



Rapid morpho-functional changes among insular populations of the greater white-toothed shrew

RAPHAËL CORNETTE^{1,2*}, ANTHONY HERREL³, JEAN-FRANCOIS COSSON⁴,
FRANÇOISE POITEVIN⁵ and MICHEL BAYLAC^{1,2}

¹UMR CNRS/MNHN 7205, 'Origine, Structure et Evolution de la Biodiversité', Muséum National d'Histoire Naturelle, 45 Rue Buffon, 75005 Paris, France

²UMS CNRS/MNHN 2700, 'Outils et Méthodes de la Systématique Intégrative', Plate-forme de Morphométrie, 45 Rue Buffon, 75005 Paris, France

³UMR CNRS/MNHN 7179, 'Mécanismes Adaptatifs: des Organismes aux Communautés', 57 Rue Cuvier, 75231 Paris cedex 05, France

⁴Centre de Biologie et de Gestion des Populations, Campus International de Baillarguet, CS 30016, 34988 Montferrier-sur-Lez cedex, France

⁵UMR CNRS 5175, Centre d'Ecologie Fonctionnelle et Evolutive, 1919 Route de Mende, F34293 Montpellier cedex 5, France

Received 6 April 2012; revised 23 April 2012; accepted for publication 23 April 2012

Islands are often considered to be natural laboratories where repeated 'evolutionary experiments' have taken place. Consequently, islands have been key model systems in our understanding of evolutionary theory. The greater white-toothed shrew (*Crocidura russula*) is of interest as it has invaded French Atlantic islands within the last few thousand years and is considered to be morphologically and genetically stable in this area. In this article, we study the shape of the mandible of the greater white-toothed shrew on four islands and compare it with that of individuals from populations on the mainland to quantify the effects of insularity. The degree of insularity (i.e. island size and distance to the continent) is thought to be linked to differences in ecological characteristics of islands compared with the mainland. We used geometric morphometric analyses to quantify differences in size and shape between populations and employed a simple biomechanical model to evaluate the potential effects of shape differences on bite force. Specimens from island populations are different from continental populations in shape and mechanical potential of the mandible. Among islands, the mandible shows various shapes that are correlated with both the distance from the coast and island area. The shape differences are located on different parts of the mandible, suggesting different ecological constraints on each island. Moreover, these shapes are linked to the 'mechanical potential', which is markedly different between islands. Mechanical potential has been suggested to evolve in response to prey size and or mechanical properties. In conclusion, our results show that, in spite of the relatively recent colonization of the Atlantic Islands, the mandible of *C. russula* possesses a distinct shape. Moreover, the shape differs among islands and is probably linked to the consumption of different prey. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, 107, 322–331.

ADDITIONAL KEYWORDS: bite force – mandible – morphometrics – shape.

INTRODUCTION

The faunas and floras of islands and archipelagos have played a key role in our understanding of evolutionary mechanisms, changes and the origin of new species (e.g. Darwin, 1845; Wallace, 1860; Losos, Warheit & Schoener, 1997; Losos, Schoener & Spiller, 2004). Islands constitute repeated, discrete and relatively simple entities and function as 'natural laboratories' that can be used to test general ideas about evolution (Whittaker, 1998). Notable differences in

*Corresponding author. E-mail: cornette@mnhn.fr

phenotype (morphology, behaviour, ecology, natural history) between continental and insular populations are often observed. The most common phenotypic difference observed is a change in body size in insular populations. Insular faunas are subjected to different ecological conditions depending on the physical, climatological and geographical characteristics of islands (Blondel, 1986). The general rule is that insular small mammals tend towards gigantism and large ones towards dwarfism (Foster, 1964; Van Valen, 1973; Lomolino, 1985). Previous studies have demonstrated that the intensity of morphological changes on islands is dependent on both the surface area of the island and its distance to the mainland (Lomolino, 2005; Millien *et al.*, 2006).

The greater white-toothed shrew, *Crocidura russula* (Hermann, 1780), is widespread in France (except Corsica), Western Europe (except Italy) and the Northern Maghreb (Wilson & Reeder, 2005). Moreover, it is present on numerous Atlantic and Mediterranean islands. Previous studies have demonstrated the genetic (Brutto, Azeuleo & Sarà, 2004; Brändli *et al.*, 2005; Cosson *et al.*, 2005), karyotypic (Brändli *et al.*, 2005) and morphological (Heim de Balsac, 1940; Poitevin *et al.*, 1987; Cosson, Pascal & Bioret, 1996) stability of this species along its European continental and Atlantic insular range. However, recent studies have shown a distinct genetic structure between the Western and Eastern Maghreb and for some Mediterranean islands (Cosson *et al.*, 2005). A biometric study based on skull measurements, however, failed to differentiate between Mediterranean insular and continental populations (Poitevin *et al.*, 1987). Moreover, a combined biometric and genetic approach was unable to demonstrate differences between insular Atlantic and continental populations (Cosson *et al.*, 1996). Thus, island and mainland populations of *C. russula* are thought to be largely undifferentiated. Yet, previous analyses of *C. russula* have been restricted to simple, mostly univariate analyses, which possibly do not capture more complex or subtle variations in shape. Advances in morphometrics (Adams, Rohlf & Slice, 2004) using multivariate approaches and geometric morphometrics analyses have permitted the quantification of small differences in form between groups.

