Body Mass in Common Loons (*Gavia immer*) Strongly Associated with Migration Distance

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Abstract.—During 25 field seasons between 1988 and 2012, Biodiversity Research Institute captured and uniquely color-banded 2,730 adult Common Loons (*Gavia immer*) on breeding territories in 11 States and seven Provinces throughout North America. Body mass was obtained from each individual; tarsus and bill measurements were obtained from more than half the birds banded. Clinal variation in body mass, tarsal width and bill length was observed. Body mass varied from 2,700 g to 7,600 g; loons from populations in the upper Great Lakes and central Canada were smallest, and size increased to the east and west. Examination of band return and satellite tracking data resulted in three migration distance groups: < 1,500 km; 1,500-3,500 km; and ≥ 3,500 km. Body mass was inversely related to migration distance. Males were significantly larger (> 20%) than associated females, and within-pair differences increased with decreasing migration distance (i.e., males from coastal States were proportionally larger than their mates compared to interior State pairs). *Received 26 February 2013, accepted 18 June 2013.*

Key words.—clinal variation, Common Loon, *Gavia immer*, migration distance.

Intraspecific variation of morphological features in birds has been observed across geographic ranges (Ainley 1980; McGillivray 1989; Leafloor and Rusch 1997; Ashton 2002). The trend for body size to be larger in cooler climates and smaller in warmer climates (often represented by latitude) is known as Bergmann's rule when it occurs among closely related species or James's rule when it occurs within species (James 1970; Blackburn *et al.* 1999). The basis is that larger body size will be favored in cool climates because lower surface area to mass ratios result in reduced heat loss and, thus, apparent increased survival. There is strong evidence for similar variation within species; however, many exceptions to the rule have been observed, particularly among migratory vs. sedentary species (James 1970; Blackburn *et al.* 1999; Ashton 2002; Meiri and Dayan 2003). In birds, this may be attributed to a decreased load-carrying capacity of an individual associated with increased body mass (Hedenström and Alerstam 1992, 1997). Further, migration speed is diminished with increased body size for birds that use flapping flight, resulting in increased migration times and, thereby, constraining the migration distances that larger-sized birds are capable of completing during their annual life cycle (Hedenström and Alerstam 1998; Alerstam *et al.* 2003; Hedenström 2003; Hein *et al.* 2012). For example, among three species of European swans, the smallest species (*Cygnus bewickii*) had the longest migration distance, the largest species (*C. olor*) the shortest distance, and the mid-sized species (*C. columbianus*) an intermediate distance between the smallest and largest species (Cramp and Simmons 1977). This pattern has also been observed in Atlantic alcids such as Thick-billed Murre (*Uria lomvia*; Vaurie 1965), Atlantic Puffin (*Fratercula arctica*; Moen 1991), Razorbill (*Alca torda*; Barrett *et al.* 1997) and Dovekie (*Alle alle*; Wojczulanis-Jakubas *et al.* 2011).

Loons are a small monophyletic group (Gaviiformes) consisting of five species worldwide (Sibley and Ahlquist 1990; Lindsay 2002; Evers *et al.* 2010). They are heavy-bodied piscivorous birds known as divers in the Old World due to their foot-propelled diving foraging strategy. Loons are a classic K-selected species with long life expectancy, delayed sexual maturity, and low fecundity; their mating system is socially and geneti-

cally monogamous (Piper *et al.* 1997). The Common Loon (*Gavia immer*) has the largest geographic range of the loon species in North America and is the only one that breeds in the contiguous USA (Sibley and Ahlquist 1990; Lindsay 2002), which makes it a good candidate to examine within-species variation. The annual life cycle of the Common Loon varies little across its broad geographical range in that it breeds on freshwater lakes throughout the northern USA, including Alaska, and Canada north to the southern edge of the taiga shield, and migrates to coastal areas in the fall, including the Atlantic and Pacific Coasts, Gulf of Mexico, and Gulf of California. Satellite tracking data indicate that the duration of migration and the timing of arrival on the wintering grounds appear to vary within and among populations (U.S. Geological Survey 2013; Biodiversity Research Institute, unpubl. data). These differences among populations seem to be associated with differences in migration distance. For example, northeastern USA Common Loon populations typically arrive in coastal wintering areas within a day of departure from breeding areas, whereas upper midwestern USA Common Loon populations that travel up to seven times the distance of northeastern USA Common Loons may take up to a few weeks to complete their fall migration (U.S. Geological Survey 2013). Less information is available regarding migration timing of Common Loon populations in interior Canada. However, limited satellite tracking data suggest that they travel the greatest migration distances of all North American Common Loons and may take up to 2 months to complete their fall migrations (Confederated Salish and Kootenai Tribes 2008; Paruk *et al.* 2014).

