

Sexing a Monomorphic Plumage Seabird Using Morphometrics and Assortative Mating

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Abstract.—This study aimed to establish a reliable method based on morphometrics to sex Long-tailed Jaeger (*Stercorarius longicaudus*), a species with slight differences in body size between sexes but no plumage differences. The presence of assortative mating based on size was also examined to determine if within-pair differences in size could improve sexing. Seventy-six Long-tailed Jaegers were measured, including 26 breeding pairs, on Bylot Island (Nunavut, Canada) during summers 2014-2018. Bird weight, wing chord, tarsus, head, and tail feathers were measured, and breast feathers were collected to determine sex with DNA extracts. A first discriminant function based on two variables (body mass and wing chord) accurately sexed 83% of birds. Some evidence for positive assortative mating based on size was found, as body mass of pair members was positively related, and 88% of females were heavier than their partner. A second discriminant function that included body mass, wing chord, length of the central tail feather, and partner's body mass accurately sexed 92% of birds. Adding a new morphometric and information from the partner allowed a reduction in sex misclassification by half (17% vs. 8%). In conclusion, external body measurements are useful to sex Long-tailed Jaegers, a slightly dimorphic species, and measurements of both members of a pair considerably improve the accuracy of sexing, likely due to the presence of assortative mating. Received 27 March 2019, accepted 13 August 2019.

Key words.—Discriminant analysis, genetic sexing, Long-tailed Jaeger, morphometrics, seabirds, sex identification, sexual dimorphism, *Stercorarius longicaudus*

Waterbirds 42(4): 380-392, 2019

Being able to correctly identify the sex of animals in the wild is essential in many situations. Indeed, most life history traits and behavior of animals differ between sexes (Roff 1992; Dingle and Drake 2007; Dobson 2013). Many bird species present conspicuous sexual dimorphism in plumage or size, which easily allows sexing of individuals in hand or even at distance. However, sexing of individuals may be very challenging in species that exhibit little or no differences in plumage or size. This is the case in many seabirds, which are often monomorphic based on their external appearance and present small size differences between sexes (Fairbairn and Shine 1993).

The Long-tailed Jaeger (*Stercorarius longicaudus*) is a typical seabird species that does not exhibit conspicuous external sexual dimorphism. Although the species shows reverse size dimorphism (Wiley and Lee 1998), the size difference between male and female

is subtle, and standard body measurements are unhelpful for sexing this species reliably according to Pyle (2008). Plumages are also virtually identical between the two sexes, even though Manning *et al.* (1956) reports that females are on average more extensively dusky on lower breast and belly than males within the same population. However, differences in coloration may be subjective and hard to observe, especially in the field. Behavioral observations can sometimes help sexing but are time-consuming and difficult to apply, especially in species where both sexes incubate, feed young, and defend the territory like jaegers (Furness 1987). Genetic analysis can reliably sex monomorphic species (Fridolfsson and Ellegren 1999). The Polymerase Chain Reaction (PCR) based method, commonly used in ecology, requires access to specialized laboratories and can be expensive. Even though recent *in situ* methods such as loop-mediated iso-

thermal amplification (LAMP) are getting more popular, specialized equipment are still needed, and they may not be adapted to all field situations (Centeno-Cuadros *et al.* 2017; Koch *et al.* 2019).

As an alternative, attempts have been made to sex seabirds with a combination of morphometrics. Several statistical methods have been used to differentiate the sex of monomorphic birds, and Linear Discriminant Analysis (LDA) is most often used in the literature. Statistical models based on a combination of morphometrics were successfully developed to sex seabirds such as the Atlantic Puffin (*Fratercula arctica*; Friars and Diamond 2011), Arctic Tern (*Sterna paradisaea*; Devlin *et al.* 2004), Black-legged Kittiwake (*Rissa tridactyla*; Jodice *et al.* 2000), Black-browed Albatross (*Thalassarche melanophrys*; Ferrer *et al.* 2016), Great Skua (*Stercorarius skua*; Hamer and Furness 1991) and Parasitic Jaeger (*Stercorarius parasiticus*; Phillips and Furness 1997).

Some studies have shown that within-pair differences in external appearance can improve the accuracy of sexing (Ainley *et al.* 1985; Jodice *et al.* 2000; Fletcher and Hamer 2003). For example, in the Short-tailed Shearwater (*Puffinus tenuirostris*), within-pair comparison of morphometrics improved the accuracy of LDA models from 84% to 92% (Carey 2011). Within-pair differences are typically due to assortative mating, defined as a pattern of non-random mating between male and female, based on some phenotypic criteria (Jiang *et al.* 2013). It can be either positive, in which case individuals tend to mate with similar partners, or negative, in which case they avoid similar partners (Jiang *et al.* 2013). Even though assortative mating appears weaker in birds compared to other phyla, it was documented in several species including in the Lesser Snow Goose (*Anser caerulescens*; Cooke *et al.* 1976), Brant (*Branta bernicla*; Abraham *et al.* 1983), Black Grouse (*Lyrurus tetricus*; Rintamäki *et al.* 1998), Brown Noddy (*Anous stolidus*; Chardine and Morris 1989), Parasitic Jaeger (Furness 1987; Phillips and Furness 1997) and several falconids (Olsen *et al.* 1998). In all those situations, researchers were able to demonstrate that

birds are not mating randomly with respect to their appearance. However, some studies did not find assortative mating based on morphometrics (Black Guillemot, *Cepphus grylle*; Berzins *et al.* 2009).

