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# Phenotypic evolution of dispersal-enhancing traits in insular voles

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Evolutionary theory predicts that in metapopulations subject to rapid extinction–recolonization dynamics, natural selection should favour evolution of traits that enhance dispersal and recolonization ability. Metapopulations of field voles (*Microtus agrestis*) on islands in the Stockholm archipelago, Sweden, are characterized by frequent local extinction and recolonization of subpopulations. Here, we show that voles on the islands were larger and had longer feet than expected for their body size, compared with voles from the mainland; that body size and size-specific foot length increased with increasing geographical isolation and distance from mainland; and that the differences in body size and size-specific foot length were genetically based. These findings provide rare evidence for relatively recent (less than 1000 years) and rapid (corresponding to 100–250 darwins) evolution of traits facilitating dispersal and recolonization in island metapopulations.

**Keywords:** biodiversity; dispersal; island populations; evolution; *Microtus agrestis*

## 1. INTRODUCTION

Studies of island populations have played an important role in generating and testing hypotheses central to the ecology and evolution of biological diversity, both historically [1,2] and currently [3–5]. Evolutionary theory predicts that in metapopulations subject to rapid extinction–recolonization dynamics, natural selection should favour evolution of traits enhancing dispersal and recolonization ability [6–8]. However, empirical evidence is relatively scarce. Populations of field voles, *Microtus agrestis*, on groups of islands in the Stockholm archipelago provide a good model system to test this prediction. These islands emerged from the sea approximately 500–1000 years ago [9] as a result of land elevation following the termination of the latest glaciations, and were colonized by field voles from the mainland [10]. These insular populations are characterized by drastic fluctuations in numbers of individuals and high turnover rates; extinctions and recolonizations from neighbouring islands are frequent [11–13]. There is evidence to suggest increased rates of emigration/dispersal before subpopulation extinctions [11,13], as well as evidence for life-history adaptations in insular environments. Laboratory breeding over several generations show that insular voles produce larger (5.27 versus 4.13) and heavier (17.06 versus 11.02 g) litters; bear larger young, which grow faster; and make a larger reproductive effort compared with mainland voles [10]. However, there is as yet no evidence that selection has favoured the evolution of traits that enhance dispersal and recolonization ability in these insular vole populations. Morphological traits linked to locomotion and dispersal capacity—such as body size [1,7,8,14–19] and hind foot length [20–22]—provide good candidates for finding such evidence [23].

There are several reasons why dispersal ability and endurance should increase with body size and foot length. Since larger individuals have a smaller surface area to body mass ratio, the effect of buoyancy is increased [24], and the proportional weight increase owing to water retention in the pelage is less for larger individuals [14]. Additionally, large individuals are less susceptible to hypothermia because their rate of heat transfer is lower [25]. Bioenergetic considerations also suggest that large individuals should have a greater maximum dispersal distance than small individuals, and treadmill experiments have confirmed this hypothesis [17,26]. Furthermore, interspecific comparisons generally suggest a positive correlation between endurance and body mass for mammals [27]. Elongated hind feet may increase surface area and cooling rates [25], but also enhance swimming ability by constituting a better propulsor [28] and increase dispersal ability across snow-covered ice by reducing the weight per unit area, so that the feet do not sink into the snow (cf. increased flotation provided by snowshoes).

We collected data on body size and relative hind foot length of field voles (*M. agrestis*) from two mainland localities and from six groups of islands at different distances from the mainland off the east coast of Sweden in the Baltic Sea (figure 1) to test whether the variation in body size and hind foot length among populations was associated with geographical isolation. We then used wild-caught voles as breeding nuclei for one mainland and one insular colony, kept in the laboratory for a period of three years in a common garden experiment, to determine whether the population differences in mean body size and foot length are genetically based