A geographic cline in the body size of the Common Loon (loons) has been observed across its North American range and appears to coincide with the differences in migration distance, where interior breeding loons are smallest and size increases to the east and west (Rand 1947; Storer 1988; Evers *et al.* 2010). The increased physiological cost of a larger body size during migration may create a selection pressure that favors smaller body sizes for loons with long migration distances. However, an opposing selection pressure for large body size may exist for loons that migrate shorter distances. A central characteristic on which several life history traits may depend is individual body size, including survival and fecundity (Boag and Grant 1981; Alisauskas 1987; Promislov and Harvey 1990; Sedinger *et al.* 1995). Loons are highly territorial during the breeding season, and competition for quality breeding territories often results in aggressive interactions between individuals and pairs (Paruk 1999; Piper *et al.* 2008; Piper 2011). Piper *et al.* (2000) found that larger-sized loons were less likely to be usurped from their territories during these interactions compared to smaller loons. Loons are also highly vocal during the breeding season and produce an array of calls, the yodel being the most complex and used solely by males often in response to territorial intrusions. Mager *et al.* (2007a) confirmed that variability in the dominant frequency of a male's yodel is influenced by body size, with larger males producing lower frequency yodels. Further, loons appeared to respond with more alarm to lower pitch yodels compared to higher pitched yodels during callback surveys (Mager *et al.* 2007b).

Over a 25-year period (1988-2012), the Biodiversity Research Institute, with the help of multiple collaborators, banded 2,730 adult Common Loons on their breeding territories in 11 States and seven Provinces throughout the species' range in North America. Of those individuals, 536 breeding pairs were sampled (i.e., the male and female of a territorial pair were captured and banded within the same breeding season). These significant banding efforts have resulted in the largest known collection of morphological data on Common Loons. We analyzed these data in an effort to determine if body size features, such as body mass, tarsus width, and bill length, are linked to differences in migration distance. We predicted that loon populations inhabiting the interior part of the continent with ostensibly longer migration distances will have smaller morphological features than coastal ones with much shorter migrations. We were also

interested in how size differences between pair members changed, if at all, across their range. If being larger is more important for a male than a female to defend and hold its territory, then selection should favor larger males relative to females when the distance between breeding and wintering areas is decreased. Our prediction was that size difference between pair members would increase as migration distance decreased.

METHODS

Study Area

During the breeding season (June-August) from 1988 to 2012, Common Loons were targeted for capture and banding efforts in their breeding territories on freshwater lakes and ponds in the following States and Provinces: Alaska, Alberta, Maine, Manitoba, Massachusetts, Michigan, Minnesota, Montana, New Brunswick, New Hampshire, New York, Nova Scotia, Ontario, Quebec, Saskatchewan, Vermont, Washington, and Wisconsin.

Capture and Measurements

Adult loons were captured on their breeding lakes with a replicable night-lighting technique (Evers 1993, 2001). Spotlights (400,000 to 1.5 million candle power) were used to search lakes, and tape-recorded and mimicked calls were used to attract loons to the boat where they were netted with large landing nets, restrained, and transported to shore. All loons were marked with U.S. Geological Survey aluminum or stainless steel bands, and a unique plastic, colored leg band combination glued with an acetone-based derivative. The following measurements were also taken using a standardized protocol developed by Evers (2001): bill length, width and depth; culmen; right and left tarsal width; and body mass. Males were distinguished from females based on yodel calls given before and/or after capture. In some cases gender was determined by placing several drops of blood on a cotton pad, which was sent to a genetics lab for analysis. Sexing was accomplished by amplifying a portion of the W-linked EE0.6 sequence and a control sequence from the *spindlin* gene on the Z chromosome with PCR (polymerase chain reaction). Female birds showed two bands on an agarose gel (~150 and 300 base pairs; the Z and W fragments, respectively) and male birds had a single band (~150 base pairs; the Z fragment) (Itoh *et al.* 2001).

Migration Distance Categories

Migration distances between breeding and wintering grounds were determined from wintering band return and satellite tracking data (Table 1). Only Common Loons banded on breeding territories and recovered outside of the breeding area during the period when loons are expected to be on the wintering grounds and not in migration (i.e., December, January, and February) were included in the development of the migration distance categories. Although loons may be found in wintering locations outside of these months, it was necessary to be conservative in the selec-

Table 1. Migration distance (km) from breeding to wintering areas of Common Loons in North America determined from band recoveries and satellite tracking data. BRI = Biodiversity Research Institute.

