



Effects of body size on sex-related migration vary between two closely related gull species with similar size dimorphism

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Studies of migration have revealed multiple trade-offs with other life-history traits that may underlie observed variation in migratory properties among ages and sexes. To assess whether, and to what extent, body size and/or sex-specific differences in competition for resources (e.g. breeding territories or winter food) may shape variation in migration distance and timing of arrival in ecologically and phylogenetically related species, we combined over 30 000 sightings of individually marked, sexually mature males and females of Herring Gulls *Larus argentatus* and Lesser Black-Backed Gulls *Larus fuscus* with biometric measurements and phenological observations at a mixed breeding colony. In *L. argentatus*, larger males migrated further from the breeding colony, whereas migration distance was independent of body size in adult females. In *L. fuscus*, no relationship between body size and migration distance was apparent in either sex. Mean arrival dates at the breeding colony did not vary with migration distances but differed between males and females of *L. argentatus* (but not *L. fuscus*). As allometry at least partly explains sexual segregation in migration behaviour in *L. argentatus*, but not in *L. fuscus*, we conclude that the effect of body size on sex-related migratory strategies may vary between closely related, sympatric species despite similar size dimorphism.

Keywords: allometry, arrival time, differential migration, sexual segregation, social dominance.

Migratory behaviour has evolved independently among many animal groups, such as birds, fish, mammals, reptiles, amphibians, insects and marine invertebrates (Alerstam *et al.* 2003), and is expressed through a wide range of movement-related behaviours (Dingle 1996, Quinn & Myers 2004, Bolger *et al.* 2008). As migration is predicted to be favoured when benefits gained from moving between habitats outweighs fitness risks and energetic costs of the journey (Calvert *et al.* 2009), seasonal and spatial variation in environmental conditions comprise primary forces in its evolution (Alerstam & Enckell 1979). Over the past decades, studies on the proximate and ultimate causes of

migration have elucidated the role of migration in the annual life cycle of migratory species. Studies on differential migration, defined as 'the situation in which migration in some distinguishable classes (ages, sexes, races) differs with respect to distance, timing or both' (Terrill & Able 1988), in particular, have revealed how migratory behaviour may trade-off against other costly activities such as breeding (Dingle 1996, Saino *et al.* 2004, Boyle 2008, McNamara & Houston 2008, Marques *et al.* 2010).

Life-history trade-offs, which are a key assumption underlying optimality models of life-history evolution (Roff 1992, Stearns 1992), also play a prominent role in the interpretation of life-history variation within populations, i.e. between ages or sexes. In many vertebrate species, males and females show a marked sexual size dimorphism

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and/or suffer from different levels of competition for breeding resources that may directly or indirectly affect fitness costs and benefits associated with migration (Catry *et al.* 2005). As a result, various properties of their migratory behaviour, such as migration distance, timing of departure or arrival, or habitat use outside the breeding season, have been predicted to differ between sexes (e.g. Cristol 1995, Cristol *et al.* 1999, Kissner *et al.* 2003, Catry *et al.* 2005, O'Hara *et al.* 2006, Palacin *et al.* 2009). Optimal life-history variation in migratory behaviour between sexes translates into three hypotheses, each of which focuses on a particular component of ecological specialization in relation to body size or other sex-related variation. The social dominance hypothesis (Gauthreaux 1982) puts forward competitive exclusion of the smaller subordinate sex from preferred habitats or habitats closer to the breeding grounds by larger and dominant conspecifics. The body size (or physiological) hypothesis (Ketterson & Nolan 1976) explains latitudinal (clinal) sexual segregation in wintering sites in relation to body size and cold resistance, with the smaller sex predicted to migrate to lower latitudes. Finally, the arrival time hypothesis (Myers 1981) explains sexual segregation in timing and distance of migration as a function of competition for breeding resources with the sex experiencing higher levels of competition for breeding opportunities predicted to arrive earlier on the breeding grounds and, with this goal, to stay closer and/or return sooner. Despite the different ecological mechanisms underlying these non-exclusive hypotheses, their predictions substantially overlap (Belthoff & Gauthreaux 1991, Jenkins & Cristol 2002) and within-sex variation needs to be taken into account to test or refute them properly (Smith & Nilsson 1987, O'Hara *et al.* 2006, Guillemain *et al.* 2009).