Our objective was to establish a reliable and simple method to sex Long-tailed Jaegers captured in the field with morphometrics. First, we examined if discriminant analysis based on a combination of body measurement could be used to sex Long-tailed Jaegers. Second, we determined if assortative mating based on size was present in this species, and if within-pair size differences could be used to improve the accuracy of sexing.

METHODS

Study Site and Field Methods

The fieldwork was conducted from 2007-2018 in the lowland tundra of Bylot Island (Nunavut) (73° 09' 00.00" N 79° 58' 60.00" W) in the Canadian High Arctic (Gauthier *et al.* 2013). A breeding population of Long-tailed Jaeger has been studied at this site since 2007. Nest searches were carried out annually in late June/early July and monitored until hatching. We captured males and females, marked them with metal and plastic bands, and took several body measurements. Birds were most often captured at the nest using a bownet trap, or in the nest vicinity using a bal-chatri trap with a live lemming inside, a noose carpet with quail or goose eggs, or a netgun when birds were not breeding.

All captured birds were weighed (± 0.5 g) with a Pesola spring scale, and we took six external body measurements. We checked the 0 on the spring scale daily, and adjusted it if needed. Culmen length (from the tip of the bill to the first feathers at the base of the maxillary), total head length (from the tip of the bill to the rear of the skull), and tarsus length (from intertarsal joint to the base of the toes) were measured with calipers (± 0.1 mm). We took two measurements of the rectrices with a ruler (± 0.5 mm): the longest central tail feather (R1) and the longest tail feather excluding R1. We measured wing chord from the carpal joint to the end of the longest primary feather using a stop-end ruler (± 0.5 mm). For birds that were measured more than once, we randomly selected one set of measurements for the analyses.

We estimated laying date of breeding pairs as follows. If the nest was found between laying of the first and second egg, laying date was considered to be the day before the visit. If only one egg was laid or if the nest was found after both eggs were laid, eggs were floated and the incubation stage was established based on Furness and Furness (1981) and Liebezeit *et al.* (2007). If

the nest was visited at hatching, laying date was estimated by subtracting the mean incubation length (24 days; Maher 1970) to the hatching date.

Molecular Sexing

We plucked three feathers on the breast of jaegers at the time of capture, or in a few cases, we took a blood sample (a few drops) from the brachial vein in order to sex birds using DNA analysis. Feathers were preserved in a paper envelope at ambient temperature and we extracted DNA from a small piece (3–5 mm) of pulp at the bottom of the calamus. Blood samples were preserved in Queen's lysis buffer (0.01 M Tris, 0.01 M NaCl, 0.01 M EDTA, and 1% n-lauroylsarcosine, pH 7.5) until analysis (Seutin *et al.* 1991). We used a salt extraction protocol modified from Aljanabi and Martinez (1997). The pulp sample was dropped in a solution of 440 μ l of salt extraction buffer (0.4 M NaCl, 10 mM Tris–HCl and 2 mM EDTA), 44 μ l of SDS 20% and 8 μ l of proteinase K (20 mg/ml). The sample was incubated overnight at 50 to 57 °C on a stirring plate, and 300 μ l of 6 M NaCl solution was added to the sample. Sample was vortexed for 30 sec and then centrifuged at 10,300 rpm for 30 min. Six hundred microliters of supernatant was transferred into a new tube to which 600 μ l of isopropanol (at -20 °C) was added and mixed by gently inverting the tubes. The sample was incubated at -20 °C for at least 1 hr and centrifuged at 13,000 rpm for 20 min. The supernatant was discarded and 200 μ l of 70% ethanol (at -20 °C) added to the tube. The sample was centrifuged at 13,000 rpm for 10 min and the supernatant discarded again. The pellet was washed a second time to remove all the remaining isopropanol. Samples were air-dried overnight at 37 °C and resuspended in 50 μ l of sterile water. Since the quantity of DNA was low in the samples, it was important to resuspend it in a small volume of water. The sample was refrigerated at 4 °C overnight before DNA amplification.

DNA was amplified by a Polymerase Chain Reaction (PCR) based on Fridolfsson and Ellegren (1999) using a GeneAmp PCR System 9700 (Applied Biosystems). PCR reaction were done with a 10 μ l volume composed of 5 μ l of AccuStart II (Quantabio) PCR SuperMix, 0.25 μ l of primers 2550F (5'-GTTACTGATTCGCTACGAGA-3') and 2718R (5'-ATTGAAATGATCCAGTGCTTG-3'), 2.5 μ l of sterile water and 2 μ l of DNA. The thermal profile was almost identical to the one described in Fridolfsson and Ellegren (1999) except the initial denaturing step lasted 4 min (instead of 2 min) and the extension in the 35 additional cycles lasted 45 sec (instead of 40 sec).