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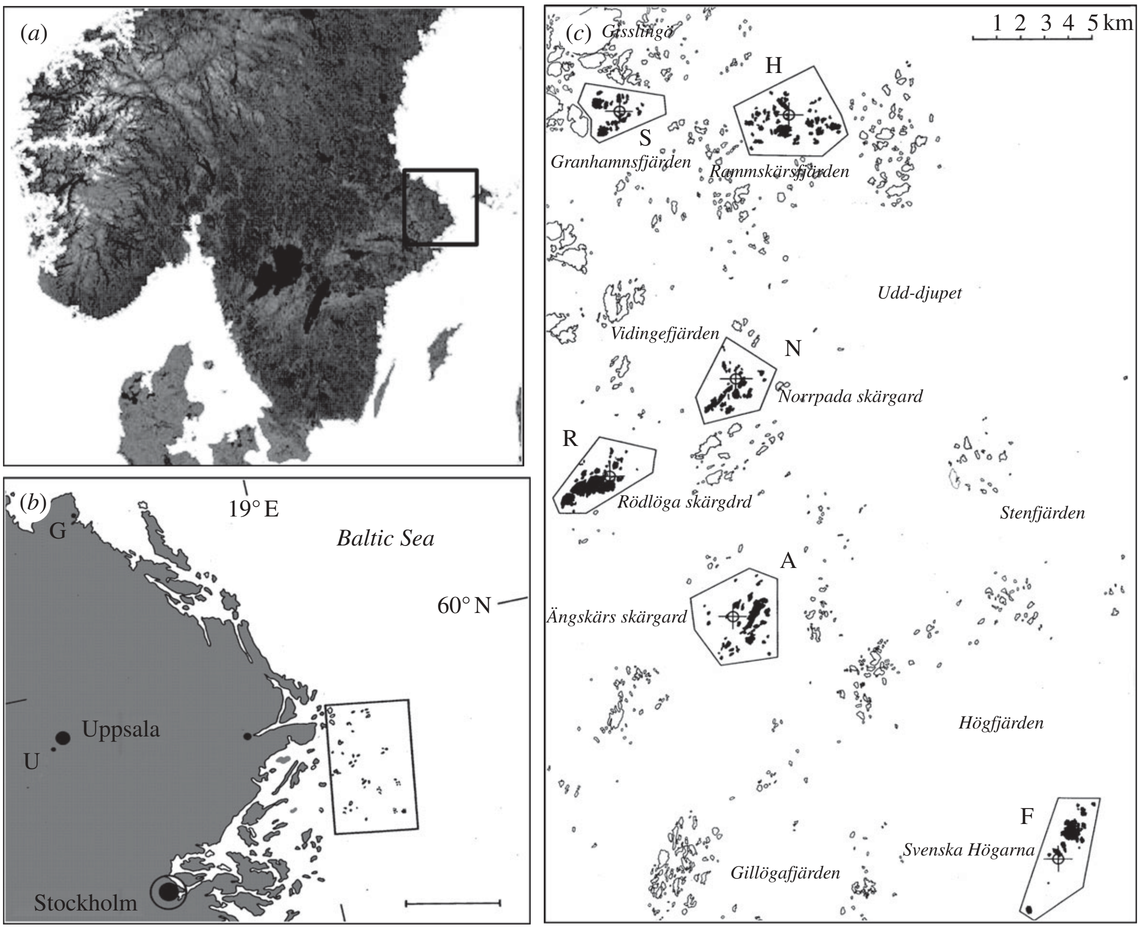

Figure 1. Map showing (*a*) study area indicated by the square. (*b*) The two mainland localities G = Granskär, U = Uppsala. (*c*) The six groups of islands in the Baltic Sea archipelago. S = Själsten, H = Inre Hamnskär, N = Norrpada, R = Rödlöga, A = Ängskär, F = Svenska Högarna. Circled plus symbol indicates the centre of each island group. Scale bar, (*b*) 30 km.

and best explained as micro evolutionary adaptations or merely reflections of developmental plasticity. Finally, we used information on the time since the islands emerged from the sea to estimate the rate of evolutionary change, expressed in darwins.

## 2. MATERIAL AND METHODS

### (a) *Study area*

We trapped field voles from two mainland localities Uppsala (U) and Granskär (G), and from six groups of islands off the Swedish east coast in the Baltic Sea (S, H, R, N, A, F; figure 1 and table 1) in July–September 1983–1987. Localities A and U were visited each year, F, G and R in three different years, and the remaining localities in two different years. About 20 traps per hectare on each site were used, combining snap-traps baited with dried apricots, and live traps (Ugglan special) baited with oats and carrots. Each trapping period lasted for 5–6 nights.

The mainland site U is a wet meadow habitat along the river Hågaån, while site G consists of small marshes surrounded by mixed forests. Potential competitors to the field vole at these sites are bank voles (*Myodes glareolus*), wood mice (*Apodemus flavicollis* and *Apodemus sylvaticus*) and water voles (*Arvicola terrestris*). Important predators at the two mainland sites are weasels (*Mustela nivalis*), stoats (*Mustela erminea*), minks (*Mustela vison*), foxes (*Vulpes vulpes*) and various birds of prey and owls.