| Population | n | Migration Distance Traveled (km) | | Data Source |
		Mean ± SD	Range	
Band Recoveries				
Maine	12	450 ± 223	190-950	BRI Banding Records
Michigan	5	2,660 ± 344	2,200-3,000	BRI Banding Records
Minnesota	4	2,869 ± 415	2,600-3,475	BRI Banding Records
Montana	3	1,967 ± 153	1,800-2,100	BRI Banding Records
New Hampshire	8	284 ± 103	175-500	BRI Banding Records
New York	3	800 ± 368	575-1,225	BRI Banding Records
Quebec	4	1,931 ± 383	1,600-2,475	BRI Banding Records
Washington	3	275 ± 150	125-425	BRI Banding Records
Wisconsin	11	2,550 ± 299	2,200-2,950	BRI Banding Records
Satellite Tracking				
Alberta	1	4,700	4,700	Confederated Salish and Kootenai Tribes 2008
Alaska	2	286 ± 10	279-293	J. Schmutz, pers. commun.
Maine	7	498 ± 313	172-1,050	BRI, unpubl. data; Kenow *et al.* 2009
Minnesota and Wisconsin	4	—	1,884-2,121	Kenow *et al.* 2002
New Hampshire	2	154 ± 3	152-156	Kenow *et al.* 2009
New York	5	430 ± 60	362-527	Kenow *et al.* 2009
Saskatchewan	3	4,005 ± 451	3,694-4,522	Confederated Salish and Kootenai Tribes 2008; Paruk *et al.* 2014

tion of recovery data to avoid inclusion of loons recovered during migration in locales that did not represent full migration distances between breeding and wintering areas. Straight-line distances between breeding territory locations and winter recovery locations were measured in ArcGIS (Environmental Systems Research Institute 2011). The same method was used to measure the distance between breeding and winter locations for the Biodiversity Research Institute's unpublished satellite tracking data. Distances were also obtained from colleagues with unpublished satellite tracking data through personal communication and from the peer-reviewed literature (Confederated Salish and Kootenai Tribes 2008; U.S. Geological Survey 2013; Paruk *et al.* 2014; J. Schmutz, pers. commun.). Three broad migration distance groups were developed based on these data: short-distance (< 1,500 km), moderate-distance (1,500-3,499 km), and long-distance (≥ 3,500 km). The short-distance migration category included Common Loons sampled in Alaska, Maine, Massachusetts, New Brunswick, New Hampshire, New York, Nova Scotia, Vermont, and Washington. The moderate-distance migration category included loons sampled in Michigan, Minnesota, Montana, Ontario, Quebec, and Wisconsin. The long-distance category included loons sampled in Alberta, Manitoba, and Saskatchewan. Loons banded in States or Provinces without band recovery or satellite tracking data, including Manitoba, Massachusetts, New Brunswick, Nova Scotia, Ontario, and Vermont, were assigned to a migration distance category based on their geographic location relative to nearby populations with known wintering locations.

Statistical Analysis

Statistical analyses were performed in Microsoft EXCEL and JMP (SAS Institute, Inc. 2010). Banding records of adult male ($n = 1,419$) and female ($n = 1,311$) Common Loons sampled on breeding territories as part of research conducted by the Biodiversity Research Institute between 1988 and 2012 were evaluated for differences in body mass, tarsus width, and bill length. Normality of sample distributions was checked with the Shapiro-Wilk test, and homogeneity of variance was examined with the Bartlett test. We examined the effects of latitude of breeding location, longitude of breeding location, the compound effect of latitude and longitude of breeding location (latitude x longitude), and migration distance category on body mass using a general linear model (GLM) framework. Candidate models of suites of covariates were ranked with Akaike Information Criterion adjusted for small sample size (AIC_c). The model with the lowest AIC_c and those having $\Delta AIC_c \leq 2$ had the most statistical support, values between 4 and 7 had considerably less support, and those > 10 had virtually no support (Burnham and Anderson 2002). The Akaike weight was also considered when determining the relative amount of statistical support for each model. The relationship between body mass and tarsus width and body mass and bill length were determined with simple linear regression. Differences in tarsus width and bill length among migration distance categories were examined with analysis of variance (ANOVA). Pairwise comparisons between categories were conducted with Tukey's honestly significant difference (HSD) test. All tests were considered significant at $P < 0.05$.

The relationship between male and female body mass within breeding pairs was examined with linear regression for short-distance migrant breeding pairs ($n = 415$) and moderate-distance migrant breeding pairs ($n = 138$). The variation in body mass, tarsus width, and bill length between a male and female of a breeding pair were tested for differences between short-distance and moderate-distance migrant breeding pairs using Student's t-test. Small sample size precluded inclusion of the long-distance category in the breeding pair analyses.