Comparison of life-history traits between closely related species is considered a strong approach for studying the nature of trade-offs underlying life-history variation between and within species (Cristol *et al.* 1999). Following this approach, we assessed variation in migratory behaviour of sexually mature male and female Herring Gulls *Larus argentatus* and Lesser Black-Backed Gulls *Larus fuscus*, two phylogenetically and ecologically closely related species that occur in sympatry in NW Europe. Although both species breed in mixed colonies, show a comparable degree of sexual size dimorphism and mature after 3–7 years (Snow

et al. 1998), they differ in their annual migration pattern along the western coastline of continental Europe. Western populations of *L. fuscus* are considered long-distance migrants between their north-western breeding colonies and main wintering grounds in Iberia and western North Africa (Wernham *et al.* 2002). Individuals of *L. argentatus*, in contrast, migrate across a much more variable, but mostly limited, predominantly coastal, radius, resulting in seasonal movements towards non-breeding areas and convergence towards breeding areas at the population level (Dingle 1996, Wernham *et al.* 2002, Roshier & Reid 2003). To assess the extent to which sex-specific constraints related to structural size and/or reproduction may shape variation in migratory behaviour within and between both species, we analyse over 30 000 sightings of individually marked adults of both species during breeding, migration and wintering, and model variation in migration distances and arrival dates in a mixed breeding colony at species, sex and individual levels.

METHODS

Study area and species

We analysed 31 256 sightings of 153 adult male and 167 adult female *L. argentatus* and 288 adult male and 270 adult female *L. fuscus* within a time frame spanning 11 annual cycles (May 1999–July 2010; database managed by the Research Institute for Nature and Forest, Belgium). All individuals were colour-ringed as pulli or breeding adults in a mixed colony at the outer port of Zeebrugge (Belgium, 51°21'N, 03°11'E). For the former, only sightings made during establishment as adult breeder (3½ years or older) in the colony were considered for this study (hereafter referred to as 'adults'). The breeding colony hosted peak numbers of 1986 pairs of *L. argentatus* (spring 2004) and 4573 pairs of *L. fuscus* (spring 2005). Outside the breeding season, adult *L. argentatus* were resighted as far north as IJmuiden (The Netherlands), southwest as far as Calvados (France) and inland as far as Tilburg (The Netherlands). Adult *L. fuscus* were resighted as far southwest as Banc d'Arguin (Mauritania), north as far as Texel (The Netherlands) and inland as far as Madrid (Spain). The majority of resightings of individuals from both species were made near the coastline and at inland refuse tips.

Because univariate proxies of body size, such as tarsus length, have been shown to provide poor measures of overall size in birds (Rising & Somers 1989, Freeman & Jackson 1990, Blas *et al.* 2009), we measured tarsus length, head length, bill length and gonys width of 97 breeding *L. argentatus* (45 males, 52 females) and 284 breeding *L. fuscus* (134 males, 150 females) to the nearest 0.1 mm using slide callipers. Using these metrics, body size was estimated as the first axis of a principal component analysis (PC1, hereafter 'body size') conducted in PASW STATISTICS 18 (SPSS Inc., Chicago, IL, USA). PC1 explained 80% of the body size variation in both species and had high positive loadings for tarsus length (*L. argentatus*/*L. fuscus*: 0.84/0.86), head length (0.95/0.95), bill length (0.88/0.90) and gonys width (0.90/0.88). Only individuals colour-ringed and measured as adult breeders were considered for the size analysis. These individuals had been captured over several years since the beginning of the study (some had already been metal-ringed as pulli) and were hence considered representative for the different cohorts/ages. Birds colour-ringed as pulli were measured at different stages of their structural growth and, if not recaptured as breeding adult, lack of measurements of fully grown traits prevented us from including these individuals in the analysis. Breeding adults were sexed by HJPV on the basis of direct size comparison of paired individuals, complemented by observations of copulation and courtship behaviour at the breeding colony. The repeatability of sex assessment of individuals recorded during subsequent breeding seasons equalled 1.00, whereas a discriminant analysis showed that males of both species were significantly larger than females, when based both on each of the univariate biometrics (see above) separately (all $P < 0.001$) and on the multivariate analysis: *L. argentatus*: ($\lambda = 0.276$, χ^2 (df = 4, $n = 97$) = 119.6, $P < 0.001$; R^2 -canonical = 0.85, 93% correct reclassification); *L. fuscus*: ($\lambda = 0.221$, χ^2 (df = 4, $n = 284$) = 422.1, $P < 0.001$; R^2 -canonical = 0.88, 98% correct reclassification). Birds for which sex identification based on direct observations (five male and two female *L. argentatus* and six male *L. fuscus*) disagreed with sex identification based on biometrics were excluded from analysis.