Mandible form, consisting of both size and shape, is a common and strongly discriminating character commonly used to study phenotypic variation, especially for small mammals (Atchley, 1993; Renaud, Alibert & Auffray, 2009). Mandible form is dependent on both developmental constraints and selective pressures. Previous authors have suggested that selection on mandibular form is mostly related to diet (Badyaev & Foresman, 2004). Moreover, previous studies have shown that the mandible of shrews is highly plastic

and offers a good model for demonstrating differences in ecology and selective regimes among populations (Young, Sweeney & Badyaev, 2010). As such, the differences in mandibular form among populations may highlight functional advantages. Considering the mandible as a simple lever, the calculation of the 'mechanical potential' provides an estimate of the functional capacity of the jaw system and may reflect selection on bite performance as a result of local dietary adaptations (Young *et al.*, 2007).

In this article, we use a geometric morphometrics approach and a simple biomechanical model with three distinct and complementary aims. First, we investigate the population-level variability in size and shape of the mandible of *C. russula* to test for differences between insular and continental populations. We predict that island populations will be different in both the size and shape of the mandible, given the predicted differences in resource availability on islands. Second, we compare patterns of form between islands. We predict that the shape of the mandible will be related to island size and the distance of the island to the mainland if natural selection is driving the observed changes. In contrast, if variation in the shape of the mandible is a result of stochastic processes or founder effects, the mandibular shape should be independent of island size and its distance to the mainland. Third, we expect that the differences in form will have direct functional consequences that may reflect the selective pressures operating on islands of different size as a result of variability in trophic resources.

MATERIAL AND METHODS

To explore the variability in mandibular form, 104 specimens from seven populations, four insular (Groix, GRO, $n = 19$; Ré, IRE, $n = 12$; Molène, MOL, $n = 10$; Oléron, OLE, $n = 15$) and three continental (Ceret, CER, $n = 19$; Commarques, COM, $n = 10$; La Garenne St Thomas, GAR, $n = 19$) were used for geometric morphometrics analyses (Fig. 1, Table 1). For insular populations, the square root of the area of the island and its log-transformed distance to the mainland were obtained (Fig. 1). Specimens were mostly collected from rejection pellets of barn owls (*Tyto alba*). Others belong to the collections of the Muséum National d'Histoire Naturelle of Paris. The barn owl swallows its prey whole and digests it in such a manner that the skeleton is nearly intact after regurgitation. After species diagnoses following Saint-Girons, Fons & Nicolau-Guillaumet (1979) and Poitevin *et al.* (1986), juvenile and very old individuals were removed from our sample. Dental abrasion patterns were used to assign age classes (Jeanmaire-Besançon, 1986).

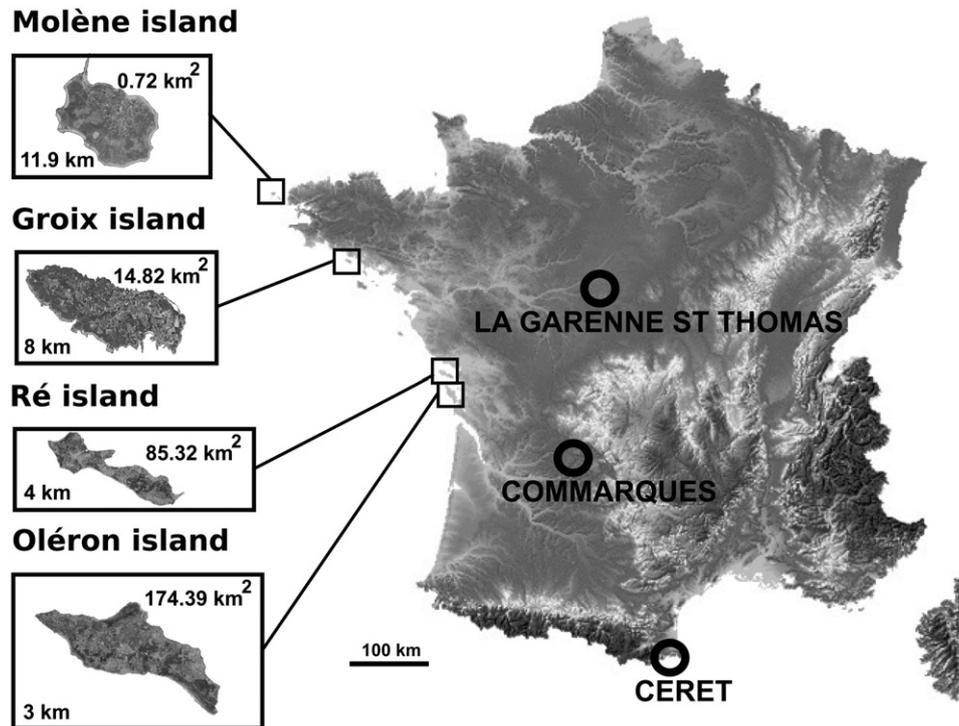


Figure 1. Geographical location of the seven populations with special emphasis on the islands included in the study. Islands are not drawn to scale. Indicated next to the islands are the island surface area and the distance to the mainland.

