States, it is only known to breed in western Alaska on the Seward Peninsula (Russell, 2002). The two species, Arctic and Pacific loons, overlap along a narrow coastal strip in North-eastern Siberia (Il'ichev and Flint, 1982). The yellow-billed loon breeds in the high arctic of Siberian Russia and western North America (Il'ichev and Flint, 1982; Fair, 2002), but its distribution is better known in the latter. All four arctic nesting species are found in western Chukotka.

The yellow-billed loon is listed in the Red Data Book of the Russian Federation as category 3—rare (*Krasnaya kniga...*, 2001), and although they were recently deemed as not threatened or endangered in the United States (*Endangered...*, 2014), they remain one of the rarest breeding birds in North America (Earnst et al., 2005). The IUCN lists the global population of yellow-billed loons as near threatened due to suspected decline in numbers, and the European population as vulnerable (based on a small wintering population). It also states that too little information is available to definitively produce global species trends (BirdLife International, 2015). Yellow-billed loon numbers in Alaska are stable or slowly increasing (Stehn, 2014; Haynes et al., 2014). Current populations face a number of environmental threats, including climate change (Leibezeit et al., 2012), subsistence hunting (Schmutz, 2009), bycatch in commercial fishnets, contaminants (e.g., mercury (Evers et al., 2014) and PCBs, (Schmutz et al., 2009), and the declining health of the marine ecosystems in Asia (Fair, 2002). The identification of both breeding and wintering areas of yellow-billed loon in Russia is critical to understanding the current status of the species. Although the other four loon species are listed as least concern, all but Pacific loon are experiencing a decreasing population trend (Solovyeva, 2012; BirdLife International, 2015).

Gavia species have been suggested as important bioindicators of ecosystem quality and contaminant presence. With looming threats to arctic habitats, including oil exploration and climate change, baseline data for arctic species will be important to inform governing bodies, industries, and conservationist organizations. We conducted surveys for the four arctic-breeding Gaviiformes, with the following objectives: (1) quantify the presence and density of each loon species, with the greatest conservation interest in the Yellow-billed Loon, (2) characterize habitat and lake size use among the congeners, and (3) estimate population sizes. Because *Gavia* young remain with their parents for a minimum of seven to eight weeks, they are a good candidate to approximate presence/absence and density using post-breeding surveys, which occur after the

young have hatched, but while they still can be observed (for loons, in August).

STUDY AREA

The study area was located in the plains and surrounding mountains of western Chukotka, Russia. The study area encompassed 28 395 km²: 137 km from north to south between 68.2 and 69.4° N, and 207 km from west to east between 166.2 and 171.3° W (Fig. 1). The primary survey areas were two lowlands, Rauchua Lowland, including the lower Rauchua River catchment, Kyttyk Peninsula, and Ayon Island, and Chaun Lowland, in the junction of the Palyavaam, Chaun, and Pucheveem rivers (Fig. 1). These arctic habitats consisted primarily of lowland tundra interspersed with numerous shallow lakes and pools. Lowlands were not contiguous, but separated by mountains. Permafrost was continuous, and the depth of ground thaw reached 0.2–1.3 m by late August. Summers are short and cool in the region, with a daily mean temperature in July of less than 10°C. The dominant vegetation consists of sedges (*Carex* spp.), willows (*Salix* spp.), and tussock-forming cottongrass (*Eriophorum vaginatum*), which cover most of the gentle slopes. Alder (*Alnus* spp.) and willow (*Salix* spp.) shrubs are common on river banks (Yurtsev et al., 2010).

METHODS

Loon Surveys

We surveyed for the four species of arctic-breeding loons using two different strategies: land-based walking surveys for lake tundra, and boat-based surveys on river and marine habitat. Red-throated and yellow-billed loons were easily identifiable due to their conspicuous markings; however, due to the similarity between Arctic and Pacific loon (Sibley, 2000) we decided to record a sighting of one or the other as *G. pacifica/arctica*. We did this for 2009 and 2010, but as we gained familiarity with the identification of each species, we began to distinguish the two during surveys in 2011. However, due to low visibility during marine surveys, some unidentified Pacific-Arctic loon appears in marine data in later years.

Surveys of Lake Tundra

Surveys for loons were conducted on land by foot. Study plots were pre-selected based on the accessibility of the area from a river or seacoast reachable by motor-boat. Plots were drawn considering lakes and adjacent tundra between lakes. Areas of each habitat type within the study area were calculated as lakes plus tundra. In late July and August of 2009–2013 and 2015, two to four personnel visited all lakes within each plot (survey efforts are given in Table 1). A total of 373 lakes were visited. We scanned lakes for loons using 8 × 10 binoculars or a 20–30× scope. Observa-