Migration distance and arrival date

For each individual *L. argentatus* (total: 12 994 sightings) and *L. fuscus* (total: 18 262 sightings)

breeding in the colony, we calculated the median of all distances (km) recorded away from the breeding colony in each month of the year over a time frame spanning 11 annual cycles ('monthly migration distance') (Great circle distance method, <http://www.movable-type.co.uk/scripts/latlong.html>). Although estimating individuals' maximum recorded migration distances following this method yielded similar migration patterns, using an extreme value in this way increases the risk of strong influences from errors in colour-ring reporting. Biases in resighting effort are unlikely to have influenced our results, as the breeding population was large and well represented by marked individuals of known sex, whose migration and wintering sites are well known and extensively visited by a large number of ring-reading volunteers. For 71 breeding *L. argentatus* and 94 breeding *L. fuscus* with known sex and body size, relationships between the median migration distance recorded while on the non-breeding grounds (*L. argentatus*: 627 sightings in October; *L. fuscus*: 757 sightings in November–January) and body size were assessed. For each adult *L. argentatus* and *L. fuscus* of known sex, the earliest sighting in the colony (arrival date) was recorded during each year an individual was observed breeding, based on meticulous observations conducted from morning to evening every second weekday between mid-winter until the start of egg-laying. Individual arrival dates were expressed as the number of days since 1 December of the previous year (earliest arrival date recorded). For 200 breeding *L. argentatus* and 119 breeding *L. fuscus*, arrival date (*L. argentatus*: 1287 arrival dates, *L. fuscus*: 2477 arrival dates) and the median migration distance during the previous year (*L. argentatus*: 627 sightings in October; *L. fuscus*: 757 sightings in November–January) were related during each year in which both estimates were available.

Statistical analysis

Monthly variation in migration distance averaged over 11 annual cycles was analysed for both species separately with a general linear mixed model (ANOVA) with Gaussian error structure (Proc MIXED in SAS 9.2 (SAS Institute Inc., Cary, NC, USA); SAS institute 2008). Categorical variables MONTH, SEX and the two-factor interaction were modelled as fixed effects. To account for statistical dependence, INDIVIDUAL was included as a random factor (Littell *et al.* 1996). Inter- and

intraspecific variation in the median recorded migration distance and relationships with body size were analysed with a general linear model (ANCOVA) with Gaussian error structure. To account for size differences between species and sexes, body SIZE was expressed as standardized residuals, i.e. within each species and sex, mean body size was subtracted from individual measurements and values were divided by the standard deviation. Categorical variables SPECIES, SEX (fixed effects), SIZE (covariate) and all two- and three-way interactions were modelled as independent variables. As the SPECIES \times SEX \times SIZE interaction was statistically significant, SEX \times SIZE interactions were tested for each species separately. Inter- and intraspecific variation in mean arrival date was also analysed with ANCOVA with Gaussian error structure. Variables SPECIES, SEX (fixed effects), median migration DISTANCE (covariate) and all two- and three-way interactions were modelled as independent variables, and INDIVIDUAL and YEAR were included as random factors. The effect of body size on arrival date could not be tested reliably due to the small number of individuals for which all data (median migration distance, arrival time, sex and body size) were known (*L. argentatus*: $n = 24$; *L. fuscus*: $n = 18$).

In each model, levels of significance of all fixed variables were tested in a stepwise backward selection procedure, and the corresponding degrees of freedom were corrected by Satterthwaite formulas (Littell *et al.* 1996). *Post-hoc* tests were carried out with Tukey tests (Proc LSMEANS in SAS 9.2). All mixed models properly dealt with putative deviations of the underlying statistical assumptions as inferred from MIXED_DX (Bell *et al.* 2010). Statistical results of all models were confirmed by non-parametric Kruskal–Wallis one-way ANOVAs (Proc NPAR1WAY in SAS 9.2) (data not shown).

