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# The role of fecundity and sexual selection in the evolution of size and sexual size dimorphism in New World and Old World voles (Rodentia: Arvicolinae)

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Evolutionary ecologists dating back to Darwin (1871) have sought to understand why males are larger than females in some species, and why females are the larger sex in others. Although the former is widespread in mammals, rodents and other small mammals usually exhibit low levels of sexual size dimorphism (SSD). Here, we investigate patterns of sexual dimorphism in 34 vole species belonging to the subfamily Arvicolinae in a phylogenetic comparative framework. We address the potential role of sexual selection and fecundity selection in creating sex differences in body size. No support was found for hyperallometric scaling of male body size to female body size. We observed a marginally significant relationship between SSD and the ratio of male to female home range size, with the latter being positively related to the level of intrasexual competition for mates. This suggests that sexual selection favours larger males. Interestingly, we also found that habitat type, but not mating system, constitutes a strong predictor of SSD. Species inhabiting open habitats – where males have extensive home ranges in order to gain access to as many females as possible – exhibit a higher mean dimorphism than species inhabiting closed habitats, where females show strong territoriality and an uniform distribution preventing males to adopt a territorial strategy for gaining copulations. Nonetheless, variation in the strength of sexual selection is not the only selective force shaping SSD in voles; we also found a positive association between female size and litter size across lineages. Assuming this relationship also exists within lineages (i.e. fecundity selection on female size), this suggests an additional role for variation in the strength of fecundity selection shaping interspecific differences in female size, and indirectly in SSD. Therefore our results suggest that different selective processes act on the sizes of males and females, but because larger size is favoured in both sexes, SSD is on average relatively small.

A common feature of many mammalian groups, including humans, is that males are larger than females (Halliday 1978, Abouheif and Fairbairn 1997, Isaac 2005, Fairbairn 2013). Male-biased sexual dimorphism in both size and/or body mass has often been attributed to sexual selection favouring larger males, because of a positive relationship between size and success at acquiring mating opportunities (Trivers 1972). Indeed, polygyny is the predominant mating system in most mammals, with males rivalling for access to breeding females (Krebs and Davies 1981). Thus, it is predicted that selection will promote phenotypic adaptations that enhance the ability to defeat same-sex rivals and to mate with as many females as possible. The most compelling evidence for this comes from empirical studies on pinnipeds and ungulates, in which there is a strong correlation between sexual size dimorphism (SSD) and the level of polygyny (Lindenfors et al. 2002, Pérez-Barbería et al. 2002, see also Krüger et al. 2014). It has therefore been argued that sexual selection is the key determinant of the evolution of male-biased SSD in mammals, especially in colonial or gregarious species (Lindenfors et al. 2007, Fairbairn 2013).

Sexual selection favouring larger body size in males is frequently regarded as the primary force behind the macroecological pattern commonly known as Rensch's rule (Rensch 1950, 1959). Rensch's rule states that the degree of SSD tends to increase with increasing average body size in taxa in which males are the larger sex, and decreases with body size in those where females are larger. So, the larger sex (males) is purportedly the driver of size divergence, while female body size co-varies passively with that of males as the result of genetic correlation between the sexes (Fairbairn 1997, Blanckenhorn 2005). This pattern, in which SSD often scales with body size seems to hold across the whole mammalian clade (Lindenfors et al. 2007), but studies conducted at a smaller scale (i.e. using more taxonomically restricted datasets) indicate that some mammalian orders (e.g. ground squirrels: Matějů and Kratochvil 2013) do not follow this pattern. In general, Rensch's rule is well supported for taxa that exhibit strong male-biased SSD but patterns of allometry among taxa with subtle SSD or female-biased size dimorphism are less clear (Ruckstuhl and Neuhaus 2005, Fairbairn et al. 2007).

Although sexual selection is believed to be the foremost cause of sexual dimorphism in taxa where males are the larger sex, it is not the only one. In some species, particularly in those exhibiting female-biased dimorphism, fecundity selection can play an important role in shaping the evolution of female body size. The 'fecundity advantage hypothesis' predicts that larger females produce more offspring than smaller females, resulting in higher lifetime reproductive success, and thereby in selection favouring larger size (Andersson 1994). From this it follows that the extent of SSD does not depend exclusively on male size, but is a function of both male and female size. Because the evolution of SSD is driven by multiple selective pressures acting on males and females in distinct ways, it is therefore paramount to differentiate between the relative role of these forces to understand the observed patterns of SSD.

Arvicoline rodents represent a fascinating example of a rapid mammalian radiation, resulting in 143 described species distributed throughout the Northern Hemisphere (Jaarola et al. 2004). Two of the best-known tribes included in this subfamily are the Arvicolini, which includes the genus *Microtus*, and the Myodini. *Microtus* is one of the most speciose rodent genera in the Holartic, which especially during the last fifty years has been subject to extensive research, mainly in the fields of population ecology and behavioural ecology (Krebs et al. 1969, Ims 1987, Lambin 1994, Lambin and Yoccoz 1998, 2001). However, relatively little attention has been paid to the evolution and maintenance of sexual dimorphism in this clade (but see Bondrup-Nielsen and Ims 1990, Yoccoz and Mesnager 1998). This is surprising, as voles are an ideal group in which to investigate the effects of sexual and natural selection on the evolution of size dimorphism for three reasons. First, they exhibit both male-biased and female-biased size dimorphism, an uncommon pattern in other mammalian taxa (Ralls 1976, 1977). Second, they are characterised by a remarkable diversity in social organisation and mating systems; whereas some species mate monogamously (e.g. *M. pinetorum*), others show a polygynous mating system in which a single male monopolises several females (e.g. *Microtus californicus*, *M. xanthognatus*), or a promiscuous mating system in which both sexes mate with multiple partners (e.g. *M. pennsylvanicus*) (Wolff 1985, Tamarin et al. 1990, Ostfeld and Klosterman 1991, Wolff and Sherman 2007). Third, voles are ecologically diverse and inhabit a wide variety of habitats; most species prefer open grasslands such as meadows and steppe-like habitats, but some also occupy ecosystems with dense vegetation (e.g. woodlands, forests). Differences in mating patterns and life-history traits contribute to selection on male and female body sizes and can therefore shape variation in SSD across taxa.