Results

Body Mass

Body mass ranged from 2,700 g to 6,200 g in females ($n = 1,311$) and from 4,350 g to 7,600 g in males ($n = 1,419$). The top supported model included longitude, latitude, longitude x latitude, and migration distance for males and females, although migration distance accounted for the greatest variation in body mass (Table 2). Body mass decreased with increased migration distance in males and females (Fig. 1). Tukey's HSD tests indicated that female short-distance migrant least squares mean (LSM) body mass [$\overline{x} = 4,505$ g (SE = 23)] was significantly greater than female moderate-distance migrants [$\overline{x} = 3,719$ g (SE = 20)] ($P < 0.001$), and both of those groups were significantly greater than female long-distance migrants [$\overline{x} = 3,430$ g (SE = 74)] (short to long: $P < 0.001$; moderate to long: $P < 0.001$). Similarly, LSM body mass of male short-distance migrants [$\overline{x} = 5,727$ g (SE = 27)] was significantly greater than male moderate-distance migrants [$\overline{x} = 4,661$ g (SE = 21)] ($P < 0.001$), and both of these groups were greater than long-distance migrants [$\overline{x} = 4,244$ g (SE = 84)] (short to long: $P < 0.001$; moderate to long: $P < 0.001$). Among State and Province populations, male and female Common Loons in Maine and New Hampshire had the greatest arithmetic mean body masses compared to loons sampled in any other States or Provinces (Appendix).

Tarsal width ranged from 20.0 mm to 28.6 mm in females and 21.1 mm to 30.8 mm in males. Right tarsal width was moderately correlated with body mass (females:

Table 2. Model selection results examining the effects of migration distance category (MD), latitude of breeding location (Lat), longitude of breeding location (Long), and the compound effect of latitude and longitude of breeding location (Lat*Long) on the body mass of female ($n = 1,311$) and male ($n = 1,419$) Common Loons sampled across their North American breeding range from 1988 to 2012. Models are ranked according to Akaike Information Criterion adjusted for small sample size (AIC_c). The table shows the variables included in the model, number of estimated parameters (K), differences between model Akaike Information Criterion adjusted for small samples size (ΔAIC_c), AIC_c weights (w_i), and the amount of variation explained by the model (r^2).

| Model	K	ΔAIC_c	w_i	r^2
Females				
MD1+Lat2+Long3+Lat*Long4	5	0.000	0.909	0.66
MD + Lat + Long	4	5.552	0.057	0.66
MD + Long	3	6.559	0.034	0.66
MD + Lat	3	19.284	0.000	0.65
MD	2	167.335	0.000	0.65
Lat*Long	3	386.360	0.000	0.54
Lat+Long	2	962.297	0.000	0.29
Long	1	1,007.851	0.000	0.26
Lat	1	1,221.432	0.000	0.13
Males				
MD+Lat+Long+Lat*Long	5	0.000	0.999	0.74
MD + Lat + Long	4	14.443	0.001	0.74
MD + Long	3	20.443	0.000	0.73
MD + Lat	3	49.510	0.000	0.73
MD	2	177.257	0.000	0.73
Lat*Long	3	529.061	0.000	0.62
Lat+Long	2	1,308.043	0.000	0.34
Long	1	1,350.686	0.000	0.32
Lat	1	1,638.399	0.000	0.16
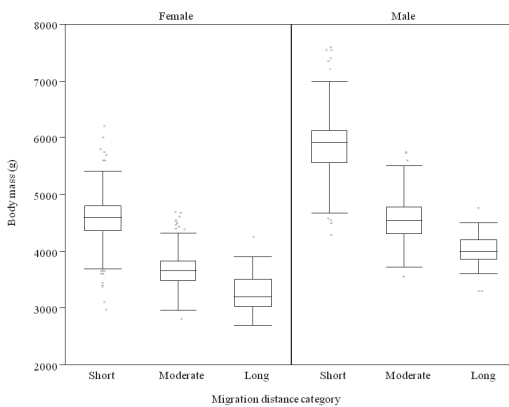
Figure 1. Differences in body mass (g) among short (< 1,500 km), moderate (1,500-3,499 km), and long (≥ 3,500 km) distance migration categories for male and female Common Loons banded on breeding territories in Canada and the United States, 1988 to 2012. Box-and-whisker plots represent median, interquartile range, overall range, and outlier values of body mass (g). Short-distance migrants: females: $n = 791$, males: $n = 813$; moderate-distance migrants: females: $n = 489$, males: $n = 572$; long-distance migrants: females: $n = 31$, males: $n = 34$.