Table 1. List of sample locations, abbreviations, sample sizes and geographical locality

Sample location	Identification code	Number of specimens	Geographical coordinates
Continental			
Ceret, Pyrénées Orientales	CER	19	42°29'N/02°45'E
Commarques, Dordogne	COM	10	45°11'N/00°43'E
La Garenne St Thomas, Indre	GAR	19	47°28'N/01°30'E
Islands			
Île de Groix, Morbihan	GRO	19	47°38'N/03°28'W
Île de Ré, Charente Maritime	IRE	12	46°12'N/01°25'W
Île de Molène, Finistère	MOL	10	48°24'N/04°57'W
Île d'Oléron, Charente Maritime	OLE	15	45°56'N/01°15'W

Landmark coordinates were taken from the left hemi-mandibles (Fig. 2 and Table 2). A Sony CCD XC-77 CE video camera and MTV software, version 1.3, were used to acquire and record the x and y coordinates of each landmark. Visualization and testing of repeatability were performed using a principal components analysis on 20 repetitions of three specimens from the same population. Variation of repetitions performed on the same specimen was much lower than the inter-individual variation, indicating the validity of our approach.

We used geometric morphometrics approaches to provide a precise description of the shape of the

mandible, allowing us to identify the areas that undergo shape change (Bookstein, 1991; Baylac, 1996; Slice, 2007). Mandibles were described by 14 landmarks and were analysed using a Generalized Procrustean Analysis (GPA; Rohlf & Slice, 1990). This analysis consists of a superimposition, normalization of size and rotation to create residual size free data. The logarithm of the centroid size was used as a global indicator of size and employed in our analyses. A multivariate analysis of covariance (MANCOVA) was performed on the shape descriptors to test for differences between populations, and between insular and continental populations. A second MANCOVA

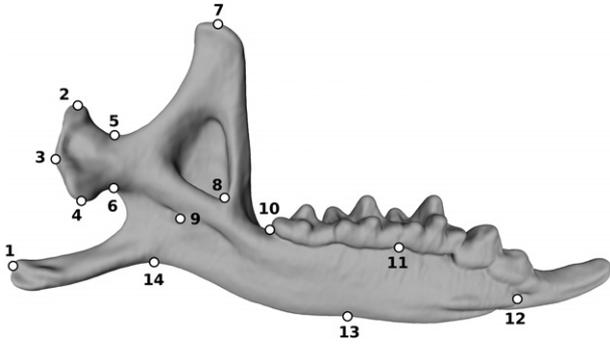


Figure 2. Illustration of the location of the 14 landmarks on the mandible used to quantify size and shape variation across populations (see Material and methods).

Table 2. Definitions and anatomical location of landmarks

Landmark	Anatomical location of landmark
1	Distal-most point of the angular process
2, 3, 4	Posterior-most, dorsal and ventral sides of the articular condyle
5, 6	Dorsal and ventral sides of the condylar neck
7	Dorsal-most point of the coronoid process
8	Anterior-most corner of the coronoid fossa
9	Posterior part of the mandibular foramen
10	Intersection of the mandible and the third molar
11	Intersection of the mandible and the second and first molars
12	Extreme part of the mandible at the base of the incisor
13	Inflexion point of the mandibular body
14	Inflexion point between the angular process and the mandibular body

was performed for insular populations, with island area and distance to the mainland as covariates. Multivariate regressions were used to estimate the impact of these two factors on the form of the mandible. To study the variability in mandibular shape, a canonical variance analysis (CVA) was carried out and visualizations of shape differences along CVA axes were performed using multivariate regressions (Monteiro, 1999). Finally, to summarize the global patterns of mandibular shape variation, a neighbor-joining tree was calculated using the Mahalanobis distances between populations. All data (traditional and geometric) were analysed using the morphometrics libraries Rmorph (Baylac, 2006), MASS (Venables & Ripley, 2002) and ape (Paradis, Claude & Strimmer, 2004) in R (R Development Core Team, 2009).

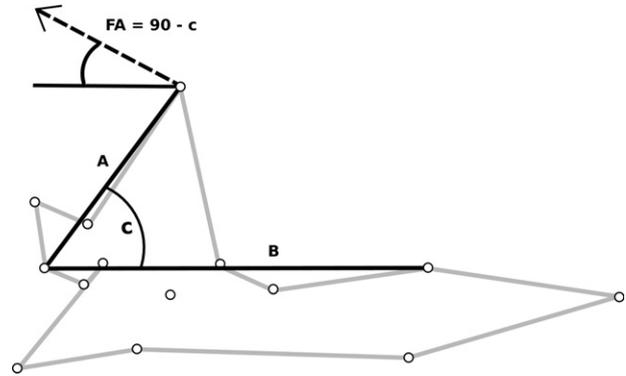


Figure 3. Graph illustrating the three measurements used for the biomechanical model: A, distance from the condyle to the middle part of the coronoid; B, distance from the condyle and the landmark situated between molar two and molar one; C, gape angle. Force angle (FA) is defined as $FA = 90 - C$.