In small mammals, and particularly in rodents, body size plays a pivotal role in shaping variation in reproductive success. For example, male voles often display intense aggression towards other males when defending their territory or mate, leading to large body size being favoured through contest competition (Yoccoz and Mesnager 1998). Furthermore, body size is frequently correlated with dominance status in males (Horne and Ylonen 1998). This implies that body size is the target of sexual selection in this clade. Additionally, fecundity selection may also favour larger size in females; previous studies on rodents have shown that female productivity is correlated with body size within species (Dobson and Michener 1995). This may be the result of larger females being better mothers in terms of parental care (e.g. they may have superior energy stores compared to smaller voles, which is likely to be beneficial during lactation). Alternatively, it may be caused by larger females being better able to protect their offspring from infanticide (Ralls 1977).With regard to sexual selection, theory predicts that in polygynous mating systems, where one single male has exclusive access to several females, sexual selection is strong and therefore should result in high sexual dimorphism. In polygamous systems on the other hand, in which males have largely overlapping home ranges, sexual selection is predicted to be less intense and accordingly, sexual dimorphism should be less pronounced in these species. Finally, monogamous species, where each male monopolises only one female, are expected to be monomorphic in size (Darwin 1871, Emlen and Oring 1977). Therefore, we predict a correlation between the mating system of a species and the degree of sexual dimorphism (Stamps 1993). Although this prediction has been tested previously in North American voles (Heske and Ostfeld 1990, Boonstra et al. 1993), both studies used a very limited dataset (no more than 16 species) and none of them accounted for the phylogenetic non-independence of taxa.

Territoriality provides exclusive access to a valuable or limiting resource (food, potential mates) (Stamps 1994). In microtine rodents, it has been postulated that food distribution determines the spatial distribution of females (Ostfeld 1990), and thereby also the behavioural tactics of males, whose territoriality is female-based (Tamarin et al. 1990) (Fig. 1). In species feeding on patchy and slowly renewing food resources (fruits, seeds; i.e. woodland voles), females are likely to exhibit strong territoriality leading to a uniform distribution pattern. As a consequence, males will be unable

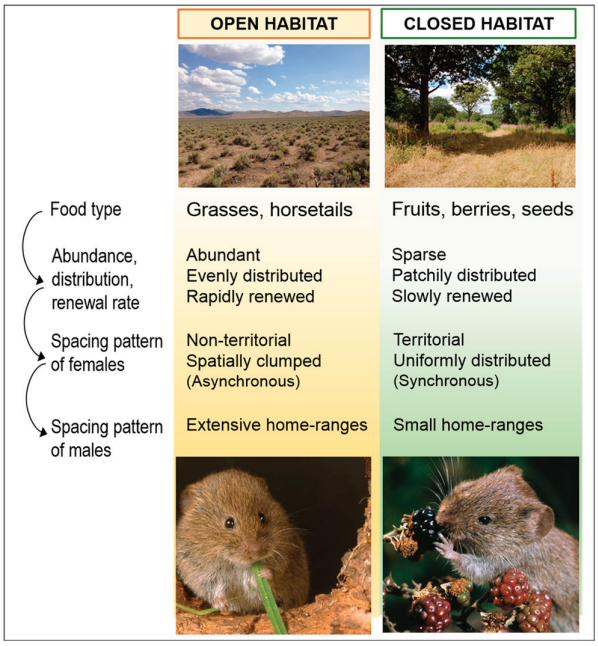


Figure 1. Graphical summary adapted from Ostfeld (1990) depicting the main predictions in relation to territoriality in both sexes for open- and closed-habitat species.

to monopolize females by defending territories, which may result in low levels of male–male competition. On the other hand, in species feeding on abundant and evenly distributed food resources (grasses, sedges, horsetails; i.e. grassland voles), females tend to be less territorial and show a more clumped distribution (Ostfeld 1985, 1990). Therefore, in such habitats male conspecifics are expected to be territorial in order to monopolize and defend these aggregations of females. In sum, in species feeding on abundant and uniformly distributed food sources and in which females tend to be spatially clumped (non-forested habitats), strong intrasexual competition for mates may favour increased dimorphism (Ostfeld 1990), making habitat type a potential driver of the evolution of SSD across taxa.

We test for the effect of sexual and fecundity selection on SSD using morphological and ecological data and a phylogenetic tree for 34 vole species belonging to the subfamily Arvicolinae. First, we aim to determine whether SSD is accentuated, diminished or remains constant as body mass (size) increases among taxa (i.e. is consistent with Rensch's rule, opposite to Rensch's rule or isometric, respectively). Second, we test whether SSD is correlated with male body mass, which is expected if sexual selection drives dimorphism, and whether male body mass is correlated with the strength of sexual selection. This allows us to test the 'intrasexual selection hypothesis', which predicts that intrasexual selection selects for large male size, resulting in larger male-biased SSD. To this end, we measured the strength of intrasexual selection as the ratio of male to female home-range area, which reflects the potential for a single male to defend multiple partners within a territory (Stamps 1983, Cox et al. 2007), assuming that the greater the potential for multiple-partner monopolisation, the more intense intrasexual selection is. Furthermore, we test whether habitat type (open versus closed habitat) and/or mating system (monogamous, polygynous, promiscuous), two traits presumably also associated with the strength of sexual selection, significantly predict variation in SSD in this group. According to the theoretical expectations, the degree of sexual dimorphism should be higher in more polygynous species and in those inhabiting open habitats. Second, we test whether female body size is related to SSD, and examine the role of fecundity selection in shaping variation in SSD by testing for a relationship between female body mass and litter size, as maternal size is frequently correlated with fecundity ('fecundity advantage hypothesis'; Parker 1992, Fairbairn and Shine 1993, Head 1995, Cox et al. 2003). Taken together, our analyses provide a comprehensive test of SSD in voles from both the Old World and the New World.