RESULTS

Variation in migration distance

In *L. argentatus*, adult females remained closer to the breeding colony than adult males during September and October (SEX \times MONTH: $F_{11,2668} = 5.76$, $P < 0.0001$; Tukey $P < 0.0001$; Fig. 1, upper panel). In *L. fuscus*, a similar pattern of sexual segregation in monthly migration distance was observed between October and December (SEX \times MONTH: $F_{11,3457} = 6.23$, $P < 0.0001$;

Tukey $P < 0.0001$; Fig. 1, lower panel). Migration distances differentially varied with body size in males and females of both species (SPECIES \times SEX \times SIZE: $F_{1,158} = 4.34$, $P = 0.04$; Fig. 2). In *L. argentatus*, larger males migrated further than smaller males ($F_{1,29} = 4.46$, $P = 0.04$; $\beta = 31.15 \pm 14.76$); however, migration distances were independent of body size in females ($F_{1,38} = 0.28$, $P = 0.59$; $\beta = -2.89 \pm 5.46$; SEX \times SIZE: $F_{1,67} = 5.64$, $P = 0.02$) (Fig. 2, upper panel). In *L. fuscus*, migration distances were independent of body size in males ($F_{1,52} = 0.82$, $P = 0.37$; $\beta = -57.04 \pm 63.05$) or females ($F_{1,37} = 0.35$, $P = 0.56$; $\beta = 52.37 \pm 88.07$; SEX \times SIZE: $F_{1,90} = 1.06$, $P = 0.31$) (Fig. 2, lower panel).

Variation in arrival date

Both species differed in the timing of arrival of males and females at the breeding colony (SPECIES \times SEX: $F_{1,347} = 5.1$, $P = 0.03$). In *L. argentatus*, males arrived significantly earlier than females (males: $\mu = 67.39 \pm 4.08$ days; females: $\mu = 80.83 \pm 4.05$ days; $F_{1,189} = 9.10$, $P = 0.003$; Fig. 3, upper panel), whereas in *L. fuscus*, both sexes arrived at nearly the same time (males: $\mu = 116.4 \pm 2.9$ days; females: $\mu = 115.6 \pm 3.1$ days; $F_{1,123} = 0.06$, $P = 0.81$; Fig. 3, lower panel). Arrival times did not vary with migration distance in *L. argentatus* ($F_{1,352} = 0.08$, $P = 0.77$), whereas in *L. fuscus*, individuals that migrated further tended to arrive later, albeit not significantly so ($F_{1,143} = 2.25$, $P = 0.13$). The effect of migration distance on arrival time did not differ significantly between species (SPECIES \times DISTANCE: $F_{1,506} = 0.25$, $P = 0.61$) or between sexes (SEX \times DISTANCE: $F_{1,448} = 0.32$, $P = 0.58$).

DISCUSSION

A large number of migratory species segregate at least partly by sex and body size on the non-breeding grounds (Cristol *et al.* 1999, Newton 2010), and variation in migration distance has been regarded as a by-product of variation in sexual size dimorphism (cf. Bennett & Owens 2002, Catry *et al.* 2005). Two hypotheses that consider allometric relationships as the biological basis of sex-related variation in migratory behaviour (i.e. body size and social dominance hypothesis) predict that individuals of the smaller sex should migrate further southward along a north–south axis. Our finding of a