To determine the sex of the amplified DNA samples, a 3% agarose gel electrophoresis was conducted in TBE buffer with ethidium bromide staining. Eight microliters of each DNA sample was placed on the agarose gel under a current of 125 V for approximately 45 min. Sex was determined by the amplification of a part of the CHD1 gene. Under UV-light, males (homogametic ZZ) display a single band (CHD1W - 400 to 450 bp) while females (heterogametic ZW) display two bands (CHD1W - 400 to 450 bp, and CHD1Z - 600 to 650 bp).

Data Analyses

Body mass can fluctuate over time and especially during the breeding season (Norberg 1981; Croll *et al.* 1991; Jones 1994), which could be a source of error when using this trait in the same analysis along with morphological measurements (van Franeker and ter Braak 1993; Lorentsen and Røv 1994). We verified if seasonal change in body mass could be a confounding factor by regressing this variable on breeding stage, estimated by number of days after laying as described above, using a linear mixed-effects model (one for each sex) with the capture year as random effect using the nlme package (Pinheiro *et al.* 2018). We used all breeding individuals captured from 2007–2018 for which the incubation date and the sex were known ($n = 44$ females and $n = 40$ males). We verified the amount of variation explained by the model using the marginal R^2_m for fixed effects (Nakagawa and Schielzeth 2013). Body mass was not significantly related to incubation stage in either females (slope = -0.83 g/day; 95% CI -1.89 to 0.22; $R^2_m = 0.07$) nor males (slope = -0.16 g/day; 95% CI -1.14 to 0.83; $R^2_m < 0.01$). Considering that most birds were measured between day 7 and 21 of the incubation period, this represents a potential mean mass loss of 11.7 g for females and 2.2 g for males over this 14 day period, or 3.7% and 0.8% of their body mass, respectively. We thus concluded that body mass could be used in our analyses without any correction.

To build equations to sex jaegers based on morphometrics, we used only birds captured from 2014–2018 because they were all measured by the same two experienced observers, which minimizes inter-individual variability. We did not attempt to do a correction for the observer and assumed that differences would be attributable to within-measurements error instead of between observers as in Devlin *et al.* (2004).

We used a Multivariate Analysis of Variance (MANOVA) with six morphometric characters to test for overall body size differences between sexes. We excluded culmen length because it was correlated with head length (Pearson $r = 0.52$; for all other measurements, $r \leq 0.35$). If the global MANOVA was significant, we further conducted univariate ANOVA on each measurement separately. MANOVA was done using a Pillai's Trace test because it is more robust to the deviation of the multivariate normality than the Wilk's Lambda (Quinn and Keough 2002).

We used Linear Discriminant Analysis (LDA) from the caret package (Kuhn 2018) with the leave-one-out cross-validation method to establish the best discriminant model. Data were scaled and centered by subtracting the mean and dividing by the standard deviation. Even if the dataset was unbalanced (see above), the prior probability was set to 0.5 for each sex since we had no reason to believe that the population was unbalanced. The model with the highest Youden's index (Youden 1950), Matthew's correlation coefficient (MCC) (Matthews 1975), and discriminant power (DP) (Blakeley *et al.* 1995) was considered as being the best-fitted model and selected to create the classification function. Homoscedasticity (homogeneity of the variance-covari-

ance matrix) was tested using Box's M test ($\chi^2_{21} = 24.4$, $P = 0.27$) and univariate normality was verified with Shapiro-Wilk's test ($P > 0.05$ for all measurements except for tarsus [$W = 0.94$, $P = 0.002$] and tail excluding R1 [$W = 0.97$, $P = 0.03$]). Because the discriminant analysis is robust to the non-respect of the normality, data were not transformed (Tabachnick and Fidell 2007).

To evaluate the presence of assortative mating, we related morphometrics of pair members with a reduced major axis regression (lmodel2 package; Legendre 2018). To evaluate within-pair differences, we performed a two-sided paired t-test for all morphometrics. We also simulated ($n = 200$ simulations) 26 random pairs (the same number as in our study) by randomly selecting with replacement females and males among the pool of individuals that we measured. For each simulation, we calculated the proportion of pairs where the female was heavier or had longer wing than their partner, and we related measurements of pair members together. Finally, we repeated the LDA by adding information from the partner to see if it could improve accuracy of our models. We added partners' variables that differed significantly within-pairs to those retained in models that presented an accuracy $>80\%$ in the previous LDA and reran all those models considering that the dataset was not exactly the same here (reduced sample size).

We evaluated the efficiency of the discriminant function equations developed in this study to sex Long-tailed Jaegers (see Results) by applying them to an independent dataset of birds measured on Bylot Island from 2007-2010 by another observer. All the analyses were done in R (R Core Team 2018).

RESULTS

We used a sample of 76 individuals (43 females and 33 males) measured by the two experienced observers from 2014-2018 for the main analyses presented in this paper. Among those, we captured both members of 26 different breeding pairs, including three pairs that had the same male or female that mated with a different individual in a subsequent year. We used an additional sample of 26 individuals (10 females and 16 males) measured from 2007-2010, including four

pairs, to test equations developed in the previous analyses. Most individuals used in the analyses were sexed using DNA, but in some cases ($n = 7$), only one member of a pair was sexed with molecular methods. As no same sex pairs of Long-tailed Jaeger were found based on DNA sexing of both partners ($n = 29$ pairs), the sex of those seven individuals was assigned based on their partner's sex.