## Methods

### Morphological and ecological data

We collected data on the size of adult males and females in 34 vole species, in the form of either a linear (i.e. total length) or a weight measure, using both empirical studies and studies summarising published and unpublished data (reviewed by Nadeau 1985, Bondrup-Nielsen and Ims 1990, Heske and Ostfeld 1990, Schulte-Hostedde 2007). Body length and body mass were significantly correlated (males: $r = 0.48$, $p = 0.017$; females: $r = 0.51$, $p = 0.012$). We therefore decided to focus on body mass only, as a large number of studies on microtines suggest that heavier males are dominant or have greater reproductive success than lighter males, and thus that body mass is the crucial measure (Iskjaer et al. 1989, Boonstra et al. 1993). This is common practice in the SSD literature, especially in studies on mammals (Lindenfors et al. 2007). In those cases in which body masses were broken down by age and/or season, we consistently chose body mass estimates reported for adult individuals during the breeding period, excluding pregnant females. We followed this criterion because most studies on microtines are carried out during the spring–summer period. All body mass estimates were based on more than 20 individuals per sex. Male and female body masses were log10-transformed prior to analysis. Mean body mass ranged from 15.43 to 58.95 g (mean: 36.77) in males, and from 15.18 to 62.96 g (mean: 34.34) in females. SSD for each species was calculated using the two-step extension of the Lovich–Gibbons index (Lovich and Gibbons 1992), as proposed by Smith (1999):

if females are larger: SSD = (larger sex/smaller sex) – 1
if males are larger: SSD = – ((larger sex/smaller sex) – 1)

Despite an extensive literature search we were unable to obtain data for sex-specific body mass for five species, in which case the SSD index was estimated from mass values obtained using predictive equations generated by regressing mass on length for the species for which we did obtain information on both mass and length. For one of the species, we found information on the mass ratio but we failed to obtain average mass values for each sex (Table 1).

Additionally, we collected information on 1) the ratio of male to female home range area, 2) habitat type, 3) mating system and 4) litter size. Although there are different methods available to calculate home range size, we used the ratio of male to female home range as a predictor (Bondrup-Nielsen and Ims 1990), and we expect this ratio to be unaffected by the method used. Habitat type was classified as open (pastures, steppe grasslands, alpine meadows and Arctic tundra) or closed (coniferous, evergreen, deciduous and cloud forests), the two main biotypes in which Arvicolinae species can be found. Mating system was recorded as monogamy, polygyny or polygamy (promiscuity). There is insufficient information in the literature for all species used in this study to generate a continuous variable (e.g. average number of monogamous pairs) that better captures variation in the degree of monogamy/polygyny found within a species. In those cases in which different mating patterns have been reported for the same species, we included the prevailing one (i.e. the mating system most frequently reported across populations). Finally, mean litter size was estimated from data on the number of embryos or pups, which ranged from 1.20 to 8.48 (mean: 4.57).

We collected morphological and ecological information from over 175 publications (including books, papers, dissertations, and online databases such as the 'Cumulative Index for Mammalian Species' powered by the American Society of Mammalogists). For most species, we found information on body mass or litter size from different populations (in the case of body mass, the modal number of populations per

Table 1. SSD index, body mass (measured as log10) and ecological characteristics of 34 species of voles (subfamily Arvicolinae, order Rodentia).

| | SSD index | Male mass | Female mass | Litter size | Mating type | Habitat | Region |
|---|---|---|---|---|---|---|---|
| *Lasiopodomys brandtii* | −0.325 | 1.740 | 1.618 | 7.0 | promiscuous | open | Asia |
| *Lasiopodomys mandarinus* | −0.020** | | | 3.9 | polygynous | open | Asia |
| *Chionomys nivalis* | −0.089 | 1.693 | 1.653 | 3.0 | promiscuous | open | Palearctic |
| *Microtus agrestis* | −0.160 | 1.539 | 1.474 | 5.1 | polygynous | open | Palearctic |
| *Microtus arvalis* | −0.002 | 1.427 | 1.426 | 5.1 | polygynous | open | Palearctic |
| *Microtus cabrerae* | 0.057 | 1.640 | 1.665 | 4.9 | monogamous | open | Palearctic |
| *Microtus californicus* | −0.147 | 1.676 | 1.616 | 4.4 | polygynous | open | Nearctic |
| *Microtus canicaudus* | −0.263 | 1.459 | 1.358 | 4.6 | promiscuous | open | Nearctic |
| *Microtus chrotorrhinus* | 0.088 | 1.486 | 1.522 | 3.2 | monogamous | forest | Neartctic |
| *Microtus duodecimcostatus* | −0.032 | 1.358 | 1.344 | 2.5 | monogamous | forest | Palearctic |
| *Microtus gregalis* | −0.012* | | | 8.5 | monogamous | open | Palearctic |
| *Microtus longicaudus* | 0.015 | 1.591 | 1.598 | 5.2 | ? | forest | Nearctic |
| *Microtus lusitanicus* | −0.016 | 1.188 | 1.181 | 2.3 | monogamous | forest | Palearctic |
| *Microtus mexicanus* | −0.006* | | | 2.4 | monogamous | open | Nearctic |
| *Microtus miurus* | −0.026 | 1.591 | 1.580 | 6.8 | promiscuous | open | Nearctic |
| *Microtus montanus* | −0.114 | 1.635 | 1.588 | 6.0 | monogamous | open | Nearctic |
| *Microtus montebelli* | −0.359 | 1.683 | 1.550 | 4.3 | polygynous | open | Asia |
| *Microtus oaxacensis* | −0.170 | 1.584 | 1.516 | 1.2 | monogamous | forest | Nearctic |
| *Microtus ochrogaster* | 0.006 | 1.613 | 1.616 | 3.6 | monogamous | forest | Nearctic |
| *Microtus oeconomus* | −0.250 | 1.666 | 1.569 | 6.3 | polygynous | open | Holartic |
| *Microtus oregoni* | −0.038 | 1.290 | 1.290 | 3.4 | ? | forest | Nearctic |
| *Microtus pennsylvanicus* | −0.026 | 1.569 | 1.557 | 4.8 | promiscuous | open | Nearctic |
| *Microtus pinetorum* | 0.112 | 1.348 | 1.394 | 2.3 | monogamous | forest | Nearctic |
| *Microtus quasiater* | 0.004* | | | 1.4 | monogamous | open | Nearctic |
| *Microtus richardsoni* | −0.149* | | | 6.3 | polygynous | open | Nearctic |
| *Microtus savii* | 0.005 | 1.262 | 1.265 | 2.5 | monogamous | open | Palearctic |
| *Microtus socialis* | −0.044 | 1.451 | 1.432 | 5.5 | polygynous | open | Palearctic |
| *Microtus tatricus* | −0.170 | 1.446 | 1.378 | 2.5 | polygynous | open | Palearctic |
| *Microtus townsendii* | −0.272 | 1.770 | 1.666 | 5.2 | monogamous | open | Nearctic |
| *Microtus xanthognathus* | −0.039* | | | 8.1 | polygynous | open | Nearctic |
| *Myodes gapperi* | 0.094 | 1.760 | 1.799 | 5.8 | promiscuous | open | Nearctic |
| *Myodes glareolus* | 0.062 | 1.674 | 1.700 | 5.2 | polygynous | forest | Palearctic |
| *Myodes rufocanus* | 0.009 | 1.600 | 1.604 | 6.0 | promiscuous | forest | Asia |
| *Myodes rutilus* | 0.081 | 1.369 | 1.403 | 6.2 | ? | forest | Holarctic |