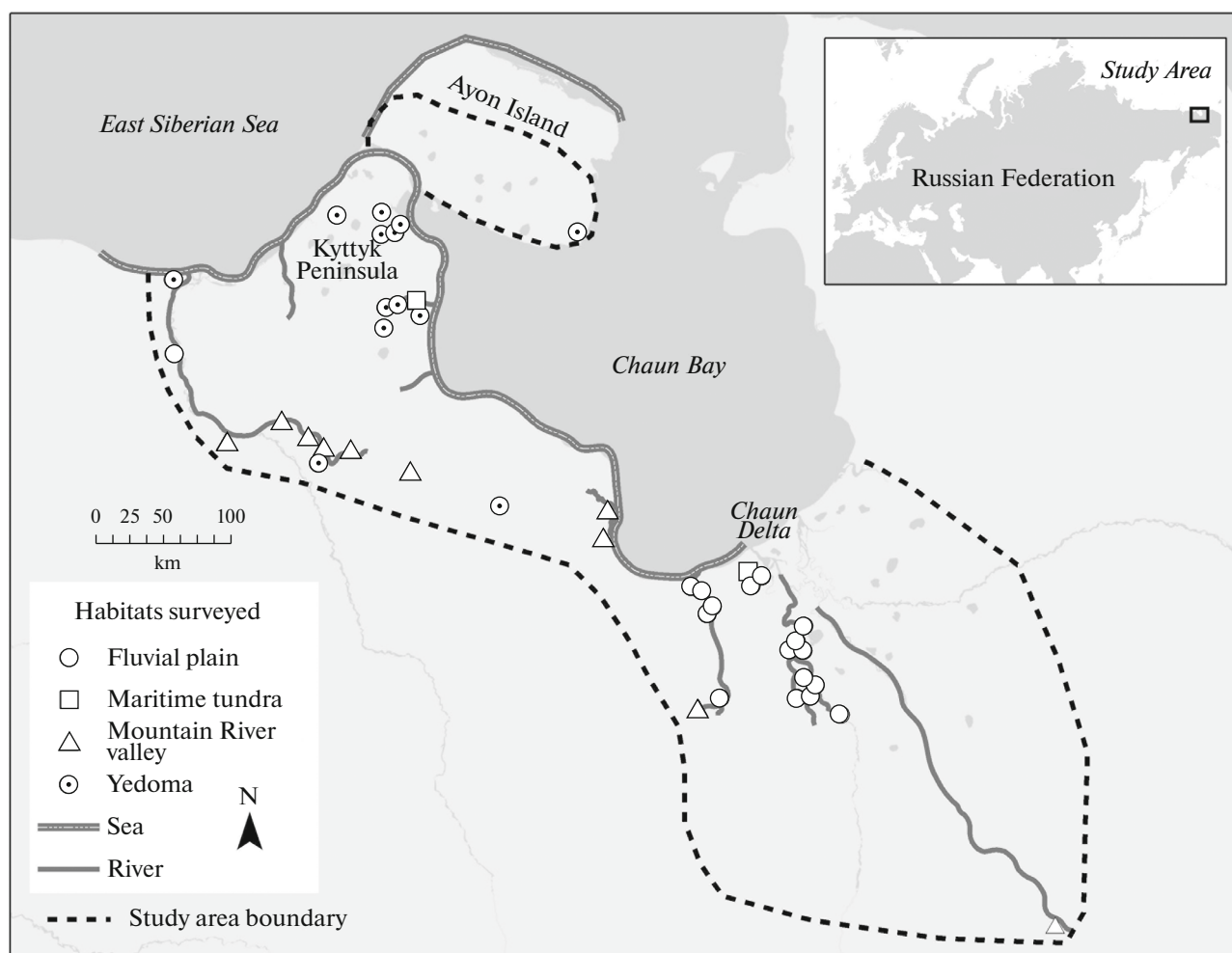


Fig. 1. Locations of loon surveys by ground (2009–2011, 2013, and 2015) and boat (2009–2015) in western Chukotka, Russia.

tions on large lakes (>1 km in diameter) lasted for 20–30 minutes to spot and identify loon species and group composition. Open areas with numerous ponds were scanned from at least two points to detect red-throated

loon. All loon sightings were recorded on a Google Earth image. The species of loon, number of adults, and number of chicks were recorded for each observation.

Table 1. Survey efforts in western Chukotka in 2009–2015. Habitat types are (S) maritime tundra (salt marsh), (Y) yedoma, (F) fluvial plain, and (M) mountain river valley

Year	Length of river surveys, km	Length of marine survey, km	Area of tundra surveys, km ²	Habitat type during tundra surveys
2009	32.4	166.3	126.8	S, Y
2010	154.8	304.1	212.3	F, M, Y
2011	132.6	43.1	226.9	F, Y
2012	142	0	22.3	M
2013	215	15.1	127.7	S, F, M
2014	136.5	196.6	0	
2015	0	0	114.7	S, Y
Total	813.3	725.2	830.7	

River and Marine Surveys

Boat surveys for loons were conducted along rivers and seacoasts from 2009–2014 (although no marine surveys were done in 2012), and sightings were opportunistically recorded when moving between field camps. One or two personnel recorded loons on the river or within 100 m of the boat when at sea. All of the rivers in lowland tundra and associated mountains were surveyed within the study area, for a survey total of 447.0 km of rivers within lowlands and 268.2 km within mountains (Table 1). Coastal marine waters of the eastern part of the East Siberian Sea and the western part of Chayn Bay were surveyed in different years; linear surveys averaged 34.5 km (range 8–82.6 km; $n = 21$; Table 1).