To evaluate the functional consequences of shape variation, a simple biomechanical model, adapted from Young *et al.* (2007), was created (Fig. 3). This model calculates the mechanical potential (MP) and estimates the theoretical bite force when the mandible is considered as a simple lever. Three measurements were taken: (1) the distance from the articular condyle to the coronoid process; (2) the distance from the articular condyle to the point situated between the second and first molars; (3) the angle formed by these two distances. The force angle (FA) is obtained as follows: $FA = 90 - C$. MP is calculated as $MP = A/B \cos(\text{FA})$. To evaluate whether differences in shape between populations imply functional differences, MP was calculated on the extreme shape configurations of the three first axes of the CVA. A histogram was constructed to visualize the difference in MP on each axis.

RESULTS

A MANCOVA performed on the Procrustes residuals showed a significant population and insularity effect (Table 3). The allometry was significant, but there were no significant interaction effects. A second MANCOVA on shape parameters restricted to island populations showed significant effects of the covariates distance to the coast and island area, as well as significant population effects (Table 4). The allometric component was significant, but there were no significant interactions, indicating a homogeneity of the observed allometric trends. Separate multiple regressions performed on shape versus size ($R^2 = 0.26$; $P < 0.002$), distance to the coast ($R^2 = 0.76$; $P < 0.001$) and island area ($R^2 = 0.81$; $P < 0.001$) were significant.

Table 3. Results of a multivariate analysis of covariance (MANCOVA) with size as covariate performed on the shape for all populations. Statistically significant results are indicated in bold

	d.f.	Pillai	<i>F</i>	num. d.f.	den. d.f.	<i>P</i>
Islands vs mainland	1	0.73	6.18	28	63	< 0.001
Populations	5	2.89	3.28	140	335	< 0.001
Size	1	0.47	2.03	28	63	0.011
Islands/mainland × size	1	0.28	0.90	28	63	0.61
Population × size	5	1.38	0.91	140	335	0.73
Residuals	90					

den., denominator; d.f., degrees of freedom; num., numerator.

Table 4. Results of a multivariate analysis of covariance (MANCOVA) with size as covariate performed on the shape for insular populations only. Statistically significant results are indicated in bold

	d.f.	Pillai	<i>F</i>	num. d.f.	den. d.f.	<i>P</i>
Distance from the coast	1	0.92	11.29	24	25	< 0.001
Area	1	0.90	9.00	24	25	< 0.001
Population	1	0.82	4.70	24	25	< 0.001
Size	1	0.65	1.96	24	25	0.05
Distance × size	1	0.42	0.74	24	25	0.76
Area × size	1	0.51	1.08	24	25	0.43
Population × size	1	0.34	0.53	24	25	0.94
Residuals	48					

den., denominator; d.f., degrees of freedom; num., numerator.

An analysis of centroid size indicated that populations from the mainland were larger than the insular populations (Fig. 4A). The effect of size on shape is shown in Figure 4B. This allometric pattern is confounded by the effects of insularity, as suggested by the small effect of size when considering island populations only (Table 4).

A CVA (Fig. 5) performed on the shape descriptors separated Oléron and Ré from Molène and Groix on the first axis (45% of the total variance). Shape differences (Fig. 5A) along the first axis separated a slender mandible for the first two islands from a more robust form for the last two. Differences in the height and width of the coronoid process and the height of the mandibular ramus were found between small and distant versus large and close islands. Specimens from Groix and Molène showed a proportionally taller and larger mandibular branch. Moreover, the angle between the coronoid and condylar processes was more obtuse than in specimens from Oléron and Ré. The height of the body of the mandible was proportionally greater in the specimens from Groix and Molène. The second axis (20% of the total variance) separated island from continental populations (Fig. 5B). Shape differences were mainly located in

the articular condyle and the coronoid and angular processes. Insular specimens showed a larger articular condyle and a more open mandibular notch. Moreover, the angular process was proportionally smaller and situated more ventrally. However, no differences were observed in the shape of the body of the mandible along this axis. The third axis (15% of the total variance) separated the two islands (Fig. 5C), Molène and Groix, from each other. The shape differences were again situated in the articular condyle and the coronoid process, as well as in the height of the mandibular ramus. Specimens from Groix had a more obtuse angle of the mandibular notch and a more robust mandibular body.

The unrooted neighbor-joining tree calculated using the Mahalanobis distances for shapes between populations illustrated the proximity in mandible shape between large islands and the mainland on the one hand, and the distinctness of small islands, on the other (Fig. 5D). Moreover, it showed that the difference between the two distant islands, Molène and Groix, was more marked than that between the islands of Ré and Oléron.

The allometric component inherent in the dataset had functional consequences, with smaller specimens