(*) In those cases in which information about body mass dimorphism was lacking, the SSD index was computed from body length measurements.
(**) There is no available information on body mass for this species, the source reference only provides the ratio.

species was 3, range: 1–8), which were summarised into a single average value. The raw data listed for each species or subspecies is provided as Supplementary material.

## Phylogeny

For the purpose of this study we reconstructed a phylogeny comprising 34 vole species based on cytochrome b (*cytb*) sequences retrieved from the PhyLota database (<http://phylota.net>) (Sanderson et al. 2008), which compiles searches for different taxa from the NCBI GenBank, and organizes them into accumulated files. Sequences were examined visually and the most complete sequence for a species was used. Sequences were aligned with ClustalW (Thompson et al. 1994). After visual inspection, they were imported into jModelTest 0.1.1 (Posada and Crandall 1998) to calculate the best-fit model of nucleotide substitution for the *cytb* gene according to the Akaike information criterion (AIC). The most complex general-time-reversible model (GTR + I + γ) was chosen as the best substitution model for this gene (Posada 2009). We searched for the most reliable tree topology using two different methods: maximum likelihood and Bayesian inference. Maximum likelihood (ML) tree reconstruction was conducted in MEGA6 (Tamura et al. 2013), and Bayesian inference analyses were performed with MrBayes 3.2 (Ronquist et al. 2012). In both cases, *Myodes* (formerly *Clethrionomys*) species were used as an outgroup, as they are ascribed to a different tribe and present the greatest genetic and phenotypic divergence from the other vole species included in the present study. Since the tree topology and clades that resulted from the ML reconstruction were more consistent with published phylogenies of microtines and provided a more intuitive output, we performed our analyses using this tree. We then used the R-package *ape* (Paradis 2015) to prune off species for which we had no morphological or ecological data (analyses including body mass: n = 28; analyses involving home range ratio: n = 24).

## Phylogenetic analyses

All further analyses were conducted in R 3.1.2 (<www.r-project.org>). To measure the strength of phylogenetic signal in our continuous variables (SSD, male

and female body mass, litter size and home range ratio), we estimated Pagel's λ (Pagel 1997, 1999) and Blomberg's *K* (Blomberg et al. 2003) using a randomisation test implemented in the *phytools* package (Revell 2011). We tested whether estimates of these two metrics of phylogenetic signal were significantly different from values expected under the null hypothesis (no phylogenetic signal). However, because assessing phylogenetic signal in the original variables is generally insufficient to determine whether a phylogenetic approach is required, we also tested for a phylogenetic signal in the model residuals (see Revell 2010 for further discussion of this issue).

Next, we evaluated whether a Brownian-motion (BM), an early-burst (EB) or an Ornstein–Uhlenbeck (OU) model was the most appropriate for explaining the evolution of SSD. The BM model (also called the random-walk model) assumes each evolutionary change is independent of the previous change (see Felsenstein 1985, 1988 for further explanation). The EB model (also called the adaptive radiation or ACDC model) predicts rapid evolution early in the radiation and an exponential slowdown in the diversification rate over time (Harmon et al. 2010). The OU model predicts that trait evolution is affected by random evolution and by stabilizing selection towards one or more adaptive optima (Butler and King 2004). Because the three fitted models have different numbers of parameters, we used the Akaike information criterion corrected for small sample size (AICc) to determine the most suitable model.

In some cases the BM does not fit the data well despite being the most suitable model; that is, the underlying process of trait evolution does not follow pure BM (e.g. when the rates of evolution change over time or for different clades). Therefore, we also tested two more complex versions of the BM model: 1) BM + λ, 2) BM + κ, and 3) BM + δ. The first one (BM + λ) is particularly suitable for traits showing a moderate phylogenetic signal, that is, intermediate values of λ, which ranges from 0 (no phylogenetic signal in the trait) to 1 (strong phylogenetic signal). The branch-length scaling parameter kappa (κ) is used to contrast punctuational *vs*. gradual evolution of a trait. When $\kappa > 1$, a disproportionate amount of evolution occurs on longer branches, $\kappa < 1$ indicates that a disproportionate amount of evolution occurs on shorter branches, and in the extreme case of $\kappa = 0$, trait changes accumulate at speciation events instead of being proportional to branch lengths. Delta (δ) is used to test if trait evolution follows a pattern of adaptive radiation or species specialisation. If $0 < \delta < 1$, most trait evolution occurs near the base of the tree; if $\delta > 1$, most trait evolution occurs near the tips of the tree; and $\delta = 1$ indicates gradual BM evolution (Hernández et al. 2013).

Because SSD is a composite trait composed of male body mass and female body mass, we also determined the most suitable model for the evolution of these traits separately. The lambda-based model (BM + λ) provided the best fit for body mass evolution in both sexes (Supplementary material Appendix 1 Table A1). The intermediate values of lambda obtained in both cases indicate that neither a pure BM nor a non-historical model ($\lambda \sim 0$) are appropriate as these models would over- and underestimate the effect of phylogeny respectively (Supplementary material Appendix 1 Table A1). In addition, the estimated evolutionary rate was similar for males and females ($\sigma^2 = 1.55$ and 1.53, respectively), which suggests that male body mass did not evolve either faster or slower than female body mass, and facilitates the interpretation of the results for SSD.