$r^2 = 0.29$, $F_{681} = 275.39$, $P < 0.001$; males: $r^2 = 0.34$, $F_{723} = 375.27$, $P < 0.001$). ANOVA results indicated significant differences in tarsal width among the migration distance categories for both sexes (females: $F_{702} = 105.21$, $P < 0.001$; males: $F_{748} = 201.10$, $P < 0.001$) (Fig. 2). Pairwise comparisons with Tukey's HSD test showed that short-distance migrants [females: = 24.86 mm (SE = 0.05), $n = 536$; males: = 26.87 mm (SE = 0.05), $n = 558$] had greater tarsal widths than moderate-distance migrants [females: $\bar{x} = 23.46$ mm (SE = 0.11), $n = 131$, $P < 0.001$; males: $\bar{x} = 24.86$ mm (SE = 0.11), $n = 153$, $P < 0.001$]; both of these groups were greater than the long-distance migrants [females: $\bar{x} = 22.68$ mm (SE = 0.21), $n = 36$; short to long: $P < 0.001$; moderate to long: $P = 0.003$] [males: $\bar{x} = 24.12$ mm (SE = 0.21), $n = 38$; short to long: $P < 0.001$; moderate to long: $P = 0.005$]. Among State and Province populations, the largest tarsal widths were observed in Alaska (Appendix).
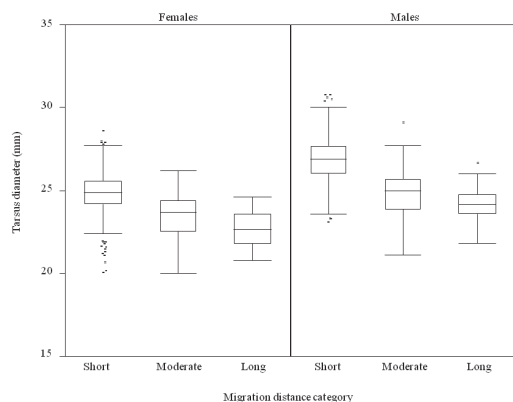
Figure 2. Differences in tarsus width (mm) among short (< 1,500 km), moderate (1,500-3,499 km), and long (≥ 3,500 km) distance migration categories for male and female Common Loons banded on breeding territories in Canada and the United States, 1997 to 2012. Box-and-whisker plots represent median, interquartile range, overall range, and outlier values of tarsus width (mm). Short-distance migrants: females: $n = 536$, males: $n = 558$; moderate-distance migrants: females: $n = 131$, males: $n = 153$; long-distance migrants: females: $n = 36$, males: $n = 38$.
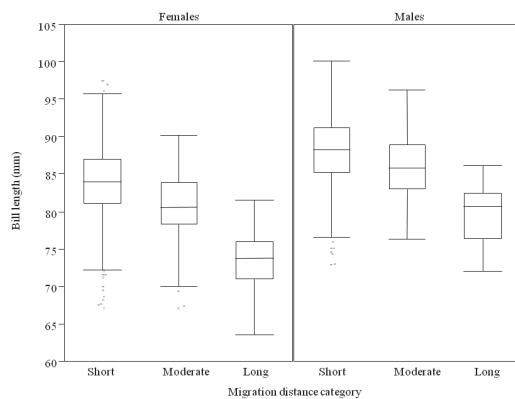
Figure 3. Differences in bill length (mm) among short (< 1,500 km), moderate (1,500-3,499 km), and long (≥ 3,500 km) distance migration categories for male and female Common Loons banded on breeding territories in Canada and the United States, 1997 to 2012. Box-and-whisker plots represent median, interquartile range, overall range, and outlier values of bill length (mm). Short-distance migrants: females: $n = 593$, males: $n = 600$; moderate-distance migrants: females: $n = 133$, males: $n = 155$; long-distance migrants: females: $n = 32$, males: $n = 36$.

Bill length ranged from 63.5 mm to 97.5 mm in females and 72.0 mm to 100.1 mm in males. Bill length was weakly correlated with body mass in both sexes (females: $r^2 = 0.20$, $F_{737} = 182.97$, $P < 0.001$; males: $r^2 = 0.10$, $F_{758} = 86.77$, $P < 0.001$). ANOVA results indicated that significant differences in bill length were observed among the distance migration categories for both sexes (females: $F_{757} = 90.45$, $P < 0.001$; males: $F_{790} = 70.06$, $P < 0.001$) (Fig. 3). Pairwise comparisons with Tukey's HSD test showed that the bill length of short-distance migrants [females: = 84.01 mm (SE = 0.19), $n = 593$; males: = 88.13 mm (SE = 0.18), $n = 600$] was greater than the moderate-distance migrants [females: = 80.78 mm (SE = 0.41), $n = 133$, $P < 0.001$; males: = 85.86 mm (SE = 0.36), $n = 155$, $P < 0.001$]. Both of those groups had greater bill lengths than the long-distance migrants [females: $\bar{x} = 73.72$ mm (SE = 0.83), $n = 32$, $P < 0.001$; males: $\bar{x} = 79.81$ mm (SE = 0.74), $n = 36$; short to long: P < 0.001; moderate to long: $P < 0.001$]. Among State and Province populations, the longest bill lengths were observed in Massachusetts (Appendix).