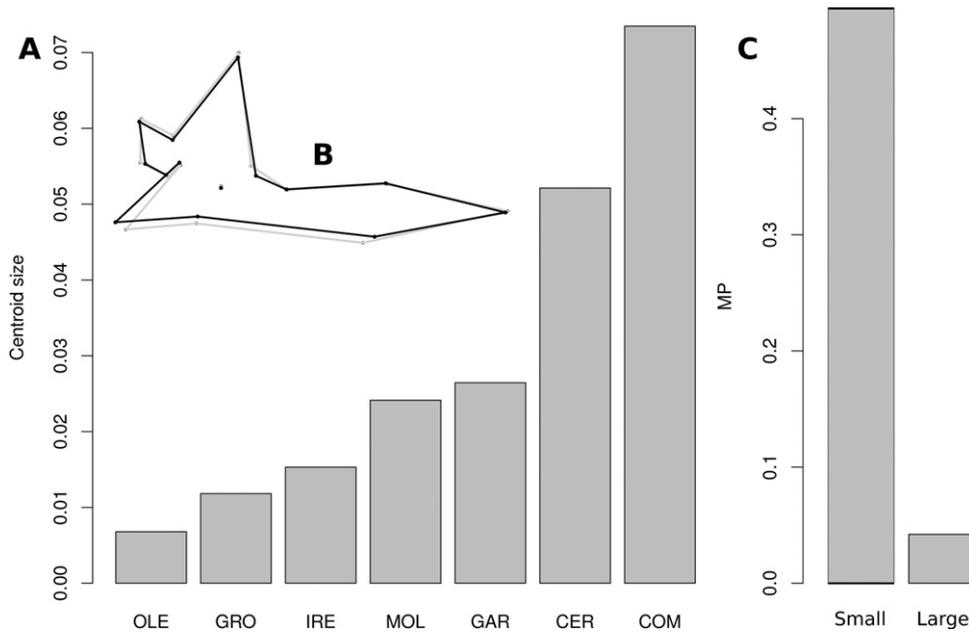


Figure 4. Graphs illustrating: A, means of the logarithms of the centroid size of each population (see Material and methods for population abbreviations); B, visualization of the allometric pattern; grey, mandible shape of small specimens; black, mandible shape of large specimens; C, mechanical potential (MP) of each of the extremes of the allometric pattern.

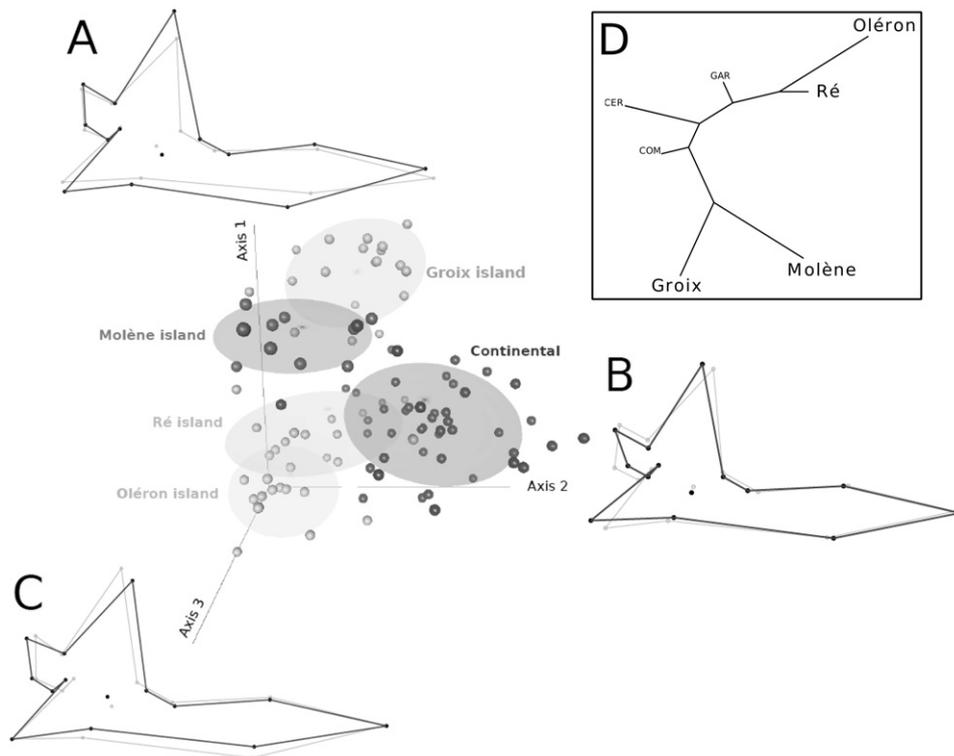


Figure 5. Canonical variance analysis performed on the shape data with seven populations: four insular and three continental. Ellipses represent the 50% confidence limits. A, B, C, Shape variation along the first three axes, respectively. Black lines illustrate the positive part of the axis, grey lines illustrate the negative part. D, Neighbor-joining tree performed using the Mahalanobis distances derived from the analysis of mandibular shape for the four insular (large type) and three continental (CER, Ceret; COM, Commarques; GAR, La Garenne St. Thomas) populations.

possessing a markedly higher MP than larger ones. With respect to shape, the first discriminant axis showed a clear difference in MP (Fig. 6, Table 5). As this axis tended to separate Groix and Molène from Oléron and Ré, this suggests that these islands differ in MP, with Oléron and Ré having a greater MP. The second axis presented no marked difference in MP between insular and continental populations, even though insular populations possessed a higher MP on average. The third axis, which tended to separate Groix from Molène, was associated with a marked difference in MP, with specimens from Molène possessing a greater MP than those from Groix.