Information on the number, size, distance from mainland and inter-island fragmentation of the insular localities is available in table 1. Distance to mainland was measured from the centre of each island group (circled plus symbol in figure 1*c*) to the nearest mainland in a straight line. For each island larger than 0.5 ha we calculated a measure of fragmentation, as a measure of isolation within an island group, by drawing a line from the centre of the island to each of the four cardinal points of the compass (N, E, S and W). If a line did not transect another island, regardless of its size, within 300 m of the shoreline, the line scored one point, and for each island the range of possible values was 0–4. The distance of 300 m was chosen since field voles are capable swimmers but rarely move more than 300 m of open-water distances [13]. The overall measure of fragmentation is the average across islands within each group. Islands less than 0.5 ha were excluded because they usually lack suitable vole habitat.

Each group of islands consists of several differently sized islands characterized by small stands of deciduous trees (*Betula* spp., *Alnus* spp., *Sorbus aucuparia*), dense shrub (*Juniperus communis*), heather (*Calluna vulgaris*) and small meadows and bare rocks. The insular locality closest to the mainland (S) is densely forested with spruce (*Picea abies*) and broad-leaved trees. There are no mammalian competitors to field voles on the insular sites except for locality S where bank voles occur. The adder *Vipera berus* occurs in higher densities on the insular localities than on the

Table 1. Characteristics of the two mainland localities (U and G) and six groups of islands in the Baltic Sea, and number of adult (estimated age more than 100 days) female and male field voles captured at each locality. (n.a. = not applicable.)

| locality | no. of islands | no. of sampled islands | mean island area (ha) | total island area (ha) | distance to mainland (km) | fragmentation | females | males |
|---|---|---|---|---|---|---|---|---|
| U | n.a. | n.a. | n.a. | n.a. | 0 | 0 | 41 | 41 |
| G | n.a. | n.a. | n.a. | n.a. | 0 | 0 | 14 | 49 |
| S | 37 | 4 | 2.32 | 86 | 6.3 | 2.05 | 19 | 21 |
| H | 57 | 8 | 2.50 | 143 | 13.4 | 2.33 | 65 | 73 |
| R | 45 | 8 | 4.30 | 194 | 14.5 | 2.09 | 18 | 33 |
| N | 36 | 9 | 2.31 | 84 | 14.7 | 2.11 | 47 | 40 |
| A | 43 | 11 | 2.92 | 126 | 22.7 | 3.02 | 47 | 47 |
| F | 23 | 2 | 4.34 | 100 | 39.6 | 2.91 | 19 | 20 |

mainland. Examination of stomach contents show that adders feed primarily on voles and frequently take entire litters of suckling voles from underground nests [29]. Experimental evidence [12] suggests that adders may limit the population growth of field voles. The only avian predators known to breed on the islands are kestrels (*Falco tinnunculus*) and short-eared owls (*Asio flammeus*). Stoats, minks and foxes occur only sporadically on the islands.

Data on air temperature and precipitation from the Swedish Meteorological and Hydrological Institute for one mainland station (Norrtälje) and two island stations (Svenska Högarna, F, and Söderarm located about 6 km east of Inre Hamnskär, H; figure 1*c*) show that in general, the island localities have cooler summers, milder winters and less variable air temperatures than the mainland localities. Owing to the buffering effect of the sea, resulting in cooler springs and warmer autumns, the vegetative period is several weeks later on the islands. The lowest monthly mean temperatures are recorded in February in all three stations (Norrtälje: −4.3°C, Söderarm: −3.0°C, F: −2.7°C), while the highest monthly means are recorded in July at the mainland station (16.8°C) and in August at the island stations (Söderarm: 15.8°C, F: 16.0°C). Precipitation is generally lower on the islands (Svenska Högarna 509 mm $\text{yr}^{-1}$; Söderarm 459 mm $\text{yr}^{-1}$) than on the mainland (Norrtälje 595 mm $\text{yr}^{-1}$).

### (b) *Laboratory common garden experiment*

We used wild-caught voles from the mainland site U and from the insular localities A + R + H (figure 1) as breeding nuclei for one mainland and one insular colony kept in the laboratory for a period of three years. Detailed information on the breeding schedule and housing conditions are given elsewhere [10]. A total of 463 litters were produced by 100 females and 101 males. For this study, we used measurements from 105 (52 females/53 males) mainland voles (representing 13 families), and from 150 (72 female/78 male) island voles (representing 16 families) of known ages.

### (c) *Morphological measurements*

From each trapped vole, total body length (from tip of nose to anus) and right hind foot length (from tip of longest digit to end of heel) to the nearest 0.1 mm, and body weight to the nearest 0.1 g was recorded. The skinned skulls were macerated in potassium hydroxide for 24 h, cleaned from soft parts and then rinsed in chloride lime for 24 h. Nine different size-descriptive skull measurements (see the electronic supplementary material, figure S1 and table S2) were then taken by the same person (T.E.) under a dissecting microscope, using vernier callipers, to the nearest 0.1 mm.