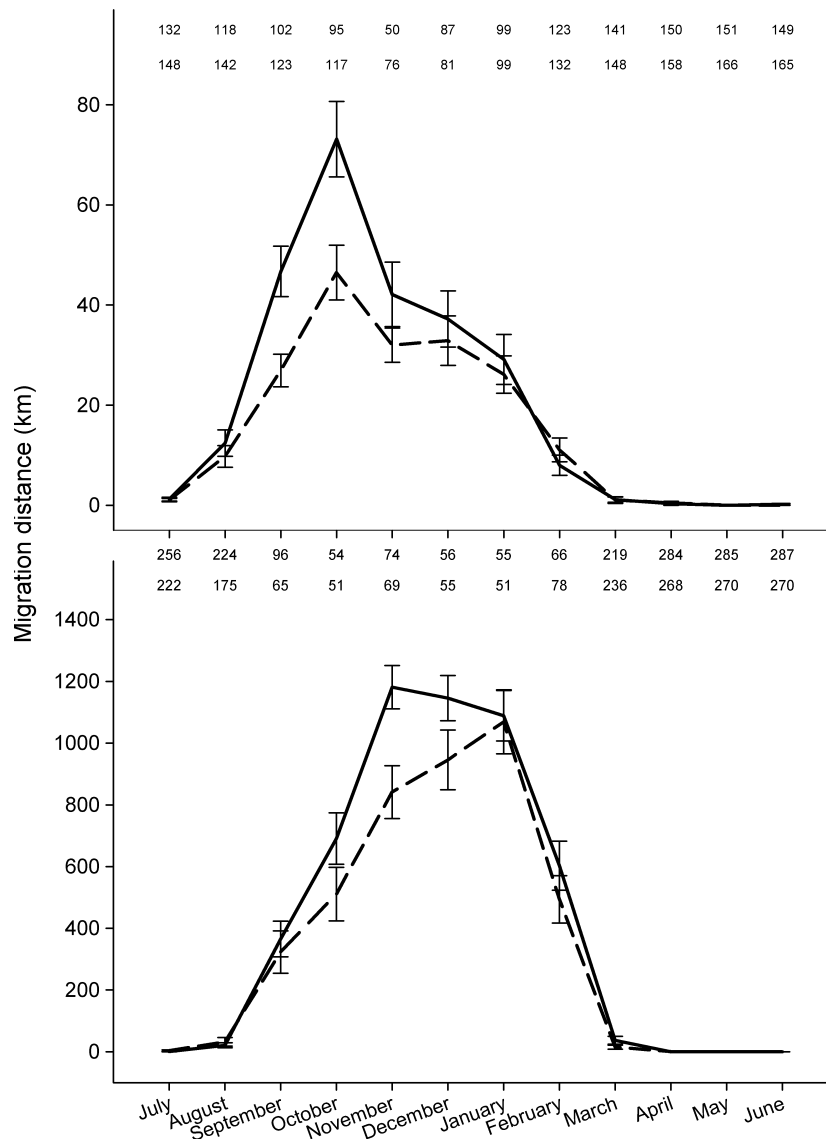


Figure 1. Monthly median migration distances (\pm se) away from a mixed Belgian breeding colony (km) averaged over 11 annual cycles, for 320 adult *Larus argentatus* (upper panel) and 558 adult *L. fuscus* (lower panel). Males are depicted by solid lines, females by dashed lines. Numbers refer to male (top row) and female (bottom row) sample sizes.

reversed pattern in two closely related Larid species was therefore unexpected, yet consistent with empirical data on sexual segregation in other migratory species (e.g. Western Sandpiper *Calidris mauri*, O'Hara *et al.* 2006; Teal *Anas crecca*, Guillemain *et al.* 2009). Mean arrival dates at the breeding colony differed between male and female *L. argentatus* in the direction predicted by the arrival time hypothesis (Ketterson & Nolan 1983), i.e. earlier arrival of the sex that is most strongly involved in breeding resource competition. In *L. fuscus*, how-

ever, males and females arrived synchronously, despite the same level of sexual size dimorphism and the much longer migration route compared with *L. argentatus* (Kissner *et al.* 2003). Possibly, a narrower time window between the end of migration and the start of the breeding activities compared with *L. argentatus* constrains the evolution of sex-differential timing of arrival in *L. fuscus* (cf. Ketterson & Nolan 1983). Within each species, median migration distances did not significantly correlate with arrival time between or within sexes.