As we found a significant phylogenetic signal in the residuals of our models, we used phylogenetic generalised least squares (PGLS) (Pagel 1997, 1999, Freckleton et al. 2002) to test for a relationship between 1) male and female body mass, 2) SSD and male or female body mass, 3) SSD and the home range ratio, and 4) litter size and female body mass, all implemented in the package *caper* (Orme et al. 2013). PGLS is a flexible phylogenetic comparative method that incorporates the phylogenetic (auto)correlation of the data in the structure of errors. We computed maximum likelihood (ML) estimates of branch-length parameters λ, κ and δ to optimise the fit of each model.

Furthermore, we used phylogenetic analyses of variance (anova) to assess whether the amount of SSD was influenced by categorical ecological variables. Specifically, we examined whether SSD variability can be explained by habitat preference (open habitats, closed habitats) or mating system (monogamous, polygynous, promiscuous). Phylanovas (10 000 iterations) were conducted in the *geiger* package (Harmon et al. 2008). Since mating system, habitat type and home range ratio are likely to be correlated and all of them are related to the intensity of sexual selection, we constructed a model including these three proxy variables using the 'crunch' algorithm in *caper* (Orme et al. 2013) to determine which is the most important factor in explaining SSD.

Finally, to characterise the evolutionary relationship between SSD and habitat preference (a significant predictor of SSD) across the Arvicolinae subfamily, we reconstructed the evolutionary history of these traits using parsimony analyses performed in Mesquite 2.74 (Maddison and Maddison 2011). Parsimony analysis weights the contribution of each character state to a node equally and assumes equal probabilities of gains and losses of a given character. We used the Pagel's (1994) discrete likelihood correlation method to test for correlated evolution between these two traits. Pagel's test compares the ratio of likelihoods of two models: one model where the rates of change in each character are independent of the state of the other and a second model where rates of change depend on the state of the other character. As only binary characters are suitable for this kind of analysis, the SSD ratio was transformed into a dichotomous variable (male-biased dimorphism; 0: absent; 1: present).

### Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.q42b2> (García-Navas et al. 2015).

## Results

### Phylogenetic signal and trait evolution

SSD and litter size were significantly influenced by phylogeny (SSD: $\lambda = 0.99$, $p = 0.009$; $K = 0.92$, $p = 0.006$; litter size: $\lambda = 0.99$, $p < 0.001$; $K = 1.07$, $p = 0.003$),

whereas both female and male body mass showed a weaker phylogenetic signal (female body mass: $\lambda = 0.49$, $p = 0.056$; $K = 0.66$, $p = 0.24$, male body mass: $\lambda = 0.53$, $p = 0.067$; $K = 0.67$, $p = 0.22$). Home range ratio did not show a phylogenetic signal ($\lambda = 0$, $p = 0.99$; $K = 0.57$, $p = 0.84$). The comparison of the continuous models using maximum likelihood showed that the Brownian-motion model had the best fit to the observed pattern of SSD evolution (AICc: BM model = –50.70; EB model = –48.29; OU model = –48.53, strength of stabilising selection $\alpha = 2.71$). The observed kappa ($\kappa = 1$) was consistent with a pure BM model. The rate of evolution of SSD was close to constant over time ($\delta = 1.37$, not significantly different from 1), suggesting the absence of 'early burst' or later changes in the rate of evolution of this trait. None of the additional models improved the BM model (AICc: BM + $\lambda$ = –48.29; BM + $\kappa$ = –48.29; BM + $\delta$ model = –48.74).

## Rensch's rule and signatures of sexual selection and fecundity selection

On average, SSD in Arvicolinae is male-biased; almost half of the species (47%) exhibit a male-biased SSD, and only 17% of all species (n = 34) exhibit female-biased SSD. Male and female body mass were strongly correlated ($r = 0.94$, $R^2 = 0.89$, $p < 0.001$), but we found no support for Rensch's rule in this clade, as indicated by the slope of the regression of log10 (male body mass) on log10 (female body mass) not being significantly greater than one ($\beta = 1.03$, CI: 0.98–1.07, n = 28). Thereby, our results indicate that the sexes in this taxonomic group are scaled isometrically (Fig. 2), which would be the result of neither sex changing body size disproportionally faster than the other through evolutionary time.

After correcting for phylogeny, we found a non-significant trend towards species in which males are large (heavy) exhibiting a more pronounced degree of sexual size dimorphism ($\beta$: –0.21, n = 28, $t = -1.75$, $p = 0.09$, $R^2 = 0.07$; Fig. 3a). The index of SSD was negatively (but marginally)

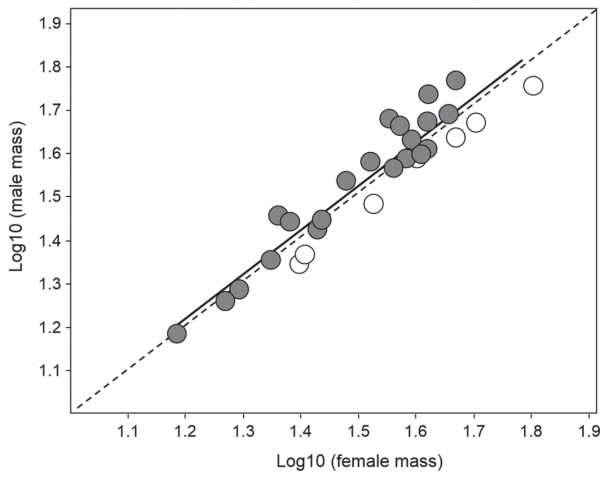


Figure 2. Relationship between male body mass and female body mass. The dashed line indicates isometry and the solid line represents the model fitted to the data; grey dots: species in which males are the largest sex, white dots: species in which females are the largest sex. The ML values for the branch length parameters were optimized as follows: $\kappa = 0.51$, $\lambda = 1$, $\delta = 1.13$.