### (d) *Age estimation of wild-caught individuals*

To identify adult wild-caught individuals older than 100 days we used the sample of skulls from 255 laboratory-reared voles of known ages (50–381 days) to examine how different morphological characters and proportions changed with age. Least-squares linear log–log regressions of relative breadth of zygomatic arches, i.e. the ratio between zygomatic breadth and braincase breadth, against age yielded the highest $r^2$ (average value = 0.78) in both sexes from both colonies, and was considered the best predictor of age. An age of 100 days corresponded with a value of relative breadth of zygomatic arches of 1.30 in all four groups of laboratory-reared voles. For untransformed data, relative breadth of zygomatic arches increased asymptotically with increasing age and levelled off at approximately 100 days in both sexes and colonies. Our ability to correctly identify and exclude individuals younger than 100 days using this ratio was high; 86 per cent (131 of 152) of the laboratory-reared individuals of known ages with a ratio exceeding 1.30 were 100 days or older. By including only wild-caught voles whose relative breadth of zygomatic arches exceeded 1.30 we obtained a dataset in which the vast majority of individuals were fully grown adults.

### (e) *Statistical analyses*

Descriptive summary statistics with means and standard deviations of body lengths, and the nine different skull measurements of adult (estimated more than 100 days) individuals are given in the electronic supplementary material, table S1. To reduce the number of morphological characters and eliminate the problem of correlations among traits, we applied a principal component analysis [30] to a correlation matrix calculated from individual measures of body length and the nine different skull characters described in the electronic supplementary material, table S1 and figure S1. Principal components were not standardized to unit variance but have variances equal to their corresponding eigenvalue. With this approach, the correlations between the original variables and the principal components are given by factor loadings (eigenvectors). The first principal component (PRIN1) explained 73.6 per cent of the variance in morphology, and because the first eigenvector showed moderate positive loadings on all 10 variables (see the electronic supplementary material, table S2) it is a good descriptor of overall body size, with high PRIN1 scores representing large body size and low scores small size. The second component (PRIN2) only explained 6.7 per cent of the variance in morphology and may be thought of as a measure of skull shape. Judging from the character loadings on this second component (see the electronic supplementary material, table S2), individuals with high scores on PRIN2 have short but broad skulls. All the remaining components each contributed less than 5 per cent to the variance in morphology. We therefore conclude that our sample of field voles vary primarily in body size but little in shape.

Statistical analyses of structural body size, body mass and body-size-specific hind foot length variation among populations relative to degree of isolation and fragmentation were performed with general linear mixed models (GLMMs) as implemented using procedure mixed in SAS [31]. Structural body size and body mass were dependent variables (in separate analyses), distance from mainland and fragmentation were regressors/fixed factors, and population was a random factor. We used the same approach to test whether body size was associated with island size or total island area. In the analyses of hind foot length, body length was used as covariate, distance from mainland and fragmentation were regressors/fixed factors, and population was a random factor. Size, body mass and size-specific hind foot length of the common garden voles were analysed with separate GLMMs, with place of origin (mainland versus island) as a fixed factor, body length as a covariate (in the case of foot length) and family as a random factor. The general Satterthwaite approximation was used for the denominator degrees of freedom in all analyses. Analyses were performed with the SAS 9.1.3 for Windows (SAS Inc., Cary, NC, USA) software package. Body size did not differ between males and females (GLMM: $F_{1,235} = 0.23$, $p = 0.63$), and sex was therefore dropped from subsequent analyses. For intuitive depiction of the results, results based on Spearman rank correlation analyses using population means are also presented.

### (f) *Rate of morphological evolution*

Current elevation (less than 20 m) of the islands, together with shore displacement curves [9], indicate that the highest islands emerged from the sea 500–1500 years ago. Since islands of a minimum size, and covered with sufficient soil and vegetation are required to sustain viable vole populations [13], our study sites probably have not been inhabited for more than 1000 years, and most populations are probably less than 500 years. We estimated the rate of evolutionary change expressed in darwins (d) as $(\log x2 - \log x1)/\Delta t$, where a structure evolved from $x1$ to $x2$ over a time in millions of years, Log is the natural logarithm and the variable $x$ is a linear measurement [32]. We used data on body length and hind foot length for the mainland population and the most isolated island locality, and assumed that island populations are 500 to 1000 years old.