Breeding Pairs

Minimal correlation was detected between female body mass and the body mass of its male mate among short-distance migrant pairs ($r^2 = 0.07$, $F_{414} = 32.29$, $P < 0.001$). However, a slightly stronger correlation was noted within pairs in the moderate-distance migrant category ($r^2 = 0.20$, $F_{137} = 33.36$, $P < 0.001$). Small sample size precluded the regression analysis of body mass for breeding pairs in the long-distance migration category. Male loons invariably weighed more than their female mates, and the difference increased with decreased migration distance (Fig. 4). Male short-distance migrants averaged 25% more in body mass [$\bar{x} = 1,293$ g (SE = 22), $n = 415$] than their female mates. In comparison, male moderate-distance migrants averaged 21% more in body mass [$\bar{x} = 875$ g (SE = 38), $n = 138$] than their female mates, which was significantly less than the body mass difference observed within short-distance migrant pairs ($t_{551} = -10.46$, $P < 0.001$).

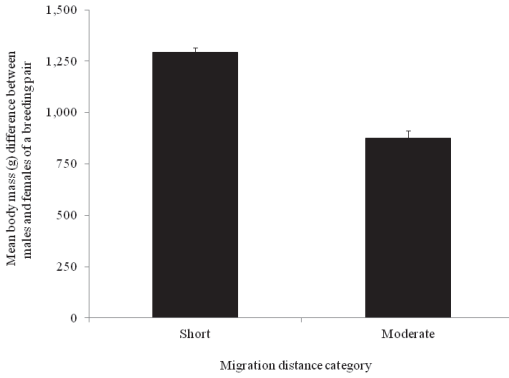Tarsal diameter showed a similar pattern as body mass; the tarsus of male short-

Figure 4. Mean plus standard error difference in body mass (g) between male and female Common Loons of a breeding pair according to migration distance category. Short-distance migration (< 1,500 km): n = 415; moderate-distance migration (1,500-3,499 km): n = 138.

distance migrants was = 2.1 mm (SE = 0.14; n = 139) larger than their female mates, which was greater than the tarsus width difference observed within moderate-distance migrant pairs [$\bar{x}$ = 1.37 mm (SE = 0.24), n = 43] (t_{180} = -2.43, P = 0.02) (Fig. 5). The bills of male short-distance migrants were = 4.69 mm (SE = 0.49; n = 122) larger than their female mates and the bills of male moderate-distance migrants were $\bar{x}$ = 4.14 mm (SE = 0.82; n = 43) greater in size than their mates (Fig. 5). No significant differences in male and female bill length were detected in ei-
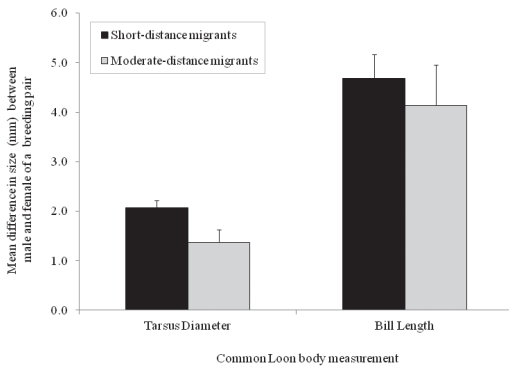

Figure 5. Mean plus standard error difference in right tarsus diameter (mm) and bill length (mm) between male and female Common Loons of a breeding pair according to migration distance category. Short-distance migration (< 1,500 km): tarsus diameter (n = 127), bill length (n = 116). Moderate-distance migration (1,500-3,499 km): tarsus diameter (n = 44), bill length (n = 51).

ther group. Small sample size precluded the comparison of tarsus widths and bill lengths for breeding pairs in the long-distance migration category.

DISCUSSION

Body masses of Common Loons varied by approximately two to threefold across their breeding range with females ranging from 2,700 g to 6,200 g and males ranging from 3,250 g to 7,600 g. The heaviest males were larger than Yellow-billed Loons (*G. adamsii*) reported to date (Evers *et al.* 2010, 2014), which were once considered as being the largest of all the loon species (North 1994). The body of the loon is streamlined to reduce drag while pursuing prey underwater, and this is further achieved by holding the wings very close to the body while swimming (Barr 1973). Consequently, loon wings are very narrow, 20 percent shorter than predicted for a bird of its size, and heavily cambered (McIntyre 1988). The resultant trade-off is one of the highest wing-loading ratios of any breeding bird in North America (2.45 g/m²), which requires a runway of approximately 200 m to achieve lift (Poole 1938; Welty and Baptista 1988). Once airborne, loons beat their wings rapidly (~240 times/min; Evers *et al.* 2010) and fly 112-129 kph to keep their bodies aloft (Kerlinger 1982). Thus, the physiological cost of transport for loons is high (Hill *et al.* 2008), and the fitness benefits associated with optimal time management in migratory species (Alerstam and Lindström 1990) would likely favor a small body size for loons that perform long-distance migrations.