Habitat Classifications

Surveys of Lake Tundra. For walking surveys, we categorized lake tundra into one of four habitat types used by loons within the study area: (1) maritime tundra, (2) yedoma, (3) fluvial plain, and (4) mountain valleys. Maritime tundra, which is also known as salt marsh, is situated along the coast and along slowly running rivers of Kyttyk Peninsula. It consists of shallow, brackish lakes with convoluted coastlines that are flooded by the sea during wind-induced tides. Only a small area of this habitat was surveyed for loons (17.7 km², or 3.1% of this habitat type). Yedoma is a remnant of Pleistocene plains dominated by fine sediments and intensive syngenetic ice wedges that make up 70–90% of the stratum volume. In yedoma landscapes, lakes are freshwater, relatively large and deep, and are of thermokarst origin. Lake depth was estimated by examining vertical thickness of ice wedges and could reach >20 m; two measured lakes had a maximal depth of 10m. A total of 597.3 km² of yedoma were surveyed (21.6% of this habitat). Fluvial plain is formed of old and recent floodplains and distinguished by lower elevations and smaller ice-wedges than yedoma. Freshwater lakes develop everywhere on fluvial plain, from immediately adjacent to rivers to 10–12 km from them. Depth of lakes was determined by vertical thickness of massive ice wedges to be less than 10 m. Three large lakes had a maximal depth of 4.5 m on fluvial plain, and a majority of lakes were >2 m in depth (frozen to the bottom in winter). Several dozen lakes were measured during searches for fish and breeding ducks. A total of 152.5 km² (4.5%) of fluvial plain were surveyed for loons within our study area. Mountain valley habitat is narrow and contains small lakes or ponds (<0.1 km) situated close to rivers. A total of 62.7 km² of mountain valley habitat were surveyed (2.9%). All totaled within the study area, the most common habitat type was fluvial plain (3375 km²), followed by yedoma (2762 km²), mountain valley (2135 km²), and maritime tundra (575 km²). Other areas were mountains without waterbodies.

River and marine surveys. Loons observed at sea were recorded as such and not placed in any of the four terrestrial habitat types. Loons observed on rivers were recorded as such, and we noted whether the river was located in mountains or lowlands.

DENSITY ESTIMATIONS

Surveys of Lake Tundra

To calculate post-nesting densities, we summed the number of individuals observed by area surveyed for each species. Because Pacific and Arctic loons could not be separated in 2009 and 2010, post-breeding densities are reported as combined densities for those years and as separate densities for each species in 2011, 2013, and 2015.

River and marine surveys. Densities along rivers were expressed in individuals/km of river and along the seacoast in individuals/km in 100 m wide strips. We ignored unidentified loons when calculating densities on rivers and at sea.

LAKE SIZE USE BY CONGENERS

The surface area of each lake was digitized and calculated using GIS. Pond sizes were measured in the field. We used an analysis of variance (ANOVA) to investigate if lake size used by congeners differed among loon species. Post hoc tests (Tukey HSD) were performed to identify differences in lake size among congeners. Data were log transformed because they did not meet assumptions of normality (Kolmogorov-Smirnov tests). We set $\alpha = 0.05$ and performed statistical analysis using R (R Development Core Team, 2008).

POPULATION ESTIMATES

We estimated loon populations for our entire study area by species as a sum of (1) loon densities in surveyed areas by habitats multiplied by areas of each habitat, (2) densities along rivers multiplied by river length by habitat, and (3) densities at sea multiplied by marine route length and for the 1 km wide strip. We increased our area to a 1 km strip rather than 100 m because loons were routinely found this distance from shore (and sometimes up to 6km from shore), and we assumed believe that 1km offshore is typical habitat for loons.

RESULTS

Species Abundance

Across all years and survey types, the combined Pacific and Arctic loon species were most abundant (1118/1788 loons; 62.5%), followed by yellow-billed loon (496/1118; 27.2%), and red-throated loon (174/1118; 9.73%). In order to determine relative abundance of Pacific loon and Arctic loon, we exam-

Table 2. Numbers of four congeneric *Gavia* species recorded at sea (S), on rivers (R) and on tundra (T) in western Chukotka, Russia, 2009–2015

Year	Red-throated loon			Pacific loon			Arctic loon			Pacific/arctic loon			Yellow-billed loon		
	S	R	T	S	R	T	S	R	T	S	R	T	S	R	T
2009	4	3	15	*	*	*	*	*	*	61	16	99	18	6	99
2010	12	9	3	*	*	*	*	*	*	60	41	120	37	10	89
2011	0	5	4	*	13	80	*	25	78	16	†	†	19	4	113
2012	—	42	7	—	32	9	—	16	2	—	†	†	—	1	0
2013	3	24	4	3	26	104	4	50	34	†	†	†	0	20	0
2014	10	26	—	53	50	—	18	18	—	27	†	—	26	4	—
2015	—	—	3	—	—	39	—	—	24	—	—	†	—	—	50
Total	29	109	36	56	121	232	22	109	138	164	57	219	100	45	351
By species	174			409			269			440			496		

* Species not distinguished ; —, survey type not conducted ; †, combined category unused.