DISCUSSION

Contrary to the findings of previous studies, we found significant differences in form among insular and continental populations of greater white-toothed

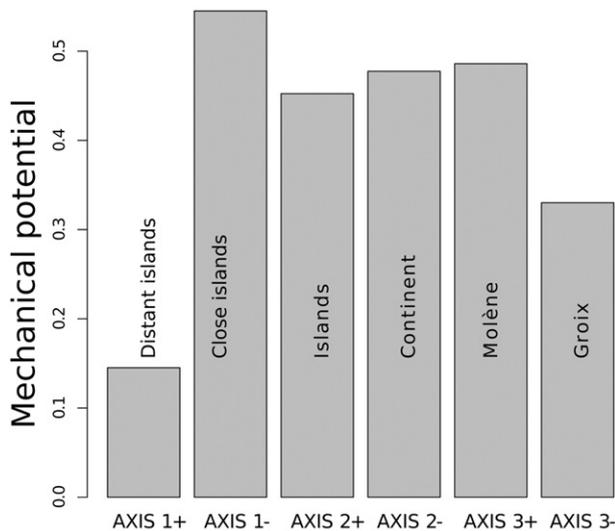


Figure 6. Comparisons of the mechanical potential (MP) of the shape of each extreme along the first three discriminant axes of the canonical variance analysis (CVA) performed using data for all populations (see Fig. 5).

shrews. This discrepancy is probably related to our use of the coherent decomposition of form into size and shape components provided by the geometric framework of Mosimann (1970). This approach highlights that shape variation is important in the segregation of populations. Moreover, our data show that the observed shape variation has functional consequences.

The observed differences in mandibular shape on islands could be caused by a host of genetic and epigenetic factors. Indeed, shape changes may imply different evolutionary processes. Mandible shape could, for example, be plastically determined depending on the consistency of food, as the mandible in shrews is known to show a late ossification during development (Renaud, Auffray & De la Porte, 2010; Young *et al.*, 2010). Moreover, environmental pressures are known to influence mandibular shape, and insularity, as a potential source of stress, could thus drive changes in shape (Badyaev & Foresman, 2004). Although founder effects may also drive the evolution of a given phenotype, especially on small islands, this is unlikely in the present case, as the same haplotype is observed on Groix and Molène as on the French mainland (Cosson *et al.*, 2005). The overall genetic homogeneity in *C. russula* is undoubtedly related to a small number of individuals who crossed the Strait of Gibraltar before colonizing the Iberian Peninsula and, later, France (Cosson *et al.*, 2005). Moreover, the observed shape differences have functional consequences and are thus presumably adaptive. In the absence of clear evidence of founder effects, it thus seems plausible that natural selection acting on mandible shape in the face of different food resources is the main driver behind the observed shape changes. The significant correlations between mandible shape and island area and distance from the coast support this suggestion, as island size and the distance to the mainland will affect the availability of food on the islands. Moreover, this hypothesis is strengthened by the observed differences in MP linked with these shapes, especially between islands.

Table 5. Results of the three measurements (Fig. 3) used to calculate the force angle (FA) and mechanical potential (MP) on the shapes situated at each extreme of the first three discriminant axes of the canonical variance analysis (CVA) and including all populations (Fig. 5)

Axis	A (pixels)	B (pixels)	C (deg)	FA	MP
Axis1+	250.84	399.45	56.78	33.22	0.145
Axis1-	226.98	406.34	49.38	40.62	0.545
Axis2+	231.22	398.72	59.26	30.74	0.452
Axis2-	258.8	431.26	49.81	40.19	0.477
Axis3+	241.98	413.94	48.57	41.43	0.486
Axis3-	242.2	406.18	57.6	32.4	0.330

These differences in shape are partly related to size differences, as shown by the significant allometric component in geometric morphometrics analyses. Our mechanical model shows that small specimens have the highest MP. This seems intuitively plausible as smaller individuals may need to compensate for their smaller absolute size to utilize the same food resources (Herrel & Gibb, 2006). Moreover, our data show that size effects are strongly associated with the observed differences between populations. Indeed, differences between the mainland and islands are associated with differences in overall size which may be a result of selection for small body size on islands. However, among islands, size does not seem to play the same role in structuring mandibular shape.

Shape variation is also related to island area and distance to the continent, suggesting that this shape variation is probably driven by natural selection rather than by stochastic processes, such as founder effects. Our results show that differences between mainland and insular populations are mainly situated on the ascending branch of the mandible, especially in the articular condyle, the coronoid process and the angular process, which are all important muscular attachment sites. Moreover, the shape of the articular condyle has been suggested to be related directly to mastication (Sarà, 1996). Yet, it is difficult to interpret the form of the condyle in terms of its function (Freeman, 1979) as, in shrews, this articulation has a double articulating surface which permits complex movements (Churchfield, 1990). In addition, the hemi-mandibles are not fused and are able to move independently (Badyaev & Foresman, 2004). Nevertheless, we demonstrate that the observed differences in shape are linked to differences in MP that may, for example, result in differences in bite force. The presence of shrews among algae, and the consumption of crustaceans by shrews on Atlantic islands, may potentially explain this change in mandible form (Rood, 1963; Churchfield, 1988). The lack of data concerning the diet of insular populations of the greater white-toothed shrew prevents more definitive conclusions and requires further investigation to confirm this hypothesis.

