# Does bite force provide a competitive advantage in shrews? The case of the greater white-toothed shrew

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Competition for resources has long been considered a major driver of evolution by natural selection. Thus, the ability to gain access to resources not available to other individuals and species should be under strong selection. In the present study, we focus on the potential role of biting in a shrew (*Crocidura russula*) because this trait may confer two advantages: (1) a broadening of the dietary niche and (2) the provision of direct superiority in interspecific interactions. The model chosen is the greater white-toothed shrew, which is considered as invasive in northern Europe and which is also known to displace native species of shrew in this area. Moreover, its distribution appears to constrain the distributional ranges of other species of shrew in the Maghreb. We use geometric morphometrics and a simple biomechanical model to describe shape variation and to evaluate the mechanical potential of the mandible of ten species of white-toothed shrews, with a special emphasis on *C. russula* and *Crocidura suaveolens*. We find that *C. russula* possesses an intermediate mechanical potential linked with an intermediate level of shape variability. Our results suggest that the higher mechanical potential may explain the observed pattern of colonization of the Atlantic islands by *C. russula* at the expense of *C. suaveolens*. Finally, our results also suggest that the ability to bite hard may be under strong selection in shrews. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **114**, 795–807.

ADDITIONAL KEYWORDS: Crocidura – feeding system – islands – mammals – mechanical potential – shape.

## INTRODUCTION

One of the hallmarks of evolution by natural selection is the idea that species compete for resources (Darwin, 1859). Indeed, competition for resources has been considered as an important factor driving the evolution of many phenotypic traits, ranging from morphology over function to life history (Lack, 1947; Losos, 1990; Pekkonen, Ketola & Laakso, 2013; Wilson, 2014). The consequences of competition for resources are apparent at the species level, with character displacement resulting when species with similar ecological requirements come into contact with one another (Lack, 1947; Losos, 1990; Schluter & McPhail, 1992; Adams, 2010). Given the importance

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of competition, any trait allowing the exploitation of different, novel or otherwise not exploitable resources will be under strong selection. The ability to bite hard, allowing an animal to capture and reduce food, may be an important trait in this context (Herrel, Vanhooydonck & Van Damme, 2004; Herrel *et al*., 2005, 2008). Moreover, biting is relevant in an interspecific context and may determine the outcome of direct aggressive interactions (Downes & Bauwens, 2002).

The mechanical potential (MP) of the feeding apparatus is directly related to biting ability and, as such, also to food intake and the ability to interact with other individuals or species (Herrel *et al*., 1999, 2001; Lailvaux *et al*., 2004). The ability to capture and reduce prey has direct consequences on diet and is strongly dependent on the morphology of a species (Ferry-Graham, Bolnick & Wainwright, 2002). A high bite force capacity thus likely offers a selective advantage (Christiansen & Wroe, 2007; Anderson, McBrayer & Herrel, 2008). Linking the differences in bite force with the geographical range of a species would be of interest because it may illustrate pathways allowing one species to become competitively superior over another.