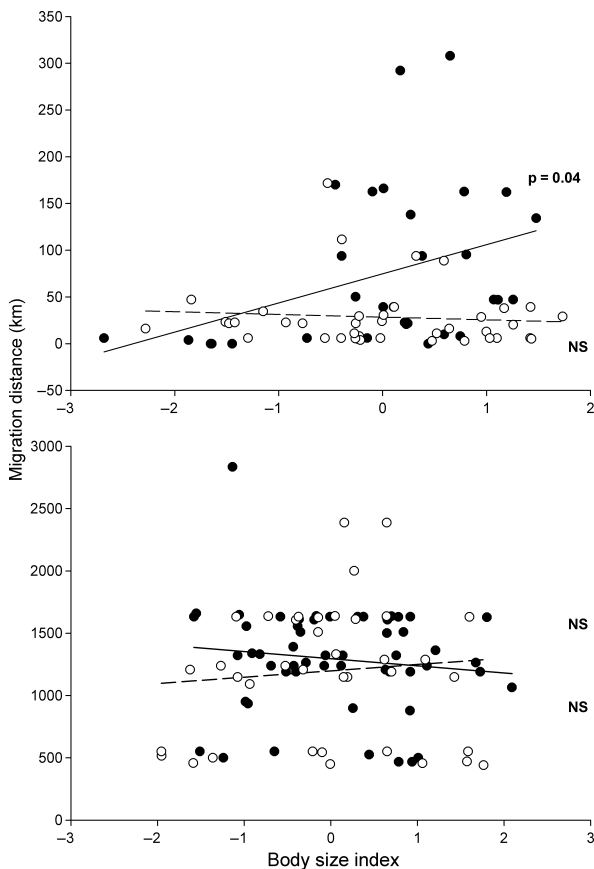


Figure 2. Relationship between median migration distance away from a mixed Belgian breeding colony (km) and standardized PC1 values, for 71 *L. argentatus* (upper panel) and 94 *L. fuscus* (lower panel). Males are depicted by closed circles and solid trend lines; females are depicted by open circles and dashed trend lines.

This result was unexpected given the inverse relationship between migration distance and arrival time predicted by the arrival time hypothesis (Ketterson & Nolan 1983).

Because of the sexual size dimorphism and predominantly north–south migration in *L. argentatus* and *L. fuscus*, variation in average migration distances between males and females directly corresponded to a latitudinal segregation in body size, with the larger sex (males) wintering further south than the smaller sex (females). Patterns of latitudinal segregation in body size are usually interpreted within the framework of Bergmann's rule, which predicts larger individuals will winter at higher latitudes because of their better ability to withstand low temperatures and food shortage (Cristol *et al.* 1999, Katti & Price 2003, Newton 2010). Results from this study, i.e. larger males wintering at lower

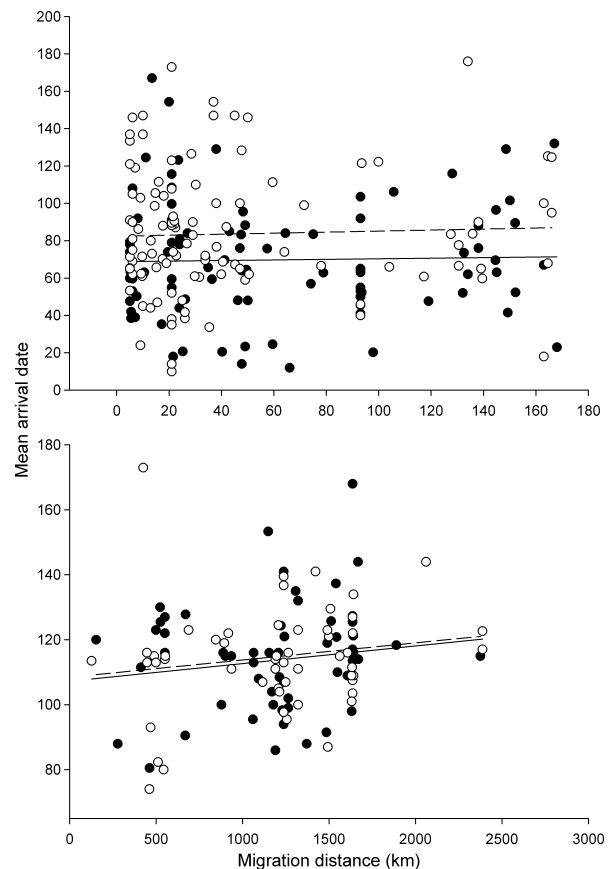


Figure 3. Relationship between median migration distance away from a mixed Belgian breeding colony (km) and mean arrival time at the colony (number of days after 1 December), for 200 *L. argentatus* (upper panel) and 119 *L. fuscus* (lower panel). Males are depicted by closed circles and solid trend lines; females are depicted by open circles and dashed trend lines.