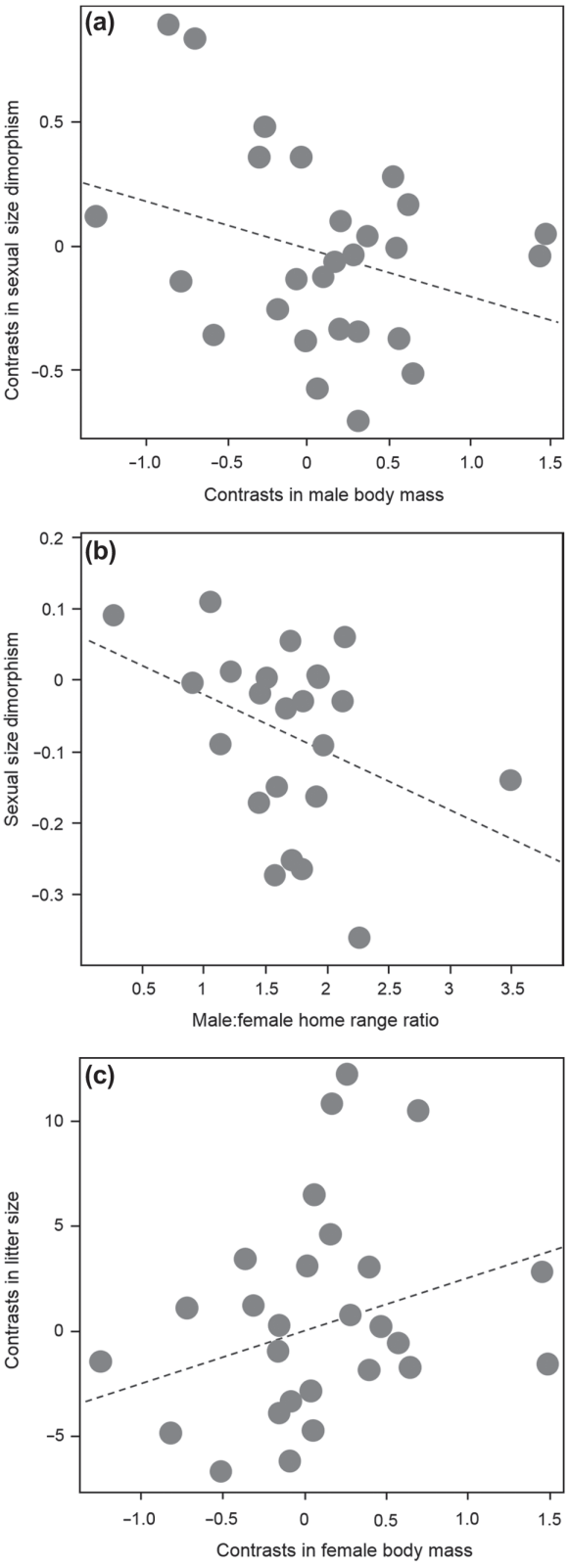


Figure 3. Relationship between (a) SSD index and male body mass (represented in the form of standardised phylogenetic independent contrasts, PIC) (b) SSD index and home range ratio (OLS), and (c) litter size and female body mass (PIC). Negative values for the SSD index indicate male-biased dimorphism. The ML values for the branch length parameters were optimised as follows: (a) $\kappa = 0.45$, $\lambda = 1$, $\delta = 1.31$; (b) $\kappa = 1.52$, $\lambda = 0$, $\delta = 0.36$; (c) $\kappa = 3$, $\lambda = 1$, $\delta = 0.27$.

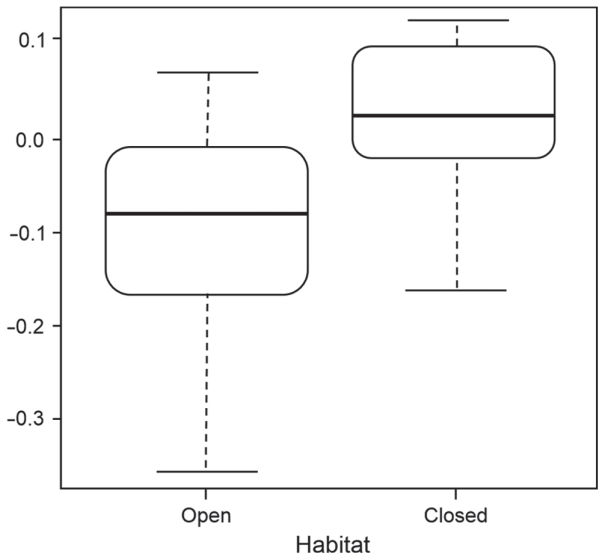


Figure 4. Difference in mean SSD between species inhabiting open habitats and species linked to closed habitats. More negative values indicate more sexual dimorphism.

associated with the ratio of male-to-female home range areas (β: –1.76, n = 24, $t = -1.91$, p = 0.068, $R^2 = 0.14$), suggesting that for species where males have home range sizes much larger than the females, SSD becomes more male-biased. Because the association between SSD and home range ratio showed a non-historical pattern (estimated λ value = 0; i.e. phylogenetic independence), the relationship between the two variables is illustrated in the form of an ordinary least square (OLS) regression (Fig. 3b). Female body mass correlated significantly with litter size (β: 1.30, n = 28, $t = 2.08$, p = 0.047, $R^2 = 0.11$); species with heavier females were more productive (Fig. 3c). There was no significant relationship between SSD and female body mass ($t = -0.37$, p = 0.71).

### Drivers of SSD: the influence of habitat type and mating system

SSD differed significantly between open habitat and closed habitat lineages ($F_{1,32} = 11.76$, phylogenetic p = 0.013); species inhabiting open habitats exhibited a higher mean dimorphism than those linked to forest habitats (Fig. 4). In contrast, we did not find a significant effect of mating system on the amount of SSD (mean SSD; monogamous: –0.035, polygamous: –0.089, polygynous: –0.119; $F_{2,28} = 1.47$, phylogenetic p = 0.32). Habitat type remained significant when including in the same model both home range ratio and habitat type as explanatory variables (home range ratio: $t = -0.28$, p = 0.78; habitat type: $t = 2.10$, p = 0.047).

Since habitat type was found to be a strong predictor of SSD, we performed a test of independent evolution of these two characters. Pagel's discrete likelihood correlation method supported a strong correlation between the evolution of SSD and habitat preference (p < 0.01, log-likelihood difference between the two models = 4.92; Fig. 5).