The heaviest loons recorded were from Maine and New Hampshire, which winter within the Gulf of Maine south to Long Island Sound—a distance of less than 500 km. In contrast, significantly smaller loons breeding in the upper Great Lakes region winter in the Gulf of Mexico—a distance of greater than 1,500 km. Satellite movement data of Common Loon migration indicate that northeastern USA loons can arrive at their wintering locations in 1 day, whereas

interior loons have a protracted migration of 4 to 10 weeks (Kenow *et al.* 2002, 2009; Paruk *et al.* 2014; Biodiversity Research Institute, unpubl. data). The geographical gradient in body size revealed by our data (i.e., interior breeding populations in the upper Great Lakes region and central Canada are smallest in size and increase to the east and west) supports the model that small body size is favored over large body size in birds using flapping flight for long-distance migrations (Hein *et al.* 2012). It also supports our original prediction that body size in Common Loons is inversely related to migration distance between breeding and wintering areas. Similar variation in body size has been observed in Canada Geese (*Branta canadensis*), a species with 11 recognized subspecies (Mowbray *et al.* 2002). However, despite great differences in body size among Common Loons, the geographic variation was clinal and the designation of subspecies originally proposed by Bishop (1921) for smaller individuals in central North America is not recommended.

Although many bird species have been shown to adhere to Bergmann's and James's Rules (James 1970; Ashton 2002; Meiri and Dayan 2003), no strong support for a relationship between body size and latitude, and therefore temperature, was found in Common Loons. For example, breeding loons in Alaska were larger than those in the interior of the continent; however, they were not larger than breeding loons in the northeastern USA. It is expected that endotherms with larger body sizes are favored in cooler environments due to a decreased surface area to volume ratio, which serves to minimize heat loss. However, studies have shown that feather mass and structure are perhaps more important than body size with regard to thermoregulation in birds (Scholander 1955; Geist 1987). It has also been proposed that larger body size is favored in more seasonal environments because larger animals can store more fat and can use those stores for greater survival during seasonal stress (Boyce 1979; Lindstet and Boyce 1985). Common Loons migrate in stages (Kenow *et al.* 2002, 2009; Paruk *et al.* 2014), which

allows them to replenish fat stores along their route, and so are likely not in need of greater fasting endurance during seasonal resource shortages.

Male loons were typically 22% heavier than females in all migration categories. Similarly, male diving seabirds may be up to 25% larger than females and it has been noted that they feed on larger prey items and have different nitrogen isotopic signatures (Croxall 1995; Bearhop *et al.* 2000, 2006; Forero *et al.* 2002, 2005). Barr (1973) examined the digestive system of Common Loons and concluded that males likely feed on larger fish than females. Furthermore, our data have shown that male loons have larger bills than females, which supports the belief of trophic segregation between the sexes in Common Loons. Another potential factor favoring size differences in loons is that males engage in aggressive intra-sexual contests for territories that can potentially result in fatalities, whereas females do not engage in such contests as often (Piper *et al.* 2008; Piper 2011). Piper *et al.* (2000) found that 40% of loon territory changes between years were due to usurpation by intruder loons. Body size, muscle mass and strength are intercorrelated in many animals (Le Boeuf 1974; Whitham 1979; Dodson 1997; Zeh 1997), and large body size is generally associated with an advantage in fighting ability among a broad spectrum of animals (Andersson 1994). If larger males are more likely than smaller males to retain territories and/or mates, then selection should favor larger-sized individuals. However, it is unclear at this time if larger females experience fitness benefits. Among breeding pairs, little correlation was detected between male body size and that of its female mate. The difference in body size was less pronounced in pairs that migrated moderate distances compared to short-distance migrant pairs, suggesting that males, freed from the energetic and physiological costs associated with longer migration, increased in size relative to females.