The MANOVA showed a significant difference between males and females based on six morphometrics ($F_{1,69} = 11.1$, Pillai = 0.49, $P < 0.001$). However, univariate comparisons revealed significant differences only for wing chord and body mass (Table 1), with females being 10% heavier than males and their wing cord 2% longer than males on average. All measurements showed a high degree of overlap between the two sexes, even for wing chord and body mass (Fig. 1).

Among the 25 LDA models tested, seven had an accuracy $> 80\%$ to discriminate between males and females, and they included between one and three variables (Appendix, Table A1). The model that performed best had the two variables that differed significantly between sexes: body mass and wing chord. This model had the highest accuracy (82.9%), Youden's index (0.655), discriminant power (1.732) and MCC (0.653; Appendix, Table A1). According to this model, the classification function was:

$$\text{Eq (1) Score} = 0.075 \cdot \text{body mass} + 0.119 \cdot \text{wing chord} - 59.915$$

where a score higher than 0 classifies the individual as a female. The test correctly classified 83.7% of the females (sensitivity or true positives) and 81.8% of the males (specificity or true negatives; Altman and Bland 1994).

Table 1. Morphometrics ($\bar{x} \pm \text{SD}$) of male and female Long-tailed Jaegers (*Stercorarius longicaudus*) and comparison between sexes based on a MANOVA ($n = 76$ individuals).

Variable	Female	Male	$F_{1,69}$	P
Head length (mm)	70.6 \pm 1.8	71.0 \pm 1.8	0.92	0.34
Tarsus length (mm)	43.5 \pm 2.1	42.9 \pm 1.5	1.89	0.17
Wing chord length (mm)	315.5 \pm 5.6	308.5 \pm 8.7	18.24	< 0.001
Tail length (R1) (mm)	298.5 \pm 24.5	298.3 \pm 21.1	< 0.01	0.97
Tail length (excluding R1) (mm)	128.9 \pm 7.3	127.6 \pm 7.7	0.62	0.43
Body mass (g)	317.8 \pm 21.1	286.1 \pm 18.5	46.74	< 0.001

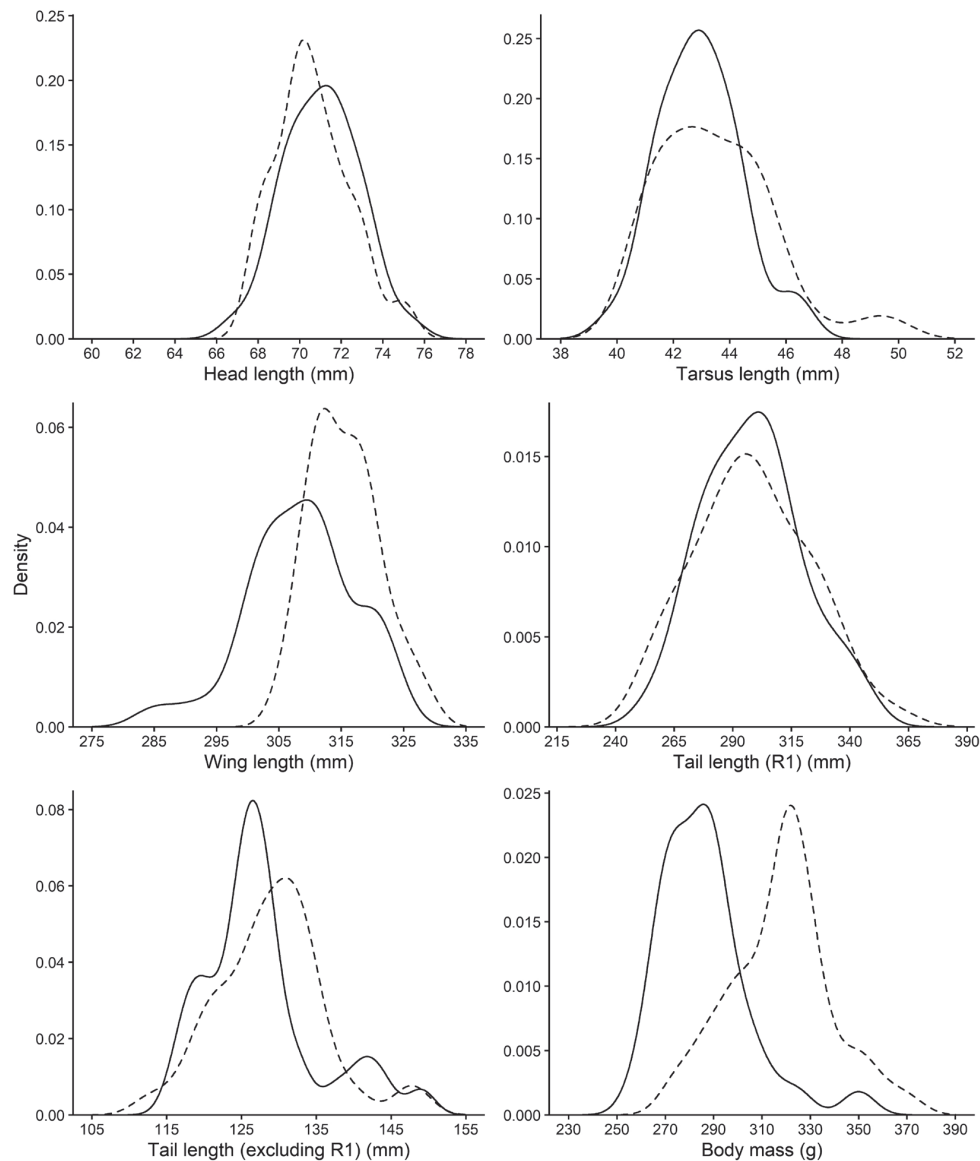


Fig. 1. Density plot of six morphometrics of male (solid line) and female (dashed line) Long-tailed Jaegers (*Stercorarius longicaudus*) ($n = 76$).