Table 3. Average (+ SE) post-breeding densities (#/km) of four congeneric *Gavia* species from boat surveys by habitat type at sea and on the rivers in western Chukotka, Russia, 2008–2014

Species	LOCALITY/HABITAT			
	marine		river	
	East-Siberian Sea	Chaun Bay	mountain	lowland
<i>G. stellata</i>	0.010 ± 0.098	0.034 ± 0.013	0.170 ± 0.082	0.139 ± 0.025
<i>G. pacifica</i>	0.366 ± 0.001	0.307 ± 0.161	0.169 ± 0.104	0.156 ± 0.053
<i>G. arctica</i>	0.114 ± 0.002	0.119 ± 0.087	0.092 ± 0.012	0.150 ± 0.030
<i>G. adamsii</i>	0.430 ± 0.315	0.317 ± 0.149	0.039 ± 0.030	0.070 ± 0.023
Total	0.920	0.777	0.470	0.515

ined numbers from 2011–2015 (when they were distinguished) and removed marine data, in which there are some cases of unidentified Pacific /Arctic loon. In this subset of data, Pacific loon is most common (353/907; 38.9%), followed by Arctic loon (247/907; 27.2%), yellow-billed loon (192/907; 21.2%), and red-throated loon (115/907; 12.7%). Red-throated loon was least common loon in all years (see table 2 for a breakdown of loon numbers by species, survey type, and habitat).

Density Estimates

Lake tundra. Loon post-breeding densities by habitat types are presented in Fig. 2 as averages across years ± SD (number of birds/km²). In yedoma habitat, yellow-billed loon was the most abundant loon with an average density (±SE) of 0.593 ± 0.081, followed by Pacific loon (0.343 ± 0.002), Arctic loon (0.273 ± 0.041), and red-throated loon (0.038 ± 0.03 birds/km²). On fluvial plain habitat, Pacific loon outnumbered other loons with density of

0.701 followed next by Arctic loon (0.260). Both yellow-billed loon and red-throated loon were uncommon in this habitat type, having densities of 0.027 and 0.017 birds/km², respectively. Fluvial plains were surveyed only in 2010 and 2013. Mountain valleys were inhabited by Pacific loon, red-throated loon and Arctic loon, with densities of 0.354 ± 0.060, 0.307 ± 0.166 and 0.213 ± 0.099 birds/km², respectively. Maritime tundra was used only by Pacific loon and Arctic loon with densities of 1.125 and 0.553 birds/km², respectively. Yellow-billed loon was not observed in mountain valleys or maritime tundra.

River and marine. In mountainous portions of rivers, sightings of red-throated loon and Pacific loon were relatively common, of Arctic loon were uncommon, and of yellow-billed loon were rare (all densities presented in Table 3). In lowland portions of rivers, densities of Pacific, Arctic, and red-throated loon were similar, and yellow-billed loon was uncommon. In contrast, at sea, yellow-billed loon had the highest density among the congeners both at the East-Siberian Sea study site and at Chaun Bay. Pacific loons

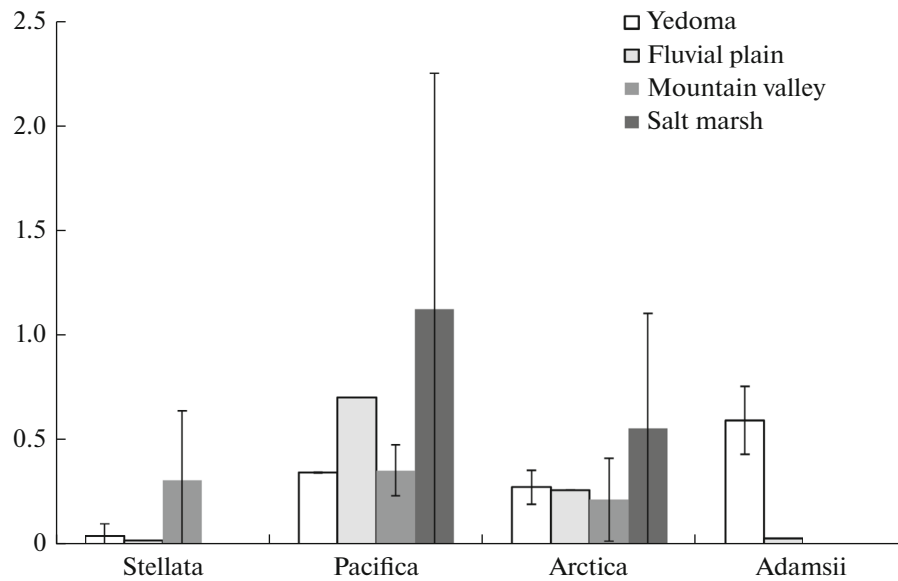


Fig. 2. Average loon densities (across years), separated by species and habitat type in lacustrine tundra in Chukotka, Russia, yellow-billed and red-throated loon from 2009–2011, 2013, and 2015, Pacific and Arctic loon from 2011–2013 and 2015. Error bars represent standard deviations.