latitudes, do not support the pattern of sex segregation predicted by the body size hypothesis, possibly because distances between male and female wintering sites were too small to result in differential climatic conditions, a basic assumption underlying Bergmann's rule (Stouffer & Dwyer 2003). Variation in migration distances has further been linked to social rank, with subordinate individuals predicted to be competitively excluded from preferred habitats or habitats closer to the breeding grounds by dominant conspecifics (Cristol *et al.* 1999). As *L. argentatus* and *L. fuscus* males are larger and socially dominant over females (Snow *et al.* 1998), yet wintered further from the breeding colony than the subordinate females, the results of this study do not support the pattern of sex segre-

gation generally predicted by the social dominance hypothesis either.

For allometry and its relationship with stress tolerance and dominance to drive sexual segregation in migration distance in the direction expected, gradients of proximity to the breeding ground should covary with gradients in habitat and ambient quality (Ketterson & Nolan 1983), i.e. *nearer* should be *better* for the predictions of the social dominance hypothesis to hold. However, this is unlikely to be the case for *L. argentatus* populations breeding in the southern North Sea area. During autumn, this species migrates southward through a heterogeneous coastal landscape, with habitats further south thought to offer better foraging opportunities and greater prey densities. Males are more often reported from the French department Somme (Fig. 4), where beaches between the Baie d'Authie and Baie de Somme provide high-quality winter habitat for *L. argentatus*. First and most importantly, large, contiguous mussel beds stretch over a distance of many kilometres. Secondly, vast cockle banks stretch near the non-protected area of the nature reserve Baie de Somme, especially near the

town of Le Crotoy. Thirdly, after periods of strong winds, there are often mass strandings of bivalves (mainly *Ensis* and the large, nutritious *Lutraria lutraria*). Similar food concentrations are not encountered elsewhere within the wintering range of this species (Harry J. P. Vercrujisse pers. obs.). Females, in contrast, are mainly reported from sandy beaches in the Belgian province of West-Vlaanderen and the French department of Nord (Fig. 4) where structures such as breakwaters provide ample feeding opportunities, albeit of lesser quality (Davy S. Bosman pers. obs.). Given this configuration of habitat, the pattern of sex segregation observed in our study might still fit a greater resource holding power of larger males and size-mediated competitive exclusion of females (and possibly smaller males, Fig. 2, upper panel) from high-quality habitat further south. Under such an assumption, the results of this study are in agreement with the social dominance hypothesis but disagree with the condition it sets that better resources are nearer. Likewise, in the Greenish Warbler *Phylloscopus trochiloides* species complex, a cline of increasing body size toward lower (not