Body mass of individuals within pairs was positively related ($r^2 = 0.245$, $P = 0.01$) but not wing chord ($r^2 = 0.001$, $P = 0.86$). Within-pair comparisons showed significant sex differences again for only two variables: wing chord and body mass (Table 2). Within a pair, 85% of the females had a longer wing than males and 88% were heavier than

males (Fig. 2). For all other measurements, the difference between sexes within-pair was close to 0 (Fig. 2). When individuals were paired randomly, body mass and wing chord of pair members were weakly related (average $r^2 = 0.042$ and 0.036 , respectively) and rarely significant ($P < 0.05$ for 6.5% of simulations for body mass and

Table 2. Results of the paired t-test for within-pair difference (female minus male) in six morphometrics ($n = 26$ pairs) of Long-tailed Jaeger (*Stercorarius longicaudus*).

Variable	Mean difference	t_{25}	P
Head length (mm)	-0.3	-0.81	0.42
Tarsus length (mm)	0.1	0.19	0.85
Wing chord length (mm)	6.1	3.79	< 0.001
Tail length (R1) (mm)	-6.8	1.30	0.20
Tail length (excluding R1) (mm)	1.4	0.84	0.41
Body mass (g)	29.8	6.81	< 0.001

3.5% for wing chord). Moreover, on average 88% of the females were heavier than their mate (range: 69% to 100%) and 76% of the females had longer wings than their mate (range: 53 to 92%). We therefore examined if adding body mass or wing chord of partners could improve the accuracy of our LDA model to determine the sex of individuals.

Adding partners' measurements to those of individuals improved their sex identification as several models using various combinations of variables had an accuracy >83% (Appendix, Table A2). The model that performed best included the body mass, wing chord and length of the central rectrice (R1) of the individual in combination with body mass of its partner. This model had an accuracy of classification of 92.3% (classification success equal in both sexes) and a discriminatory power of 2.740 (Appendix, Table A2). The classification function of this model was:

$$\text{Eq (2) Score} = 0.113 \cdot \text{body mass} + 0.107 \cdot \text{wing chord} - 0.051 \cdot \text{tail length (R1)} - 0.129 \cdot \text{partner's body mass} - 13.525$$

where a score higher than 0 classifies the individual as a female.

When we tested Equation 1 on the dataset measured from 2007-2010, only 62% of the 26 individuals were correctly sexed. On the other hand, Equation 2 correctly sexed 100% of the eight individuals. Close examination of this dataset revealed that the mean body mass of females was 23.5 g lower than in the dataset we used to establish the function ($t_{51} = -3.17$, $P = 0.003$) though not for males (difference of 3.7 g, $t_{47} = -0.57$, $P = 0.57$).

DISCUSSION

As previously reported (Wiley and Lee 1998), we found reversed size dimorphism in Long-tailed Jaegers. However, dimorphism was weak and only present for body mass and wing chord. Nonetheless, combining body mass and wing chord in a discriminant analysis allowed us to accurately sex 83% of the individuals. Interestingly, the model was simple as it required only two variables that are relatively easy to measure to predict the sex. Errors in taking those measurements are often quite small compared to other measurements such as tarsus, head length and culmen (Winker 1998).

The sex classification success that we obtained is comparable to other studies in seabirds which typically ranges from 72% to 93% based on individual measurements (Coulter 1986; Lorentsen and Røv 1994; Mallory and Forbes 2005; Mischler *et al.* 2015; Ferrer *et al.* 2016). A similar study in Parasitic Jaeger, a closely related species, produced a discriminant function to sex individuals with an accuracy of 91% using the same two variables as in our Equation 1 (Phillips and Furness 1997). The higher accuracy of their model compared to ours may be due to a higher dimorphism in that species, as females were 15% heavier than males on average.