The model chosen for the present study is the greater white-toothed shrew, *Crocidura russula* (Fig. 1). This species has a long record of expansion and an anthropophilous behaviour (Churchfield, 1990), which is the cause of its accidental introduction into many insular territories. As such, this species represents an excellent case when studying the role of the mechanical potential for biting in competitive interactions. In France, the current range of this small insectivorous species is the result of a natural expansion from Southern Europe coupled to human-mediated transport (Pascal, Lorvelec & Vigne, 2006). It arrived in France relatively recently (approximately 6000 years ago) from the Iberian Peninsula (Poitevin *et al*., 1986). Phylogeographical studies based on cytochrome *b* analyses suggest an origin in Morocco, from where it would have crossed the Gibraltar strait approximately 60 000 years ago (Cosson *et al*., 2005). The colonization of Europe likely took place by a limited number of individuals, as suggested by the remarkable genetic and morphological homogeneity of this species across its distributional range. Its current northern distribution lies in the north of Germany. It is also found on many Mediterranean and Atlantic Islands where it is considered to have arrived recently (Poitevin *et al*., 1986; Vigne & Marinval-Vigne, 1990; Cosson, Pascal & Bioret, 1996). The most recent phenomenon of colonization concerns Ireland (Tosh *et al*., 2008) where *C. russula* has become established over the past 10 years to the detriment of the native species *Sorex minutus* (McDevitt *et al*., 2014), suggesting the competitive superiority of *C. russula*.
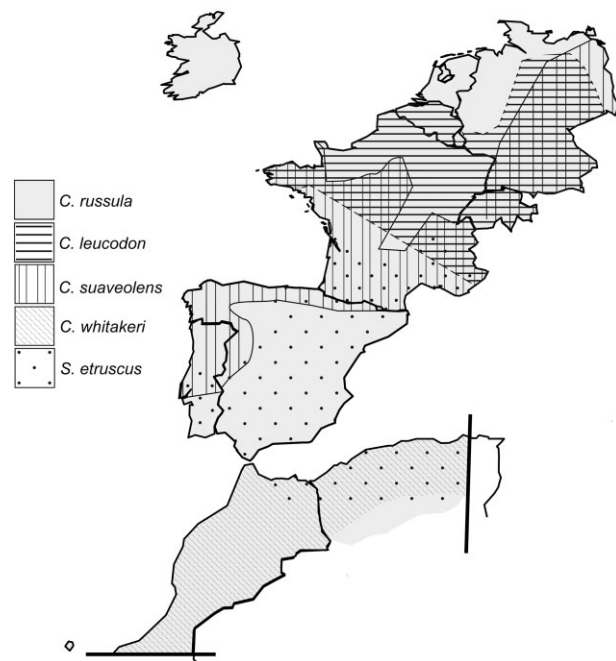
In Europe, there are two other sympatric white-toothed shrews: the bicoloured shrew *Crocidura leucodon* and the lesser white-toothed shrew *Crocidura suaveolens*. In the Maghreb, four species, the Mauritanian shrew *Crocidura lusitania*, the Saharan shrew *Crocidura tarfayensis*, the savanna path shrew *Crocidura viaria*, and the Whitaker's shrew *Crocidura whitakeri* (Wilson & Reeder, 2005),
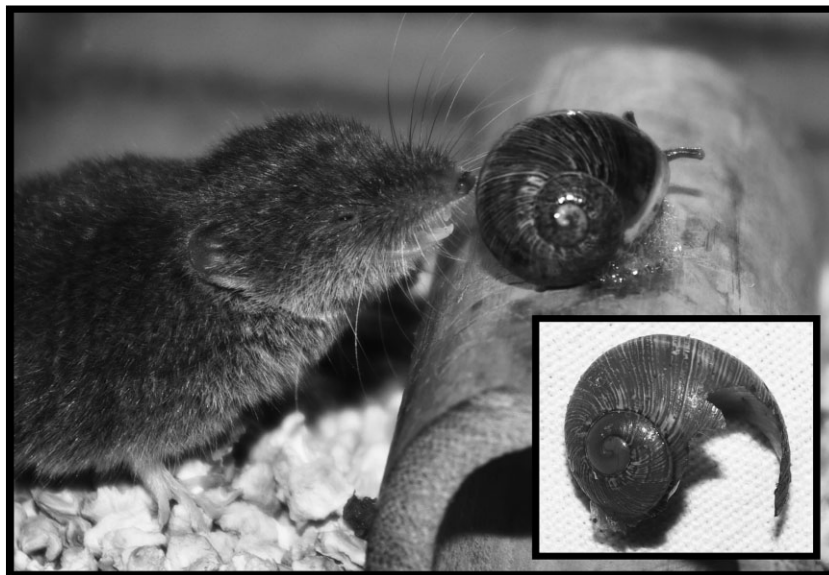


**Figure 1.** A greater white-toothed shrew, *Crocidura russula*, eating a snail. In detail: the shell of the snail after consumption showing tooth marks.