Interestingly, the shape differences observed between insular populations are different from those observed between insular and mainland populations and are located in another part of the mandible. The islands of Molène and Groix, in contrast with those of Ré and Oléron, show the strongest differences in mandibular shape and MP. Among them, shrews from Ré and Oléron are phenotypically more similar to mainland populations. The height and width of the mandible (which are greater for specimens from Ré and Oléron) are linked to the size of the masseter muscle, suggesting a potential change in diet that

could be linked to the inclusion of smaller, yet more resistant, prey in the diet. Moreover, these differences in shape produce a marked difference in MP, suggesting the presence of different trophic niches in individuals of these islands. Indeed, MP is dramatically lower in specimens from Molène and Groix, suggesting a specialization on softer or smaller prey (Young *et al.*, 2007).

Interspecific interactions with other small mammals, even other shrews, could also potentially influence the form of the mandible and MP, either directly or indirectly. The high density of potential competitors on islands may thus provide an additional selection pressure on mandibular shape if direct interactions involving biting exist (Poitevin *et al.*, 1987; Dayan & Simberloff, 1998; Lomolino, 2005; Millien *et al.*, 2006; White & Searle, 2007). This is exemplified by the elimination of the black rat, *Rattus rattus*, on some islands (not those included in the present study), which resulted in an explosive expansion of *C. russula* with an increase of up to 30% in population density (Pascal *et al.*, 2008). The role of changes in predation pressure on population density and structure in insular shrew populations remains unclear (Dayan & Simberloff, 1998) and seems to have no direct consequences on insular shrews (White & Searle, 2007). Moreover, no clear correlation was observed between the composition of mammal communities on Atlantic islands and variation in form, except for the presence of the rodent *Microtus agrestis* on Groix (Saint-Girons & Nicolau-Guillaumet, 1987). Yet, direct interactions between voles and shrews have been observed (Chanudet & Saint-Girons, 1966).

CONCLUSION

In this study, we demonstrate that the mandible of *C. russula* on the French Atlantic islands has morpho-functional patterns specific to the islands. The observed differences in shape have functional consequences, and suggest an adaptive change in the mandibular shape of *C. russula* which took place in a rather short time span. These morpho-functional particularities are related to the geographical isolation from the mainland and island area, and are thus potentially driven by differences in food availability and changes in diet on islands.

ACKNOWLEDGEMENTS

We are greatly indebted to S. Moulin, A. Evin, V. Debat, A.-C. Fabre and C. Houssin for reading a preliminary version of this article. We also thank three anonymous reviewers for helpful comments which greatly improved the final version of the article.

REFERENCES

- Adams DC, Rohlf FJ, Slice DE. 2004. Geometric morphometrics: ten years of progress following the 'revolution'. *Italian Journal of Zoology* **71**: 5–16.
- Atchley WR. 1993. *Genetic and developmental aspects of variability in the mammalian mandible*. In: Hanken J, Hall BK, eds. *The skull*. Chicago, IL: University of Chicago Press, 207–247.
- Badyaev AV, Foresman KR. 2004. Evolution of morphological integration. I. Functional units channel stress-induced variation in shrew mandibles. *The American Naturalist* **163**: 868–879.
- Baylac M. 1996. Morphométrie géométrique et systématique. *Biosystema, Systématique et Informatique* **14**: 73–89.
- Baylac M. 2006. *Rmorph: an R geometric and multivariate morphometrics library*. Available from the author: baylac@mnhn.fr.
- Blondel J. 1986. *Biogéographie évolutive*. Paris: Masson.
- Bookstein FL. 1991. *Morphometric tools for landmark data: geometry and biology*. New York: Cambridge University Press.
- Brändli L, Handley LJ, Vogel P, Perrin N. 2005. Evolutionary history of the greater white-toothed shrew (*Crocidura russula*) inferred from analysis of mtDNA, Y, and X chromosome markers. *Molecular Phylogenetics and Evolution* **37**: 832–844.
- Brutto SL, Azeuleo M, Sarà M. 2004. Mitochondrial simple sequence repeats and 12S-rRNA gene reveal two distinct lineages of *Crocidura russula* (Mammalia, Soricidae). *Heredity* **92**: 527–533.
- Chanudet F, Saint-Girons MC. 1966. Combat entre une musaraigne et un campagnol. *Penn Ar Bed* **44**: 175–176.
- Churchfield S. 1988. *Shrews of British Isles*. Shire Natural History 1st edn. Oxford: Shire Publications Ltd.
- Churchfield S. 1990. *The natural history of shrews*. Ithaca, NY: Comstock Publishing.
- Cosson JF, Hutterer R, Libois R, Sarà M, Taberlet P, Vogel P. 2005. Phylogeographical footprints of the Strait of Gibraltar and Quaternary climatic fluctuations in the western Mediterranean: a case study with the greater white-toothed shrew, *Crocidura russula* (Mammalia: Soricidae). *Molecular Ecology* **14**: 1151–1162.
- Cosson JF, Pascal M, Bioret F. 1996. Origine et répartition des musaraignes du genre *Crocidura* dans les îles bretonnes. *Vie et Milieu* **46**: 233–244.
- Darwin CR. 1845. *Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world*, 2nd edn. London: John Murray.
- Dayan T, Simberloff D. 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review* **28**: 99–124.
- Foster JB. 1964. Evolution of mammals on islands. *Nature* **202**: 234–235.
- Freeman PW. 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats. *Journal of Mammalogy* **60**: 467–479.
- Heim de Balsac H. 1940. Faune mammalienne des îles littorales atlantiques. *Comptes Rendus de l'Académie des Sciences* **3**: 212–214.
- Herrel A, Gibb AC. 2006. Ontogeny of performance in vertebrates. *Physiological and Biochemical Zoology* **79**: 1–6.
- Jeanmaire-Besançon F. 1986. Estimation de l'âge et de la longévité chez *Crocidura russula* (Insectivora, Soricidae). *Acta Oecologica* **7**: 355–366.
- Lomolino MV. 1985. Body size of mammals on islands: the island rule re-examined. *The American Naturalist* **125**: 310–316.
- Lomolino MV. 2005. Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography* **32**: 1683–1699.
- Losos JB, Schoener TW, Spiller DA. 2004. Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature* **432**: 505–508.
- Losos JB, Warheit KI, Schoener TW. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* **387**: 70–73.
- Millien V, Lyons SK, Olson L, Smith FA, Wilson AB, Yom-Tov Y. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters* **9**: 853–869.
- Monteiro L. 1999. Multivariate regression models and geometric: the search for causal factors in the analysis of shape. *Systematic Biology* **48**: 192–199.
- Mosimann JE. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *Journal of the American Statistical Association* **65**: 930–948.
- Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**: 289–290.
- Pascal M, Siorat F, Lorvelec O, Yésou P, Simberloff D. 2008. A pleasing consequence of Norway rat eradication: two shrew species recover. *Diversity and Distributions* **11**: 193–198.
- Poitevin F, Catalan J, Fons R, Croset H. 1986. Biologie évolutive des populations ouest-européennes de Crocidures. I-Critères d'identification et répartition biogéographique de *Crocidura russula* (Hermann, 1780) et *Crocidura suaveolens* (Pallas, 1811). *Revue d'Ecologie (Terre Vie)* **41**: 299–314.
- Poitevin F, Catalan J, Fons R, Croset H. 1987. Biologie évolutive des populations ouest-européennes de Crocidures (Mammalia, Insectivora). II-Ecologie comparée de *Crocidura russula* Hermann, 1780 et de *Crocidura suaveolens* Pallas, 1811 dans le midi de la France et en Corse: rôle probable de la compétition dans le partage des milieux. *Revue d'Ecologie (Terre Vie)* **42**: 39–58.
- R Development Core Team. 2009. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing, ISBN 3-900051-07-0. Available at: <http://www.R-project.org>