Body mass must be used with caution when attempting to discriminate sexes because it varies over time, especially during the breeding season, and possibly differently between sexes (Norberg 1981; Croll *et al.* 1991; Jones 1994). However, we did not find any significant change in body mass according to the incubation stage in both sexes despite a trend for a decrease in females. Since most birds were measured over about half of

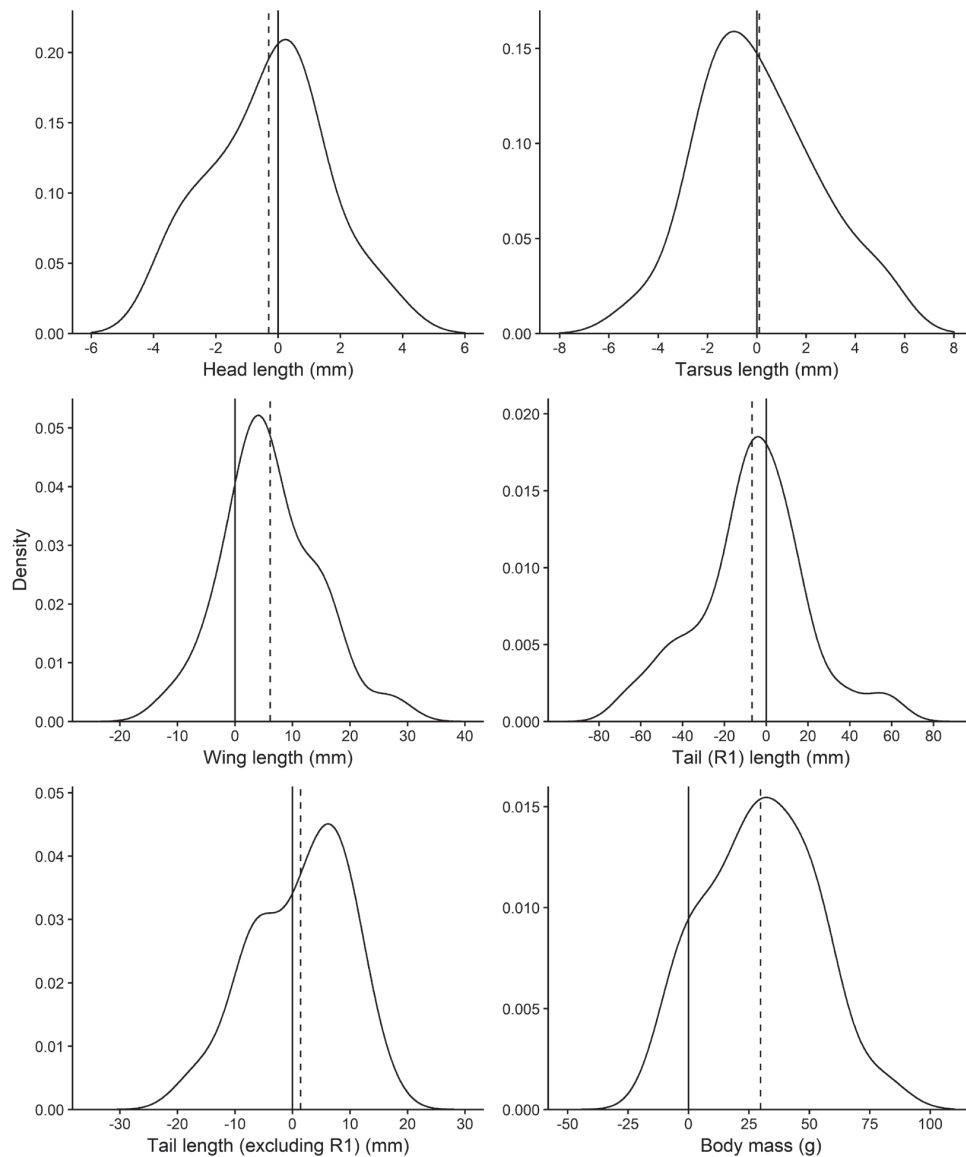


Fig. 2. Density plot of the within-pair size difference for six morphometrics in Long-tailed Jaegers (*Stercorarius longicaudus*) ($n = 26$). The vertical solid line represents no difference (0) and a positive value means that females are bigger than males. The vertical dashed line represents the within-pair mean difference.

the incubation period only (day 7 and 21), it is possible that this limited our ability to find a significant decrease in females. Thus, even though variation in body mass may be source of errors in some circumstances, our results suggest that it remains an important variable to discriminate the sex of Long-tailed Jaegers on the breeding ground.

We concluded that there is a positive assortative mating based on body mass, as heavy females tended to mate with heavy males and light females with light males on average, but not based on wing chord. Positive assortative mating, which occurs when individuals tend to mate to individuals similar to them, has been reported in a wide va-

riety of species such as in Brant (Abraham *et al.* 1983), Feral Pigeons (*Columba livia*; Johnston and Johnson 1989), Parasitic Jaegers (Phillips and Furness 1997) and in several falcon species (Olsen *et al.* 1998). Despite this positive assortative mating, it is interesting to see that within-pairs, 88% of females were still heavier and 85% had longer wings than their partner, which suggests that females also prefer to mate with males smaller than themselves. Female preference for a male smaller than them has been reported in many raptor and owls species that present reversed size dimorphism (Earhart and Johnson 1970; Andersson and Norberg 1981; Safina 1984). Nevertheless, we do not know exactly what is the mechanism leading to the mating pattern found in Long-tailed Jaeger, as we lack behavioral observations. For instance, we cannot totally exclude the possibility that the observed pattern of assortative mating could be a consequence of other confounding variables, such as selection for high-quality territories defended by heavy individuals.