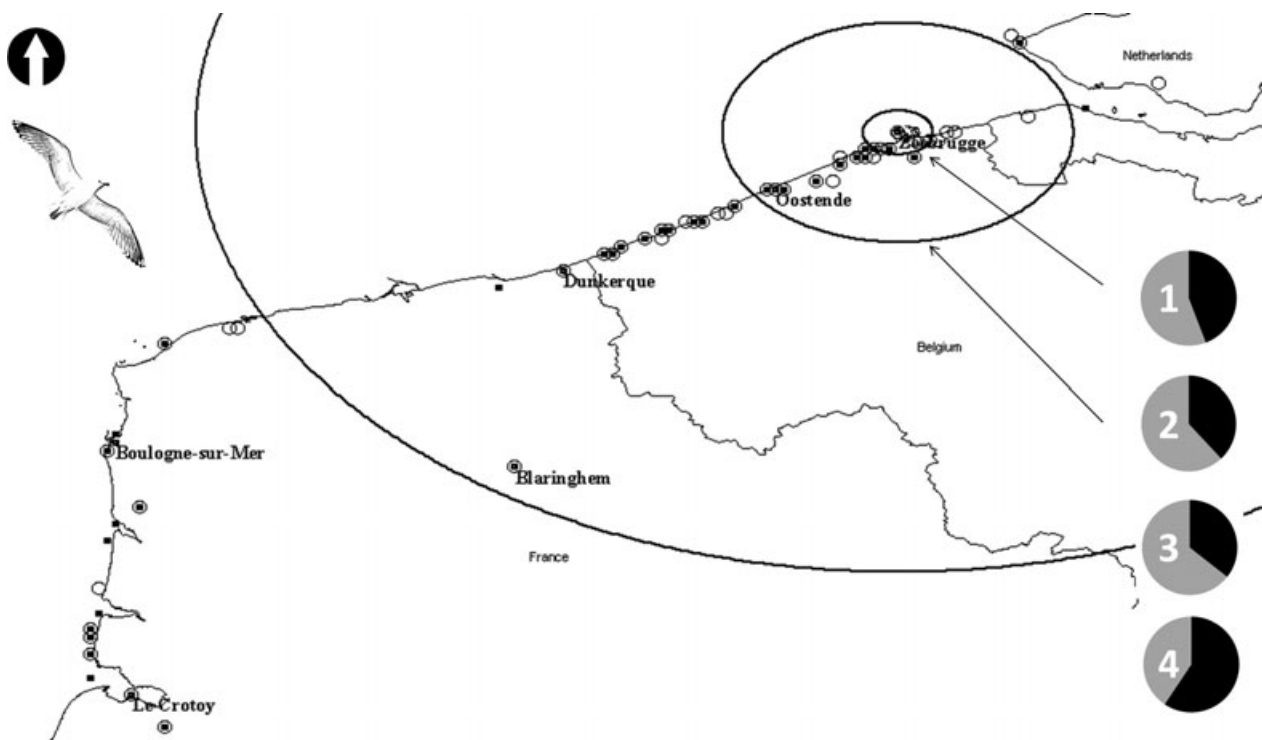


Figure 4. Variation in sex ratio of colour-ringed adult *L. argentatus* resighted during October (1999–2010) at progressive distances from their Belgian breeding colony. Closed squares, male resightings only; open circles, female resightings only; closed squares in open circles, resightings of both sexes. Sex ratios are calculated for four zones (males: black, females: grey): (1) ≤ 5 km (19 males, 24 females); (2) ≤ 25 km (19 males, 31 females); (3) ≤ 100 km (21 males, 38 females); (4) > 100 km (38 males, 26 females).

higher) latitudes was explained by a corresponding spatial distribution of critical resources, mediated by competitive interactions (Katti & Price 2003). Alternatively, the observed latitudinal segregation between wintering males and females of *L. argentatus* may reflect sex-specific niche specialization. Although Greig *et al.* (1985) found differences in feeding efficiency and foraging behaviour between males and females on the shared use of landfill areas by *L. argentatus*, they also reported that individuals of both sexes regularly feed in mixed-sex flocks at a variety of feeding sites. However, to the best of our knowledge, sex-related differences in foraging habitat preference on a larger spatial scale have not yet been described in *L. argentatus*. How social dominance, optimal foraging and sexual segregation are interrelated in *L. argentatus*, and to what extent body size mediates these relationships, remains a topic of further research (Catry *et al.* 2005). In the longer-distance migrant *L. fuscus*, no relationship between body size and migration distance was apparent in males or females.

The results of this study do not support the overall hypothesis that allometric relationships drive variation in migration behaviour within and between *L. argentatus* and *L. fuscus*. Although allometry partly explains sex-related relationships in migration distance in *L. argentatus*, data from the closely related *L. fuscus* do not seem to fit such a pattern. As longer migration routes did not result in a significantly later return at the breeding grounds in either species, presumed sex differences in the intensity of selection for early arrival cannot explain patterns of latitudinal sexual segregation in *L. argentatus* and *L. fuscus* either. The results of this study therefore show that the effect of body size on sex-specific life-history strategies related to migration may vary between closely related, sympatric species despite a similar size dimorphism. Future comparative research of related species pairs that are very similar in many aspects of their ecology but strongly differ in their use of space may help to identify important life-history distinctions (Cristol *et al.* 1999). In conclusion, it seems likely that a complex life-history trait like migration did not evolve in relation to any one selection pressure, but that multifactorial explanations will be required (Catry *et al.* 2005).

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