- Renaud S, Alibert P, Auffray JC. 2009.** Mandible shape in hybrid mice. *Die Naturwissenschaften* **96**: 1043–1050.
- Renaud S, Auffray JC, De la Porte S. 2010.** Epigenetic effects on the mouse mandible: common features and discrepancies in remodeling due to muscular dystrophy and response to food consistency. *BMC Evolutionary Biology* **10**: 28.
- Rohlf FJ, Slice DE. 1990.** Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* **39**: 40–59.
- Rood JP. 1963.** Ecological studies on the small mammals of the Isles of Scilly. PhD Thesis, Southampton University.
- Saint-Girons MC, Fons R, Nicolau-Guillaumet P. 1979.** Caractères distinctifs de *Crocidura russula*, *Crocidura leucodon* et *Crocidura suaveolens* en France continentale. *Mammalia* **43**: 511–518.
- Saint-Girons MC, Nicolau-Guillaumet P. 1987.** Les phénomènes d'insularité dans les îles du Ponant (France). Mammifères et Oiseaux. *Bulletin de la Société Zoologique de France* **112**: 61–79.
- Sarà M. 1996.** A landmark-based morphometrics approach to the systematics of Crocidurinae: case study on endemic shrews *Crocidura sicula* and *C. canariensis* (Soricidae, Mammalia). In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE, eds. *Advances in morphometrics NATO science series A: life sciences* 284. Hamburg, Germany: Springer Verlag, 335–344.
- Slice DE. 2007.** Geometric morphometrics. *Annual Review of Anthropology* **36**: 261–281.
- Van Valen L. 1973.** Pattern and the balance of nature. *Evolutionary Theory* **1**: 31–49.
- Venables WN, Ripley BD. 2002.** *Modern applied statistics with S*, 4th edn. New York: Springer-Verlag.
- Wallace J. 1860.** On the zoological geography of the Malay archipelago. *Zoological Journal of the Linnean Society* **4**: 172–184.
- White TA, Searle JB. 2007.** Factors explaining increased body size in common shrews (*Sorex araneus*) on Scottish islands. *Journal of Biogeography* **34**: 356–363.
- Whittaker RJ. 1998.** *Island biogeography: ecology, evolution and conservation*. Oxford: Oxford University Press, 285.
- Wilson DE, Reeder DM. 2005.** *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn. Baltimore, MD: Johns Hopkins University Press.
- Young RL, Haselkorn TS, Badyaev AV. 2007.** Functional equivalence of morphologies enables morphological and ecological diversity. *Evolution* **61**: 2480–2492.
- Young RL, Sweeney MJ, Badyaev AV. 2010.** Morphological diversity and ecological similarity: versatility of muscular and skeletal morphologies enables ecological convergence in shrews. *Functional Ecology* **24**: 556–565.