## 3. RESULTS

### (a) *Comparisons of body size among populations*

If the invasion and colonization of insular localities by voles from the mainland and the metapopulation-like dynamics of these subdivided island populations has favoured improved dispersal ability, then voles in the archipelago should have evolved larger body size and longer hind feet than expected for their body size compared with mainland voles. As expected, we found that the voles from mainland populations were on average smaller (mean principal component scores of body length and nine different skull traits (PRIN1) + s.d. $= -2.09 + 1.86$, $n = 73$) than voles from insular populations ($0.91 + 2.52$, $n = 168$; $F_{1,239} = 83.52$, $p < 0.0001$). Average body size also increased with the increasing distance from nearest mainland (GLMM, linear effect of distance: $F_{1,11.8} = 13.79$, $p = 0.003$; nonlinear effect of distance: $F_{1,10.8} = 11.04$, $p = 0.007$; Spearman rank correlation, $r_s = 1.0$, $n = 6$, $p < 0.0001$; figure 2*a*). Body size also increased with degree of fragmentation, as measured in degree of inter-island isolation (GLMM: $F_{1,11.9} = 4.91$, $p = 0.047$; $r_s = 0.77$, $n = 6$, $p = 0.072$), suggesting that voles were larger in archipelagos where islands were more scattered (figure 3*a*). There was no significant effect of population of origin on structural body size ($Z = 0.49$, $p = 0.31$), other than that mediated by geographical isolation. The results were qualitatively similar for body mass: body mass increased both with the degree of fragmentation ($F_{1,5.39}=12.05$, $p = 0.0158$) and with distance from mainland ($F_{1,6.63} = 8.26$, $p = 0.025$; figure 2*b*). The variation in body size among the six island groups was not associated with average island size (GLMM, effect on: structural body size; $F_{1,3.83}=2.23$, $p = 0.21$; body mass: $F_{1,5.58}=1.74$, $p = 0.24$) or with total island area (structural body size: $F_{1,3.74}=0.09$, $p = 0.78$; body mass: $F_{1,5.04}=0.42$, $p = 0.54$).

### (b) *Evaluating effects of among year variation in body size*

Among-year variation is unlikely to have biased our comparisons of body size, because the associations were still evident when we included year as a random explanatory factor in the analyses (GLMM, effect of year: $Z = 1.11$, $p = 0.13$; linear effect of distance: $F_{1,13.6} = 17.77$, $p = 0.0009$; nonlinear effect of distance: $F_{1,11.7} = 15.09$, $p < 0.0023$; linear effect of inter-island isolation: $F_{1,13.7} = 7.83$, $p < 0.0144$). There was also an almost perfect association between least squares mean estimates of body size for the different populations generated by a model that did and a model that did not include year as an explanatory variable ($r = 0.98$, $n = 8$ populations, $p < 0.0001$).

### (c) *Comparisons of hind feet length for a given body size*

Insular voles had longer hind feet than expected for their body size. Mean size-specific hind feet length differed significantly among populations and increased with inter-island fragmentation (GLMM: $F_{1,5.87} = 14.92$, $p < 0.0001$; $r_s = 0.89$, $p = 0.019$, $n = 6$; figure 3*b*), but was not associated with distance from nearest mainland (GLMM: $F_{1,7.25} = 0.03$, $p = 0.86$; $r_s = 0.94$, $p < 0.005$, $n = 6$). However, when fragmentation was dropped from the model, hind foot length increased with the increasing distance from mainland (GLMM: $F_{1,6.29} = 11.16$, $p = 0.0145$; figure 2*c*). There was no significant effect of population of origin, other than that mediated by geographical isolation ($Z = 1.20$, $p = 0.12$). Results were similar when the first principal component, rather than body length, was used as a measure of overall body size.