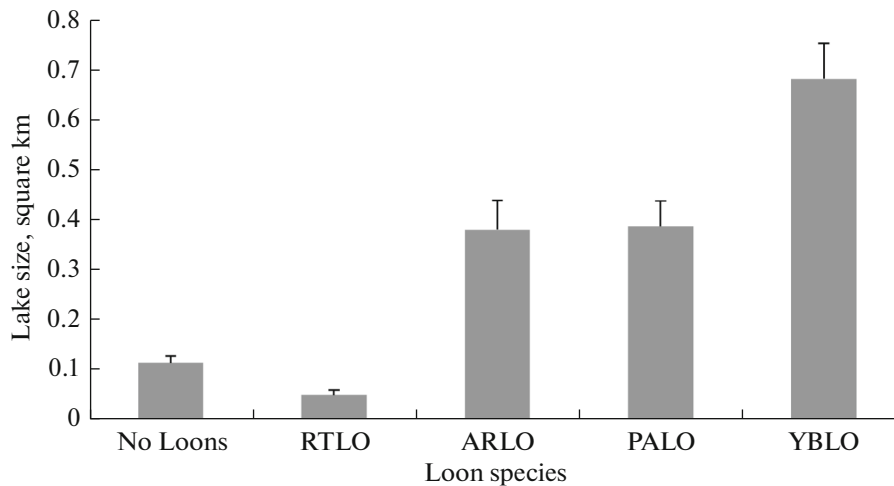


Fig. 3. Lake size (average \pm SE) utilized by four *Gavia* species in Western Chukotka, Russia.

were also common at both sites on the sea, and Arctic loon was less common. Red-throated loons were uncommon at both sea study sites.

Lake Size Use by Congeners

Different species utilized different lake sizes ($F = 4.520$, $p = 0.004$); yellow-billed loon used larger and red-throated loon used smaller waterbodies than the grouped Pacific and Arctic loons (Fig. 3). The average lake occupied by yellow-billed loon alone ($0.69 \text{ km}^2 \pm 0.09$; range $0.065\text{--}1$; $n = 135$) was nearly twice as large as the average lakes utilized by Arctic loon ($0.38 \text{ km}^2 \pm$

0.05 ; range $0.006\text{--}1.89$; $n = 66$) and Pacific loon alone ($0.39 \text{ km}^2 \pm 0.05$; range $0.003\text{--}2.29$; $n = 89$), and 35 times larger than lakes used by red-throated loon alone ($0.02 \text{ km}^2 \pm 0.002$; range $0.00006\text{--}0.14$; $n = 13$; Fig. 3). In 11 of 13 cases (85%) red-throated loons were observed on small ponds that were not considered lakes (ponds were waterbodies too small to be recognizable using Google Earth). Lakes with no loons averaged $0.11 \text{ km}^2 \pm 0.02$ (range $0.06\text{--}2.03$; $n = 162$).

Lake sharing. It was more common for a lake to be used or occupied by a single loon species (125/162, 77.2%) than by two or more species (37/162, 22.8%). All red-throated loon ($n = 13/13$), 78.5% of Pacific

loon (51/65), 65.1% of yellow-billed loon (43/66), and 58% of Arctic loon (29/50) occupied a lake with no other loon species. Of the lakes where 2 or more *Gavia* species were observed, all potential pairwise species combinations were documented, except for red-throated loon, which was never seen sharing a lake. The most commonly observed pairwise combination was Pacific and Arctic loon (43.5%, 10/23), followed by Pacific and yellow-billed loon (34.8%, 8/23), and Arctic and yellow-billed loon (21.7%, 5/23).

When multiple species or multiple pairs of conspecifics were found on a lake, average lake size was larger. For example, lakes occupied by yellow-billed loon alone were $0.69 \pm 0.08 \text{ km}^2$, but average size increased to $1.08 \pm 0.38 \text{ km}^2$ when shared with either Arctic or Pacific loon. Lakes with three congeners were $0.83 \pm 0.71 \text{ km}^2$ ($n = 3$). Lakes occupied by both a Pacific loon and an Arctic loon were smaller in size ($0.69 \pm 0.16 \text{ km}^2$, $n = 10$) than lakes shared by either Arctic or Pacific and yellow-billed loon (1.08 km^2). Lakes $\geq 0.33 \text{ km}^2$ had the potential to support two *Gavia* species, and ones $\geq 0.83 \text{ km}^2$ had the potential to support three congeners.

Population Estimates

We estimated a total of 2831 yellow-billed loon for the entire study area, with 1732 birds on lakes, 1033 at sea, and 66 on rivers. Pacific loon outnumbered other loons with an estimation of 5674 birds, with 4540 on lakes, 935 at sea, and 199 on rivers. The Arctic loon had an estimated number of 2800 birds (2327, 326, and 147 from lakes, sea, and river, respectively). The red-throated loon was the least numerous loon with an estimated total of 1073 birds (820, 64, and 190 from lakes, sea, and river, respectively). These population estimations are relevant for the Raichua Lowland, western part of Chaun Lowland, and mountain valleys.

DISCUSSION

Species Abundance

We demonstrated that this area in northern Russia is rich in both *Gavia* diversity and abundance. All four arctic-breeding species were observed with young in our study area. Successful breeding of all four loon species indicates that this area serves as important habitat for loon species.