For body size (phenotypic variation) of a species to be considered an adaptation, the differences must also be genetic (Stillwell

2010). Limited genetic research has been conducted on Common Loons (Dhar *et al.* 1997; McMillan *et al.* 2004); more results will be forthcoming (A. Lindsay and A. McMillan, pers. commun.). Barbraud *et al.* (1999) concluded that body size differences in Snow Petrels (*Pagodroma nivea*) across a broad geographic scale were at least partly attributable to genetic variation. Larger-sized petrels associated with coastal environments made significantly shorter foraging trips compared to smaller-sized individuals in more interior environments. It was suggested that the larger individuals made shorter trips to offset the increased energetic costs associated with flapping flight for larger-bodied birds. Across North America, Common Loons undertake short, moderate, and long-distance migrations between their seasonal environments. Our findings suggest that the body size of regional populations is strongly influenced by migration distance. Migration has evolved as a strategy to maximize fitness in a seasonal environment (Alerstam *et al.* 2003), and, although we did not test for genetic differences between our sampling areas, it is likely that there is some genetic component to body size variation in Common Loons. However, we recognize the caveat of making adaptive conclusions from phenotypic data (Gienapp *et al.* 2008).

In conclusion, the morphometric data collected from multiple Common Loon populations across North America indicate that short-distance migrants do not have the physical constraints of long-distance migrants and, therefore, selection favors larger individuals that can more effectively compete for limited high quality breeding territories. Further research on the heritability of body size and other characteristics in loons will likely better characterize underlying reasons for geographically based variability in Common Loon morphology.

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Appendix. Body mass, right tarsus width, and bill length of adult male and female Common Loons banded on breeding territories in Canada and the United States, 1988-2012.

State	Males Body Mass (g) Mean (SE)	n	Tarsus Width (mm) Mean (SE)	n	Bill Length Mean (SE)	n	Females Body Mass (g) Mean (SE)	n	Tarsus Width (mm) Mean (SE)	n	Bill Length (mm) Mean (SE)	n
Canadian Provinces												
Alberta	3,963 (75)	24	24.48 (0.23)	29	79.45 (0.82)	26	3,255 (65)	23	22.77 (0.22)	30	72.80 (0.92)	24
Manitoba	4,156 (131)	8	23.00 (0.44)	8	81.24 (1.48)	8	3,341 (128)	6	22.40 (0.55)	5	76.10 (1.85)	6
New Brunswick	5,420 (111)	11	26.70 (1.25)	1	90.16 (2.42)	3	4,562 (90)	12	NA		83.99 (1.71)	7
Nova Scotia	5,751 (87)	18	26.96 (0.36)	12	87.86 (1.12)	14	4,461 (68)	21	25.06 (0.33)	14	83.14 (1.13)	16
Ontario	4,927 (99)	14	—		—		3,646 (104)	9	NA		NA	
Quebec	4,867 (53)	49	25.22 (0.21)	36	86.52 (0.69)	37	3,819 (50)	39	23.85 (0.21)	33	81.26 (0.83)	30
Saskatchewan	3,792 (261)	2	22.60 (1.25)	1	—		3,267 (221)	2	21.1 (1.23)	1	77.55 (3.20)	2
U.S. States												
Alaska	5,667 (77)	23	28.22 (0.51)	6	82.10 (1.16)	13	4,429 (63)	23	25.48 (0.50)	6	75.52 (1.51)	9
Maine	5,982 (18)	409	26.93 (0.07)	283	87.91 (0.24)	296	4,672 (16)	400	24.89 (0.08)	266	84.41 (0.26)	300
Massachusetts	5,666 (64)	33	26.18 (0.26)	23	90.31 (0.84)	25	4,672 (56)	31	25.25 (0.27)	20	85.92 (0.94)	23
Michigan	4,605 (33)	126	24.40 (0.34)	14	89.08 (0.76)	30	3,662 (30)	108	23.97 (0.46)	7	84.77 (1.07)	18
Minnesota	4,310 (33)	126	24.57 (0.17)	53	85.13 (0.79)	28	3,497 (31)	105	22.83 (0.19)	43	80.37 (0.83)	30
Montana	4,690 (54)	47	25.40 (0.19)	43	82.60 (0.66)	40	3,863 (45)	48	23.98 (0.19)	42	78.79 (0.71)	41
New Hampshire	5,972 (28)	170	26.85 (0.12)	115	88.72 (0.37)	129	4,679 (25)	155	24.84 (0.11)	114	84.23 (0.41)	120
New York	5,593 (33)	123	26.90 (0.13)	95	88.83 (0.42)	101	4,295 (29)	119	24.75 (0.12)	97	83.50 (0.46)	97
Vermont	5,490 (111)	11	26.79 (0.40)	10	88.17 (1.32)	10	4,374 (90)	12	24.60 (0.39)	10	83.44 (1.36)	11
Washington	5,132 (95)	15	25.96 (0.35)	13	81.49 (1.40)	9	4,032 (78)	16	24.24 (0.41)	9	79.43 (1.43)	10
Wisconsin	4,550 (26)	210	22.73 (0.47)	7	87.34 (0.94)	20	3,651 (23)	180	21.72 (0.50)	6	81.36 (1.21)	14