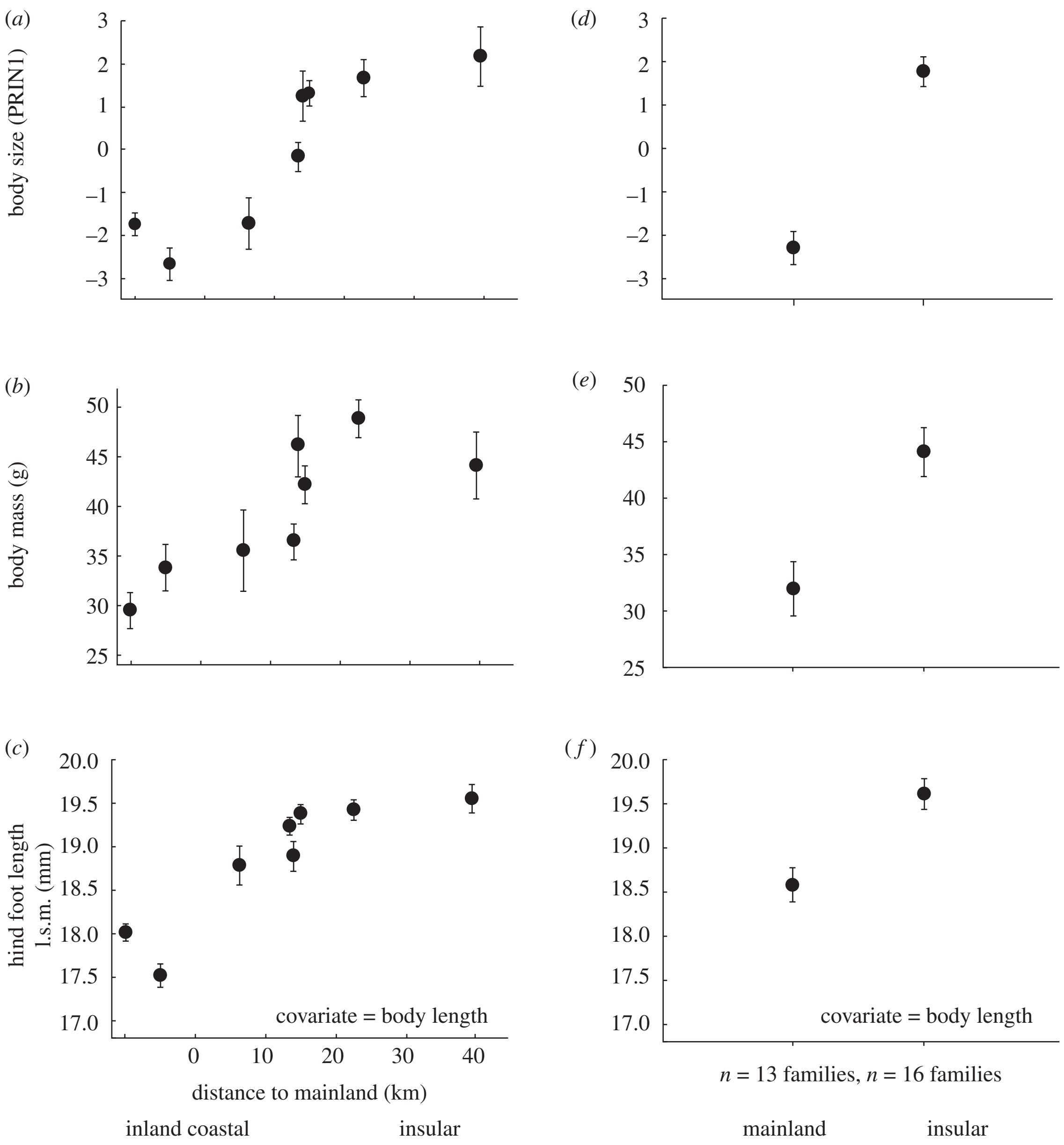

Figure 2. (*a*,*d*) Mean (± s.e.) structural body size (measured as the first principal component based on body length and nine different skull traits); (*b*,*e*) body mass in g; and (*c*,*f*) size-specific hind foot length (expressed as least squares means (l.s.m.) from linear regression of hind foot length on body length). (*a*,*b*,*c*) data for populations of *Microtus agrestis* from two mainland six insular localities in the Stockholm archipelago. (*d*,*e*,*f*) data for descendants to mainland and insular voles reared in the laboratory using a common garden experimental design.

### (d) *Comparison among mainland and insular voles reared in a common environment*

Since the results above are based on data from wild collected voles, a critical question arises: are the phenotypic differences genetically determined, rather than environmentally induced [33,34]? Data from a common garden experiment confirmed that the observed differences are likely to be genetic: laboratory-born insular voles had larger body size (GLMM: $F_{1,27} = 68.79$, $p < 0.0001$; figure 2*d*), were heavier (44 versus 32 g: $F_{1,28.6} = 13.92$, $p < 0.0008$; figure 2*e*), and had longer hind feet than expected for their body size ($F_{1,33.5} = 31.5$, $p < 0.0001$; figure 2*f*) compared with laboratory-born mainland voles. There were significant effects of family on structural body size ($Z = 1.73$, $p = 0.042$) and hind foot length ($Z = 2.36$, $p = 0.0091$), but not on body mass ($Z = 1.23$, $p = 0.11$). Analyses of body mass (see above) and physical condition (see the electronic supplementary material for the supporting results) also indicate that our results were not influenced to any important degree by developmental plasticity in response to food or other environmental conditions.