Population Densities

We found low densities of yellow-billed loon on mountain and lowland rivers (0.039, 0.070 birds/ km^2 ; Table 3), and even lower densities on fluvial plains, maritime tundra, and mountain valleys (0.027, 0.00, and 0.00 ind./ km^2). The 4-year average density of yellow-billed loon on yedoma (Kyttyk Peninsula and Ayon Island) was 0.593 ind./ km^2 , with a peak post-

nesting density of 0.781 ind./ km^2 in 2009. This density is high compared to other estimations of this loon density in the region. Solov'ev (1992) reported a breeding yellow-billed loon density of 0.18 pairs/ km^2 from the Belyaka Spit in eastern Chukotka. Similarly, N. Poyarkov and colleagues (2000), using fixed-winged aircraft, found concentrations of approximately 0.01 yellow-billed loon/ km^2 on the North coast of Chukotka Peninsula (including Belyaka Spit). Surprisingly, yellow-billed loon was not found in the Kyttyk Peninsula during their aerial survey, although 170 Arctic/Pacific loon were reported (Hodges and Eldridge, 2001). The high densities seen at our study site may be due to the specificity of our data to yedoma habitat; the yedoma plains of Kolyma delta are also an important breeding location, as density there was approximately 1 ind./ km^2 but was less precisely estimated (A. Andreev, personal communication). Our densities on yedoma were similar to those observed for yellow-billed loon in the highest density areas of the Arctic coastal plain of Alaska (Uher-Koch et al., 2015) and were much higher than previously thought for this region of Russia. The high densities of yellow-billed loon observed on the yedoma habitat of Kyttyk Peninsula and Ayon Island identify these areas as potential key locations for global yellow-billed loon conservation and management.

Densities of Pacific loon ranged from 0.343 birds/ km^2 on yedoma to 1.13 birds/ km^2 on maritime tundra, and it was common in all four lake habitat types. Pacific loon were common in our sea surveys (0.366, 0.307 birds/ km^2 ; Table 3), but were less common on mountain and lowland rivers (0.169, 0.156 birds/ km^2). A previous study on Belyaka Spit recorded a density of 0.25 pairs/ km^2 (Solov'ev, 1992). This number is between our lowest and highest densities, possibly due to our habitat-specific densities, or to methodological counting differences (breeding pairs versus individuals in post-breeding period). Additionally, Pacific loon is the only loon believed to have an increasing population trend (BirdLife International, 2015), which could account for higher densities seen in our study than in Solov'ev's (1992) study.

Arctic loon densities ranged from 0.213 birds/ km^2 in mountain river valleys to 0.553 birds/ km^2 on maritime tundra, and along with Pacific loon, Arctic loon was present in all four habitat types. Arctic loon was common in the sea surveys (0.114, 0.119 birds/ km^2 ; Table 3) and more abundant in lowland rivers than in mountain rivers (0.150 vs 0.092 birds/ km^2). Our recorded densities of Arctic loon in lake tundra were similar to the density of 0.15 pairs/ km^2 recorded from Belyaka Spit in a previous study (Solov'ev, 1992).

Our densities of Arctic + Pacific loons were higher than densities reported from the same area during aerial surveys of 1994 in 0.32 birds/ km^2 (Hodges and

Eldridge, 2001). Possible explanations for this discrepancy include: (1) an increase in loon numbers between the two surveys; (2) gatherings of non- and failed-breeding loons in the fall (August) causing inflation of our numbers; and (3) missed loons during aerial surveys (for example, diving loons may not be counted during a pass), leading to a lower density estimates than our foot based surveys. Rigorous ground and aerial surveys in northern Alaska found that about one third of loons are not detected during aerial surveys (Haynes et al., 2014), so this explanation seems feasible. Further, aerial surveyors didn't report Yellow-billed loon even though it has been known to be abundant in this area since the first two bird studies of the region (Lebedev and Filin, 1959; Stishov, 1990).

In our study area, red-throated loon densities ranged between 0.0 birds/km² on maritime tundra and 0.307 birds/km² in mountain valleys. Our red-throated loon densities on maritime tundra, fluvial plain (0.017 birds/km²), and yedoma (0.038 birds/km²) are low compared to other localities that included areas of prime breeding habitat, range of 0.15–2.1 birds/km² (Bergman and Derksen, 1977; Dickson, 1993; Solov'ev, 1992; Mineev, Yu.N. and Mineev, O.Yu., 2009). However, our highest red-throated loon densities in mountain valleys were comparable to the lower range of densities from other studies. Marine densities were again low (0.010, 0.034 birds/km), but densities on mountain and lowland rivers are at the low end of previously reported values (0.170, 0.139 birds/km) (Mineev, Yu.N. and Mineev, O.Yu., 2009). Red-throated loon densities at our study area were comparable to the recent densities found at Belyaka Spit (0.13 pairs/km²; (A. Dondua *in litt.*)). Our sample size and areas surveyed were larger and more diverse than in Belyaka Spit (27.6 km²), which primarily consists of one habitat type, the old coastal spit (most similar to our maritime tundra). Belyaka spit is different than our study area in that it lacks rivers and there is an absence of fish in lakes, necessitating that birds there forage on the sea. Red-throated loon in our study site preferred rivers and were absent from maritime tundra, so differences in available habitat may have caused increased red-throated loon density in the suitable areas of Belyaka Spit. One hypothesis is that oceanic conditions in the North Pacific undergo decadal scale variation in temperature and foraging conditions (Anderson and Piatt, 1999), leading to boom or bust outcomes for predators of marine forage fish, such as red-throated loon (Schmutz, 2014). It is unclear why this wouldn't affect other marine foraging species, such as yellow-billed loon, however.