A preference of females for males smaller than themselves can explain why including body mass of the partner in our discrimination analysis considerably improved the accuracy of our model to predict the sex. Indeed, the proportion of misclassified individuals decreased by half (17% vs. 8%) with the partner's measurement and the addition of the tail length to the model. Therefore, efforts should be made to capture and measure both members of a pair if sex identification is an important variable. Few studies attempted to improve the classification success using within-pair comparison and, to our knowledge, none did by developing new discriminant functions taking into consideration measurements from the other individual. Nevertheless, a simple within-pair comparison of the discriminant score reduced the proportion of misclassified individuals from 26-28% to 10-16% in two tern species (Fletcher and Hamer 2003; Devlin *et al.* 2004) and from 5-15% to 0-11% in Cape Petrel (*Daption capense*; Weidinger and Franeker 1998).

When we tested Equation 1 with the set of measurements taken by another observer from 2007-2010, we were surprised of the poor success of the equation in assigning sex. The large difference in female body mass found between the two datasets may be responsible for this poor success. Several factors may explain this large difference, including annual effects, difference in the incubation stage at which individuals were measured or miscalibration of the spring scale. Among those, difference in incubation stage may be an important one, because birds were captured on average significantly later in the 2007-2010 dataset than in the 2014-2018 dataset used to establish the equations (23 days vs. 17 days of incubation, respectively; $t_{22} = 3.0$, $P = 0.006$). This further emphasizes the need to be cautious when using equations that include body mass, as mentioned above. However, it is reassuring to see that, when using Equation 2 with this same dataset, classification success was 100%. It thus appears that any factor that may have biased low female body mass in that other dataset was controlled by including body mass of the partner. This comparison therefore provides a strong argument to justify the measurement of both breeding partners and the use of our Equation 2. Furthermore, when measuring breeding individuals, we strongly suggest recording the reproductive phenology. Even though our data did not show any significant decrease in body mass of incubating females, more data covering the whole incubation period are needed to better document this. A decrease in female body mass throughout the incubation period would not be surprising, considering that females assume about two-third of the total incubation time in this species (Andersson 1971).

We were able to establish two simple equations to sex Long-tailed Jaegers based on morphological measurements. Depending on the objectives of the study, the sexing method we presented in this paper may be sufficient to avoid the need to do expensive and tedious DNA analyses to sex individuals. However, the timing of the measurements may affect the reliability of Equation 1 due to possible

variations of female body mass during incubation. The equation should be most accurate when individuals are measured during mid-incubation, between 7 and 21 days. However, using measurements from the partner apparently overcomes this limitation and this is why, when working with breeding pairs, we recommend capturing both individuals. Also, geographical differences in size are possible between populations of the same species (Waugh *et al.* 1999; Angel *et al.* 2015) and differences in body mass between sites were previously reported for the Long-tailed Jaeger (Wiley and Lee 1998). Thus, care should be taken when applying these equations elsewhere in the Arctic.

ACKNOWLEDGMENTS

We are grateful to all the people who contributed to this project in the past years. Jaimie Vincent, Kamil Chatila-Amos, Audrey Robillard and Andréanne Beardsell for their help in the field and Damien Boivin-Delisle, Guillaume Côté and Alysse Perreault for their help with the genetic analysis. Special thanks to Marie-Christine Cadieux for her assistance with the data management and the field logistic. Funding for this project was provided by the Natural Sciences and Engineering Research Council of Canada, the Fonds de recherche du Québec Nature et Technologies, the Network of Centre of Excellence ArcticNet, the Polar Continental Shelf Program of Natural Resources Canada and the Northern Scientific Training Program of Polar Knowledge Canada. All protocols were approved by the Animal Care Committee of Université Laval in accordance with the guidelines of the Canadian Council of Animal Care in Research. YS, GG and JFT collected the data in the field. YS conducted the laboratory analyses and statistical analyses and wrote the manuscript with the assistance of GG. LB helped with the laboratory analyses. LB and JFT contributed to the revision of the manuscript. We thank two anonymous reviewers for helpful suggestions to improve the manuscript.

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Table A1. Results of the 25 linear discriminant analysis models tested to predict the sex of individual Long-tailed Jaegers (*Stercorarius longicaudus*) using various combinations of their morphometrics. Models are sorted from the highest to the lowest accuracy.