### (e) *Estimated rates of evolution*

We estimated rate of morphological evolution [32] in these vole populations based on the assumption that islands have been inhabited for 500–1000 years. For body length, the estimated rate of evolutionary change is ((log 125 mm − log 110 mm)/0.001) 128 darwins, assuming populations are 1000 years old and 256 darwins assuming that populations are 500 years old. For hind foot length (least squares mean values in figure 2*c*), estimated rate of evolutionary change is

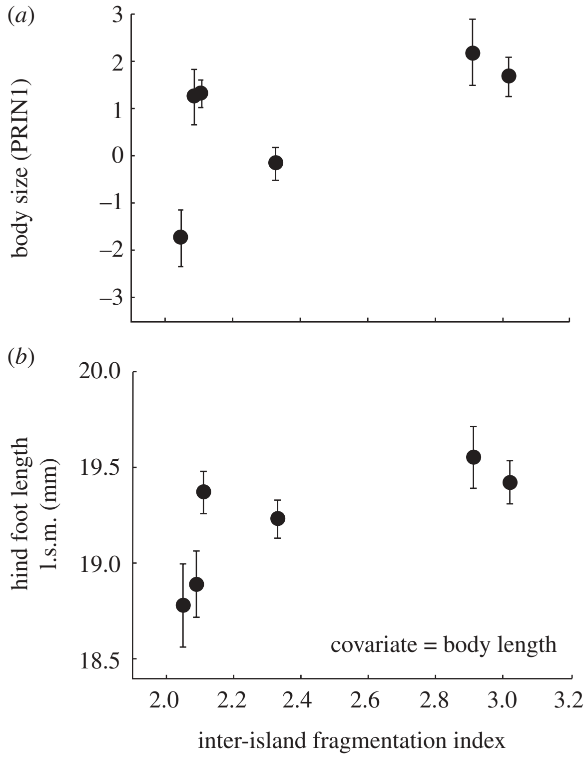

Figure 3. (*a*) Variation in mean body size and (*b*) size-specific hind foot length among insular populations of *Microtus agrestis* as a function of inter-island fragmentation. Body size measured as first principal component. Hind foot length measured as least squares means (l.s.m.) from linear regression of hind foot length on body length. Error bars depict ± s.e.

((log 19.5 mm − log 17.5 mm)/0.001) 108 darwins for 1000 years and 216 darwins for 500 years.

## 4. DISCUSSION

Does selection associated with colonization, extinctions and recolonizations in subdivided island populations promote the evolution of morphological traits that enhance dispersal ability, as predicted by theory? Across two mainland and six insular populations of *M. agrestis*, we found that body size and length of hind feet—both traits facilitating the likelihood of successful dispersal over water—were larger on islands than on the mainland and also increased with increasing island isolation towards the outer archipelago (figure 2). A common garden breeding experiment confirmed that the population differences in body size and size-specific foot length were genetically based, indicating that the observed population divergence reflects evolutionary adaptation. We do not at the moment have genetic data to assess the phylogenetic relationship and reconstruct colonization history of populations. We therefore cannot dismiss the possibility that founder events, serial bottlenecking and drift may have contributed to the evolution of larger body size in insular voles. However, we can see no reason why such random processes should generate a continuous increase in body size and relative foot length according to distance from mainland or fragmentation. Hence, the results provide rare empirical evidence—in line with theoretical predictions—that traits enhancing dispersal and recolonization ability should evolve in island metapopulations [6–8].

### (a) *Alternative explanations for evolution of larger body size on islands seem unlikely*

Several factors may have contributed to the evolution of larger body size of field voles on islands in the Stockholm archipelago, such as competitive release [16,18,35,36], size selective predation imposed by gape-limited snake predators [12,37], and correlated responses to selection for life-history traits that enhance reproductive performance in metapopulations [8,10]. While these factors may have contributed to the evolution of a larger body size of island voles compared with mainland voles, they do not provide a satisfactory explanation for the increase in body size and size-specific hind foot length with distance from mainland and inter-island fragmentation.

There are more competitor mammal species to field voles on the mainland than on islands in the outer archipelago [29]. Some models posit that competitive release promotes evolution of larger body size on islands [18]. In keeping with this line of argument, access to higher quantity or quality of food may have contributed to the evolution of larger body size with increasing distance from the mainland (figure 2). However, comparisons of physical condition of voles do not support this interpretation (see the electronic supplementary material, supporting results in the appendix for details.) Wild-caught voles from the mainland were heavier for a given body size than laboratory-raised mainland voles. This contradicts the hypothesis that mainland voles were smaller than insular voles because they were food stressed. Furthermore, differences in average physical condition among wild-caught voles from different insular populations were not associated with population mean structural body size. This argues against the interpretation that among-population divergence in body size reflects responses to food availability.