Pacific loon was the most common of the congeners in our study area, followed by similar numbers of yellow-billed and Arctic loons, and the least abundant red-throated loon. In 1986–88, red-throated loon outnumbered all other loon species at Belyaka Spit,

where all four congeners co-existed with densities red-throated loon—0.54 pair/km²; Pacific loon—0.25 pairs/km²; yellow-billed loon—0.18 pairs/km² and Arctic loon—0.15 pairs/km² (Solov'ev, 1992). It seems that Pacific loon is very common throughout the region, and we suspect that our higher density of yellow-billed loon was due to the prevalence of yedoma in the study area, which this loon prefers (see niche differentiation section). The most notable difference is that red-throated loon were most common at Belyaka Spit in the 1980s, but were least common at our study site. Between 1986 and 2014, the density of red-throated loon declined four times on Belyaka Spit to 0.11 pairs/km², while the densities of other three congeners didn't change from 1986 to 2014 (A. Dondua *in litt.*). At our study site, densities were similarly low in all years.

Habitat Use by Congeners

Multiple organisms within a geographic area must partition resources in a manner that allows them to coexist; this is especially true for congeneric species that often utilize similar resources. Interspecific competition is a major factor determining niche separation of sympatric species at both ecological and evolutionary levels (Diamone, 1978; Pianka, 1982). It can be difficult to identify or measure niche differences among similar congeners. Lack (1971) emphasized that niches of congeneric bird species are most often separated by feeding and habitat type (Davis, 1972; Bergemann and Derksen, 1979; Eriksson and Sundberg, 1991). In our lake tundra study area, the four congeneric loon species utilized lakes differentially by habitat type and size.

Yellow-billed loon used large lakes and showed a strong preference for yedoma habitat (99.4% of records). Yellow-billed loon likely require large lakes due to their large size; large loons have inefficient wing-loading ratios and require long lengths of open water for running take-offs. While lake size and habitat type were correlated, both yedoma and fluvial plain included large lakes, leading us to believe that yellow-billed loon chose yedoma lakes for reasons other than size. Yedoma lakes are large, deep, and contain a variety of fish species. Fish sampling on Ayon Island indicated that all yedoma lakes contained fish, which may be true for Kyttyk Peninsula as well (information from local people). Fish species available included Arctic char (*Salvelinus alpinus*; length 18.7–51.3 cm) and least cisco (*Coregonus sardinella*; length 22.8–30.5 cm), both of which are preferred by yellow-billed loon in Alaska (T. Haynes, pers. comm.). By contrast, only 10% of fluvial plain lakes contained fish, and the fish species were mainly pond smelt (*Hypomesus olidus*), as well as European whitefish (*Coregonus lavaretus pidschian*). The majority of fluvial plain lakes (97%) didn't have the large *salvelinus* or *coregonus* pre-

ferred by yellow-billed loon. It is likely that yellow-billed loon prefer yedoma habitat based on fish availability as well as large lake sizes (North and Ryan, 1989).

Pacific loon was ubiquitous in all habitats and had the greatest densities in all but yedoma habitat. Pacific loon was most commonly found in maritime tundra and was also frequent in fluvial plains. Because Pacific is small loon, it likely has fewer requirements for lake size. Average lake sizes chosen by Pacific loon were no different than average lake size for the survey area, indicating that lake size was not a factor in habitat choice. Shallow, brackish lakes in maritime tundra contained no fish, which may not be a problem for smaller Pacific loon that can take off more easily to forage on seas and rivers, where they were common. Small fish like pond smelt, common in fluvial plains, are likely good prey species for small loons such as Pacific loon. It is unclear whether Pacific loon chose other habitats or was relegated to these habitats due to interspecific competition. Haynes et al. (2014) showed strong competition between Yellow-billed and Pacific loons in western Alaska (where no Arctic loon occur), suggesting Pacific loon had a tenfold reduction in occupancy when yellow-billed loon were present. Similar competition for yedoma lakes may take place among congeners at our site. As an indicator of this possibility, in yedoma where yellow-billed loons were the most common congener, Pacific loon density was lower; but everywhere else, where yellow-billed loon were scarce, Pacific loon had the highest density.

Arctic loons were most common on maritime tundra and were less common on all other habitats. Arctic loon in our study area did not appear in different densities based on habitat type. Because the densities were similar regardless of which other congeners are present, there did not appear to be direct competition, although further study would be needed to determine this definitively. Arctic loon lake sizes were similar to the average lake size for the area, which was slightly larger than previously reported lakes used by this species (0.18 km²) (Petersen, 1979). This may simply be due to more yedoma habitat, and hence, larger available lakes in our study area compared to other studies.

Red-throated loons were most common along mountainous parts of rivers and in mountain valley lakes. Lakes on mountain valleys did not contain fish, but red-throated loon's small size and greater flight efficiency likely allow it to forage on rivers, where other species are less common. Lakes or ponds occupied by red-throated loon were significantly smaller than the lakes occupied by other congeners, which was expected, as it is the smallest of the congeners. This loon may select smaller lakes to avoid competition with larger congeners abundant in our study area.