#	Model	Accuracy	95% CI	MCC	Youden	DP
11	Body mass + Wing	0.829	0.725 - 0.906	0.653	0.655	1.732
9	Body mass + Head + Tail	0.816	0.710 - 0.895	0.634	0.639	1.683
10	Body mass + Head	0.816	0.710 - 0.895	0.634	0.639	1.683
4	Body mass + Wing + Tail (R1)	0.816	0.710 - 0.895	0.629	0.632	1.643
7	Body mass + Wing + Tail	0.816	0.710 - 0.895	0.629	0.632	1.643
12	Body mass	0.803	0.695 - 0.885	0.611	0.616	1.608
8	Body mass + Head + Wing	0.803	0.695 - 0.885	0.604	0.609	1.562
6	Body mass + Head + Wing + Tail	0.789	0.681 - 0.875	0.581	0.586	1.487
2	Body mass + Head + Tarsus + Wing + Tail (R1)	0.776	0.666 - 0.864	0.557	0.562	1.418
3	Body mass + Head + Wing + Tail (R1)	0.776	0.666 - 0.864	0.557	0.562	1.418
5	Body mass + Head + Tarsus + Wing + Tail	0.776	0.666 - 0.864	0.557	0.562	1.418
1	Body mass + Head + Tarsus + Wing + Tail (R1) + Tail	0.763	0.652 - 0.853	0.535	0.539	1.352
18	Head + Wing + Tail	0.737	0.623 - 0.831	0.464	0.464	1.117
19	Head + Wing	0.737	0.623 - 0.831	0.464	0.464	1.117
15	Head + Wing + Tail (R1)	0.711	0.595 - 0.809	0.416	0.418	0.982
21	Wing + Tail (R1)	0.697	0.581 - 0.798	0.392	0.395	0.920
17	Head + Tarsus + Wing + Tail	0.697	0.581 - 0.798	0.382	0.381	0.897
13	Head + Tarsus + Wing + Tail (R1) + Tail	0.684	0.567 - 0.786	0.357	0.357	0.832
14	Head + Tarsus + Wing + Tail (R1)	0.684	0.567 - 0.786	0.357	0.357	0.832
22	Wing	0.632	0.513 - 0.739	0.256	0.257	0.582
23	Tail	0.579	0.460 - 0.691	0.178	0.178	0.408
20	Head + Tail	0.566	0.447 - 0.679	0.140	0.141	0.315
16	Head	0.566	0.447 - 0.679	0.126	0.127	0.282
25	Tarsus	0.539	0.421 - 0.655	0.102	0.101	0.231
24	Tail (R1)	0.105	0.047 - 0.197	-0.793	-0.800	-2.514

Table A2. Results of the 28 linear discriminant analysis models tested to predict the sex of individual Long-tailed Jaegers (*Stercorarius longicaudus*) using various combinations of their morphometrics, and body mass and wing chord of their partner. Models are sorted from the highest to the lowest accuracy.

#	Model	Accuracy	95% CI	MCC	Youden	DP
30	Body mass + Wing + Tail (R1) + Partner's Body mass	0.923	0.815 - 0.979	0.846	0.846	2.740
44	Body mass + Wing + Tail (R1) + Partner's Body mass + Partner's Wing	0.904	0.790 - 0.968	0.808	0.808	2.493
27	Body mass + Wing + Partner's Body mass	0.885	0.766 - 0.956	0.772	0.769	2.310
46	Body mass + Partner's Body mass + Partner's Wing	0.885	0.766 - 0.956	0.772	0.769	2.310
41	Body mass + Wing + Partner's Body mass + Partner's Wing	0.885	0.766 - 0.956	0.769	0.769	2.246
45	Body mass + Wing + Tail + Partner's Body mass + Partner's Wing	0.885	0.766 - 0.956	0.769	0.769	2.246
33	Body mass + Head + Wing + Partner's Body mass	0.865	0.742 - 0.944	0.736	0.731	2.161
47	Body mass + Head + Wing + Partner's Body mass + Partner's Wing	0.865	0.742 - 0.944	0.736	0.731	2.161
29	Body mass + Head + Partner's Body mass	0.865	0.742 - 0.944	0.731	0.731	2.063
31	Body mass + Wing + Tail + Partner's Body mass	0.865	0.742 - 0.944	0.731	0.731	2.063
42	Body mass + Head + Tail + Partner's Body mass + Partner's Wing	0.865	0.742 - 0.944	0.731	0.731	2.063
43	Body mass + Head + Partner's Body mass + Partner's Wing	0.865	0.742 - 0.944	0.731	0.731	2.063
28	Body mass + Head + Tail + Partner's Body mass	0.846	0.719 - 0.931	0.692	0.692	1.880
32	Body mass + Partner's Body mass	0.846	0.719 - 0.931	0.692	0.692	1.880
34	Body mass + Wing + Partner's Wing	0.846	0.719 - 0.931	0.692	0.692	1.880
40	Body mass + Head + Wing + Partner's Wing	0.846	0.719 - 0.931	0.692	0.692	1.880
37	Body mass + Wing + Tail (R1) + Partner's Wing	0.827	0.697 - 0.918	0.654	0.654	1.731
38	Body mass + Wing + Tail + Partner's Wing	0.827	0.697 - 0.918	0.654	0.654	1.731
7	Body mass + Wing + Tail	0.808	0.675 - 0.904	0.623	0.615	1.674
11	Body mass + Wing	0.808	0.675 - 0.904	0.617	0.615	1.604
4	Body mass + Wing + Tail (R1)	0.808	0.675 - 0.904	0.617	0.615	1.604
12	Body mass	0.788	0.653 - 0.889	0.581	0.577	1.490
9	Body mass + Head + Tail	0.769	0.632 - 0.875	0.545	0.538	1.387
8	Body mass + Head + Wing	0.769	0.632 - 0.875	0.538	0.538	1.328
39	Body mass + Partner's Wing	0.769	0.632 - 0.875	0.538	0.538	1.328
36	Body mass + Head + Partner's Wing	0.750	0.611 - 0.860	0.510	0.500	1.291
10	Body mass + Head	0.750	0.611 - 0.860	0.503	0.500	1.238
35	Body mass + Head + Tail + Partner's Wing	0.731	0.590 - 0.844	0.467	0.462	1.142