## Discussion

Like most rodent species, Arvicolinae exhibit relatively subtle size differences between males and females. In accordance with this lack of strong dimorphism, we did not find evi-

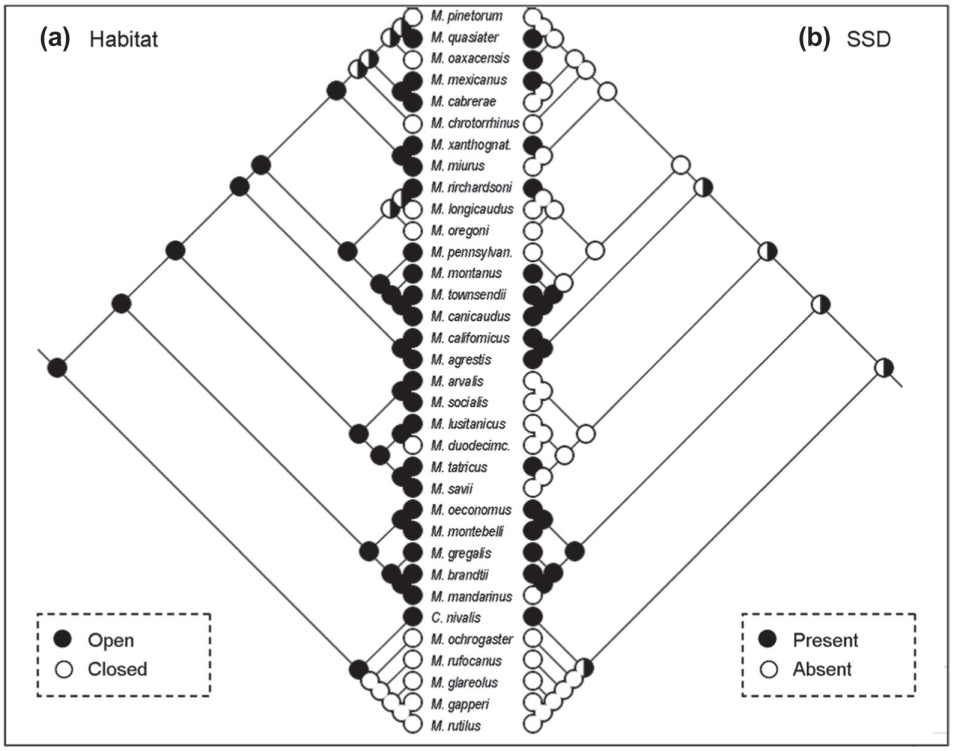


Figure 5. Ancestral reconstruction of (a) habitat type and (b) male-biased SSD in voles (Arvicolinae subfamily), as shown along the phylogeny.

dence for a decoupling of male and female size evolution. Model fitting revealed no directional evolutionary tendency in either sex-specific size or SSD. Instead, SSD exhibited a random walk-like pattern on the phylogeny, with both male and female body size evolving in no particular direction. This result is noteworthy because the *Microtus* genus constitutes a clear example of explosive speciation (Jaarola et al. 2004), and theory would thus predict a pattern of rapid evolution followed by relative stasis (Schluter 2000). For example, in a study on Tanganyikan cichlids, González-Voyer et al. (2009) found that body size indeed exhibited early burst (EB) of rapid evolution. On the contrary, Harmon et al. (2010) found little support for the EB model of adaptive radiation in a comparative study involving many classic adaptive radiations, concluding that radiations characterised by early bursts of morphological evolution followed by slowdowns are in fact rare.

The observed mode of evolution – Brownian Motion – is difficult to reconcile with Rensch's rule (1950). Rensch's rule implies that male body size increases at a faster evolutionary rate than female body size, suggesting that male body size is the main driver of the evolution of SSD, likely as the result of sexual selection (Fairbairn et al. 2007). However, our results indicate that Arvicolinae species show a scaling pattern (isometry), which implies that there is no trend in the direction of body size changes of any sex. Furthermore, we found that the evolutionary rate for body size was similar in both sexes ($\sigma^2 \sim 1.5$); that is, male body mass did not evolve faster than female body mass. Both these findings are not consistent with Rench' rule. Given they possess an extensive variability in social systems and moderate range of body sizes, at first sight our finding that voles do not conform to this macroevolutionary trend may be unexpected. However, these results are in line with previous work on SSD in rodents, as two recent studies showed that ground squirrels (Ctenomyidae: *Ctenomys*) and tuco-tucos (Sciuridae: *Marmotini*) do not follow Rensch's rule either (Matějů and Kratochvil 2013, Martínez and Bidau 2015). Similarly, although a previous study carried out at a higher taxonomic level found support for Rensch's rule when considering all extant mammalian orders, this pattern disappeared when the analysis was restricted to rodents (Lindenfors et al. 2007).

Several factors may explain why Rensch's rule was not validated in voles. First, the limited extent of SSD in this group reduces statistical power to detect a trend if it exists. Second, the existence of low variation in SSD may, in turn, be attributable to the action of different selective forces preventing the evolution of extensive sexual dimorphism. Selection may operate on both sexes independently, but the optimal size for males and females could be very similar. Finally, while our results suggest that there is selection for an increase in body size, this pressure may be constrained by other selective (ecological) pressures common to both sexes, such as adaptation to life underground. Most Arvicolinae species have a fossorial lifestyle (i.e. they dig subterranean burrows) or live among rocks and in crevices, which may be a constraining factor for the evolution of larger body sizes in both sexes (Begall et al. 2007).

Sexual selection is considered a major determinant of size differences between males and females (Darwin 1871, Andersson 1994, Ralls 1977). Previous comparative studies have shown that evolutionary shifts in male aggression and territoriality are generally correlated with changes in SSD in many mammalian taxa (Owen-Smith 1993, Armitage 2014). Here, we found a marginally significant relationship between male body mass and SSD, as expected if sexual selection is the main driver of dimorphism. In addition, SSD tended to be correlated with home range ratio, a measure of the level of competition over females (Arnold and Duvall 1994), indicating that the level of SSD is higher in species with a greater intensity of intrasexual selection. Male–male competition for mates is expected to select for traits that increase an individual's ability to efficiently monopolise females, and several studies on microtines have shown that being large male confers an advantage in terms of male aggression and territoriality (Borowski 2003). Nonetheless, when including both home range ratio and habitat type as predictors in the same model, habitat type, but not home range ratio, remained significant, suggesting that the effect of territoriality – home range – is mediated by the spatial distribution of females.