Lake sharing between congeners was fairly common in our study area (22.8%; 37/162) compared to Belyaka Spit (1.5%; 1/66; only Arctic-Pacific loon) (Soloviev, 1992). This could be explained by differ-

ences in habitat types between study locations; our study site contained more yedoma habitat, which appears to be the most suitable habitat for multiple loon occupation. Additionally, different survey timing may influence results. Territorial loon pairs were counted in the spring on Belyaka Spit, while our study counted birds in August, after breeding. Post-breeding loons seem to be less aggressive to congeners than pre-nesting loons.

Occurrence of two or more congeners was more frequent on yedoma (83.8%; 31/37) than on fluvial plain (10.8%; 4/37), and in other habitats, there were only single cases of lake sharing. Lake size appears to dictate the potential to support more than one species: lakes > 0.33 km² had the potential to support two *Gavia* species and ones > 0.83 km² had the potential to support three congeners. Although fluvial plain also has large lake sizes, the abundance and variability of prey species likely makes yedoma habitat more desirable. In a previous study, lakes with more convoluted shorelines were more likely to contain both Yellow-billed and Pacific loons because the visual and spatial separation allowed the two species to coexist with reduced interactions (Haynes et al., 2014). It is likely that lake size combines with shoreline configuration to determine the suitability of a lake to sustain multiple loon species.

The largest congener (59.5% of shared lakes), was the most likely to be observed sharing a lake with another congener. Arctic loon, the second largest congener, was also frequently seen sharing lakes (42% of shared lakes). Arctic and yellow-billed loons were the least likely to share a lake with one another (21.7% of shared lakes); this may be because the two larger-bodied birds require larger territories, which may be incompatible unless the lake is very large. The two most similar species, Pacific and Arctic loons, were most commonly together (43.5% of shared lakes). It is possible that the two require small enough territories to coexist on one lake. Pacific loon shared with yellow-billed loon in 34.8% of shared lakes; smaller Pacific loon likely requires smaller territories; and the size difference likely transfers to a difference in prey preferences. Due to their smaller body size and feeding habits, red-throated loon can use smaller lakes than its congeners. Its preference for small ponds likely precludes it from sharing lakes with other congeners, which cannot make use of such small waterbodies due to biomechanical and prey resource limitations. Pacific loon is only slightly larger than red-throated loon, and also was the only species on a lake the great majority of the time (78.5% of Pacific loon cases).

Food sources, lake size, and shoreline configuration are all dimensions that can lead to spatial separation, and further study into these areas could help us to better understand the niche overlap among *Gaviiformes* (Haynes et al., 2014; Schmidt et al., 2014). In addition, both territorial and encounter competition

(Elmhagen et al., 2002; Schoener, 1983) can lead to habitat segregation, further separating niche use. Investigations into niche partitioning among Gaviiformes, as well as possible congeneric competition, are important foci for future research (Sargeant, 2007; Broennimann et al., 2012).

Population Estimates

Our study area in western Chukotka supported large loon populations of all four species. The Pacific loon outnumbered other loons with an estimate of 5674 birds, followed by yellow-billed and Arctic loon, with 2831 and 2800 birds, respectively, and red-throated loon was the least numerous (1073 birds). Although our population estimates are crude, they are important contributions to obtaining better world population estimates and are an important starting point for developing future decisions on status and estimating trends of the species. In Chukotka, yellow-billed loon inhabits three of four lowlands: the Chaun-Rauchua Lowland, Valkaray Lowland, and Vankarem Lowland; it is absent on Anadyr Lowland (Krechmar et al., 1991; Solov'ev, 1992; Hodges and Eldridge, 2000; A Dondua, *in litt.*; this study). Our estimate indicates that the Chaun-Rauchua Lowland is the largest and the most densely populated by yellow-billed loon habitat in eastern Russia; and the habitat is critical for the entire yellow-billed loon population in the Eastern Russian arctic. Many opportunities exist for further research on Gaviiformes distribution and population trends, as relative abundance and diversity throughout northern Russia are unknown. Additionally, quantifying breeding success and productivity for yellow-billed and other loons in western Chukotka would be valuable to better understand their population demographics and growth.

CONCLUSION

Our study site in western Chukotka, Russia, provides important breeding habitat for all four species of arctic breeding loons. Densities of loon species here are similar to or higher than densities reported from nearby areas and past surveys, with the exception of lower densities of red-throated loon in our study area. The four species of loons are differentially abundant based on habitat types: yellow-billed loon is the most common in yedoma and at sea, Arctic loons are most common on fluvial plains and maritime tundra, Pacific loons are ubiquitous in all habitats, and red-throated loon is the most common in mountain valley lakes. The four species of loons also utilize different lake sizes, with yellow-billed loon using large lakes, Arctic and Pacific loons using average lake sizes, and red-throated loon using small ponds. Significant populations of all species likely occur in this area.

ACKNOWLEDGMENTS

We are grateful to Evgeny Kuzmin and Michael Ettuvgee assisted with the field work. We are extremely grateful for the transportation (helicopter and plane flights) and logistic support from Kinross Gold Corporation, Chukotka subdivision, during 2010–2015. We also thank two anonymous reviewers for providing helpful comments on an earlier draft of the manuscript. This study was funded by US Fish and Wildlife Service, Biodiversity Research Institute, and Wildlife Conservation Society.

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