Predation by mammals and birds is believed to select for decreased body size in small prey species [16,17,25]. Since there are fewer predator species on islands in the outer archipelago than on the mainland [12,29], reduced predation provides an alternative explanation for the evolution of large body size in insular populations. Likewise, high density of adders (*Vipera berus*)—which are gape-limited predators that are only able to consume prey below a certain body size [37]—on insular populations [12,29] may have contributed to the evolution of larger voles in the isolated island populations. However, neither relaxed competition nor differential predation provides satisfactory explanations for the association between mean vole body size and inter-island fragmentation (figure 3).

It has been suggested that the relative importance of major determinants of body size (e.g. predation, food availability, competition and predation) may change as a function of island area, such that island size may influence the evolution of body size [38–41]. However, our analyses uncovered no association across insular localities of vole body size with average island area or with total island area.

Body size is a complex trait that is associated with many important ecological, physiological and life-history characteristics [25,42]. Local extinctions and recolonizations from neighbouring islands are frequent in insular populations of field voles [11–13], and breeding experiments have demonstrated that insular voles have evolved different life-history characteristics (i.e. produce more and larger young that grow faster, and make a larger reproductive effort) than mainland voles [10]. The larger body size with increasing distance from the mainland and increasing inter-island fragmentation may thus represent a correlated response to selection for traits that enhance reproductive performance in dynamic metapopulation systems [11,13,42,43].

### (b) *Selection for enhanced dispersal ability can explain the evolution of larger body size and longer hind feet on islands*

None of the mechanisms discussed above can explain why vole populations in more isolated and fragmented island groups have evolved longer feet than expected for their body size compared with mainland voles. However, larger animals with long hind feet are better swimmers, float better, lose less heat and have higher energetic capacity for moving long distances in water and on land [14,15,24,26,28,44]. We therefore suggest that the associations of body size and foot length with geographical isolation demonstrated in these field vole metapopulations provide rare evidence for evolution and local adaptation in response to natural selection for enhanced dispersal capacity. Selection, favouring large, long-footed individuals, may have operated during the founder events when islands were first colonized by voles from the mainland, but given the metapopulation like dynamics, selection for enhanced dispersal is probably an ongoing process within each island group.

Previous studies on range expansion of cane toads (*Bufo marinus*) suggest that longer hind legs facilitate dispersal ability [23], but have not established that the differences in leg length had a genetic basis. By contrast, our common garden experiment demonstrates that the geographical differences in body size and foot length were genetically based. Together with the functional importance of both of these traits for dispersal ability, this confirms that the divergence among these vole populations represents adaptive evolution.

### (c) *Evolution in insular vole populations have been unusually rapid*

The estimated rate of contemporary morphological evolution in these vole populations (100–250 darwins) was very rapid compared with a median rate of morphological evolution of 2.88 darwins, based on data for island and mainland populations from a large number of mammal species [4]. That evolution has been unusually rapid in these vole populations is evident also when the strong negative relationship between rates of evolution and the time interval over which the evolutionary rates were estimated [4,45] is taken into consideration. Millien found that the average rate of evolution over a 1000 year time period was 53 darwins for island mammals and 26 darwins for mainland mammals (see fig. 2 and table S1 in Million [4])—our estimated rates of evolution for body length (128 darwins in 1000 years) and hind foot length (108 darwins) are two to five times higher.

## 5. CONCLUSIONS

In their review of empirical demonstrations of contemporary adaptations in natural populations, Reznick & Ghalambor [46] found that rapid evolution appeared to be associated with colonization and establishment in novel or modified environments, as well as with heterogeneous environments and a metapopulation [43] structure. These settings are associated with changes in many aspects of the biophysical environment that result in strong directional selection and provide at least a short term opportunity for population growth [46]. Our insular voles conform to this general pattern. To this end, our findings provide as yet a rare example of rapid morphological evolution in mammals inhabiting northern Europe, where levels of biodiversity and diversification that have evolved *in situ* are thought to be low owing to the recency of the last glaciations. Furthermore, the results highlight the continued value of island populations in enhancing our understanding of the evolution and maintenance of biological diversity, especially in respect to body size [1,16,18,35] and dispersal traits [14,17,20].

All experiments were conducted with the approval of the concerned Swedish authorities.

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