Understanding the evolution and maintenance of sexual dimorphism requires consideration of the selective pressures acting on both sexes. From the female perspective, the fecundity advantage hypothesis states that fecundity selection favouring larger females is the main cause of female-biased SSD (Isaac 2005, Lindenfors et al. 2007, Fairbairn 2013). However, across a wide range of mammalian taxa there is a negative relationship between litter size and female body size (reviewed by Carranza 1996), which instead would suggest that fecundity selection tends to favour smaller females (Lee et al. 1991, Charnov 1993, Purvis and Harvey 1995). The latter can explain why female-biased SSD is an uncommon pattern in mammals. Here, we observed larger females have higher fecundity, which is consistent with the model developed by Tuomi (1980). This model predicts a positive correlation between litter size and body weight in small mammals ($< 1$ kg) (as shown by previous authors; Myers and Master 1983, Dobson and Michener 1995, Frynta et al. 2011) and a negative correlation in large mammals. This implies that in rodents and other small mammals, both sexual selection on males and fecundity selection on females are expected to favour large size (i.e. selection acts in the same way in both sexes), which may explain the absence of strong SSD in these groups (Lu et al. 2014, Zidarova 2015).

Microtine species are thought to have originated 1.2–2 Ma from the fossil genus *Allophaiomys* (Chaline et al. 1999). The putative origin of this group has been postulated to be located in southern Asia, from where three major colonisation events took place: one colonisation wave from southern Asia to northern Asia, another to Europe, and a third over the Beringian land bridge to North America (Fink et al. 2010). Regrettably, we were unable to locate information on size dimorphism for several Asian species, including those comprising the genus *Neodon* which are considered relics of the Pleistocene epoch and whose morphology resembles the extinct *Allophaiomys* (Musser and Carleton 2005). Many vole species endemic to Russia, China and central Asia (Mongolia, Afghanistan, Iran) are poorly described and basic data about morphometry, life-history traits and reproductive behaviour are lacking for most of them. This information would be very useful to determine if ancestral lineages are typically monogamous and monomorphic as predicted by

the Jarman's (1974) hypothesis for the evolution of sexual dimorphism in ungulates. This hypothesis states that ancestral antelopes were closed habitat-dwelling, monogamous and monomorphic species. These species then evolved into open habitat specialists, where animal aggregation and increased group size favoured the evolution of polygyny, which in turn favoured the evolution of dimorphism (Jarman 1974).

Here, we found that open habitat species exhibit a higher degree of SSD than those inhabiting thickets, woodlands and forests. This is in line with Jarman's hypothesis, which relies on the assumption that in many mammalian groups, food distribution determines the probability of encounters among individuals in both space and time, and thus, affects the intensity of sexual selection in males, which largely depends on the degree of clumping of females (Jarman 1974, see also Emlen and Oring 1977). In closed habitats where food resources show a more patchy distribution, it is expected that females will show strong territoriality. When females tend to be hyperdispersed, a single female may be defended by a given male, leading to monogamus mating and non-overlapping home ranges. In species occupying habitats with abundant food, or where food is evenly distributed across space, female voles tend to aggregate, resulting in males attempting to monopolise several females by defending territories. This forces males to search more widely for receptive females (extensive-home ranges), which increases their probability of encountering other males (Ostfeld 1985). Accordingly, we observed that the male-to-female home range ratio was larger in grassland voles compared to forest voles (open habitat species: $1.69 \pm 0.09$, closed habitat species: $1.44 \pm 0.21$; $F = 4.36$, $p = 0.050$). Therefore our results fit Ostfeld's prediction regarding the presence of female territoriality in species feeding principally on sparse and patchy food resources, and male territoriality in species feeding on abundant and homogeneous food sources (Ostfeld 1990).

The second premise of Jarman's (1974) hypothesis (polygyny favours dimorphism), was not fulfilled. Although the differences in SSD between mating systems were congruent with the expected pattern (monogamous $<$ polygamous $<$ polygynous), these were not statistically significant. This result could be explained taken into account that information on mating systems comes from recent molecular studies (Ishibashi and Saitoh 2008, Borkowska and Ratkiewicz 2010) but also, and mostly, from observational studies where the mating pattern is inferred on the basis of social organisation (Batzli and Henttonen 1993). As a consequence, for a large number of species there is no information on levels of multiple paternity. In fact, parentage analyses are rare in studies of mating behaviour in arvicoline rodents (Ishibashi and Saitoh 2008). Because social organisation does not necessarily reflects the prevailing mating system (as demonstrated in other taxa; Griffith et al. 2002), inferences about mating systems made solely on social behaviour may be misleading (i.e. social monogamy does not necessarily imply genetic monogamy; Solomon et al. 2004). Therefore, it would be appropriate to examine mating systems on the basis of both ecological and genetic information, to ascertain unambiguously whether more polygynous species exhibit a more pronounced SSD compared with monogamous species in this taxonomic group.

SSD is thought to evolve when selective pressures on body size are stronger in one sex than another, or when selective forces push the sexes in opposing directions. Although we observed that male-biased SSD is the prevailing pattern in Arvicolinae, the amount of SSD observed in this subfamily (average SSD $= 1.07 \pm 0.02$; Lovich–Gibbons index: $-0.07 \pm 0.02$) is substantially lower in comparison to that reported across different mammalian lineages ($>1000$ species; average SSD $= 1.18$), and even within the Rodentia order (300 species; average SSD $= 1.09$) (Lindenfors et al. 2007). In line with this, our analyses do not provide evidence for the size of one of the sexes evolving disproportionally faster. Furthermore, the absence of a pattern consistent with Rensch' rule suggests that, across all lineages, neither sex is driving the evolution of body size of the other sex (or they both do so equally). The prevalence of male-biased SSD in voles seems to result from sexual selection for large male size, which presumably confers an advantage in terms of acquiring mates. However, we also found evidence suggesting that larger body size is associated with higher fecundity in females, as is predicted by the fecundity advantage hypothesis. In conclusion, our results therefore suggest that the low amount of SSD observed within this group reflects the combined action of sexual and fecundity selection. This study reinforces the view that selective forces operate on both sexes simultaneously, and any hypotheses and tests related to sexual dimorphism must take this into account.

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Supplementary material (available online as Appendix oik-03026 at <www.oikosjournal.org/appendix/oik-03026>). Appendix 1.