co-occur with *C. russula*. Interactions of *C. russula* with these other species appear to be largely in favour of the former. The competitive superiority of *C. russula* can be illustrated by the fact that, on the Atlantic islands, it replaces the native *C. suaveolens* each time that it is introduced to an island (Cosson *et al.*, 1996). An example of a recent replacement has been observed on the island of Sein where only *C. suaveolens* was captured in the sixties and where *C. russula* is the only species present today, as shown by extensive trapping performed in the 1990s (Pascal *et al.*, 2006). Two others examples are provided by the displacement of *C. leucodon* by *C. russula* in Switzerland over the past 20 years (Vogel *et al.*, 2002) and by the decrease in abundance of the local shrew, *S. minutus*, in Ireland in favour of the expanding *C. russula* (McDevitt *et al.*, 2014). The current distributional ranges of the white-toothed shrew in the Maghreb highlight a geographical segregation of *C. russula* and other shrew species, supporting the idea that *C. russula* may be competitively superior and capable of excluding or limiting others shrew species as competitors (Fig. 2).

The present study aimed to evaluate the mechanical potential of the greater white-toothed shrew and nine other species of shrews with which it is sympatric or in contact (currently or historically). We use geometric morphometric approaches to accurately describe the form of the mandible, and then apply a biomechanical model that permits the calculation of the mechanical potential for each specimen, species, and population. We also evaluate the shape variability of each species to investigate its links with the calculated mechanical potential. Moreover, we explore functional relationships between mechanical potential and mandible shape using different populations of greater and lesser white-toothed shrews in insular and continental contexts (Vitousek, 1988; Fritts & Rodda, 1998; Mooney & Cleland, 2001). If the ability to bite hard plays a role in the superior competitive ability of *C. russula*, then it should have a greater mechanical potential compared to other species and populations with which it is in contact.
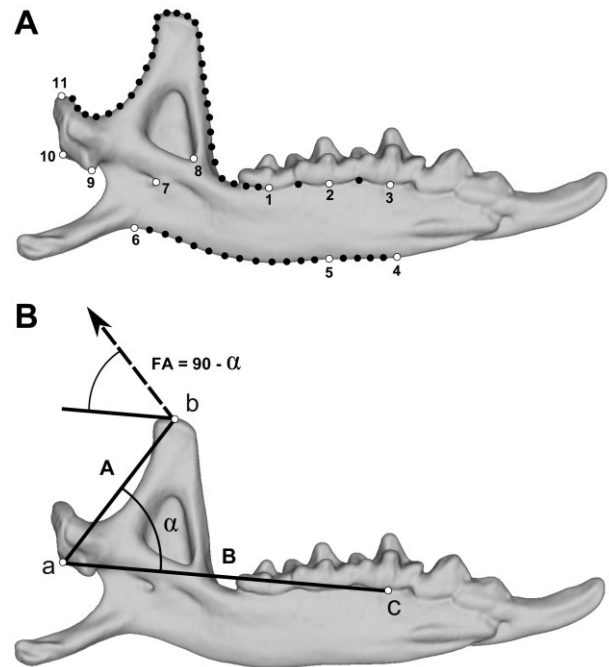
## MATERIAL AND METHODS

To allow a quantitative comparison, 372 mandibles of ten species of shrews were measured, as summarized in Table 1. The specimens are deposited in the following collections: Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFAKB), Department of Ecology and Evolution of the University of Lausanne (DEEUL), the University of Barcelona (UB), Agrocampus ESE of Rennes (AESE), and the Museum National d'Histoire Naturelle (MNHN), Paris (for details, see Supporting information, Table S1). They represent the great majority of species of white-toothed shrews found in Europe and the Maghreb (10 out of 12; Wilson & Reeder, 2005), with the exception of two insular species: *Crocidura zimmermanni* and *Crocidura canariensis*. Among these species, *C. russula* is directly sympatric with *C. suaveolens*, *C. leucodon*, and *Suncus etruscus* in Europe, and with *C. whitakeri* and *S. etruscus* in the Maghreb. Contact zones at the periphery of its distributions exist between *C. russula*, *C. ichnusae*, *C. lusitania*, and *C. viaria* in the Maghreb (Aulagnier, 1987) or have existed as with *C. tarfayensis* (Cornette, 2012). A special emphasis was placed on the relationships between *C. russula* and *C. suaveolens*. Both species were sampled throughout their continental ranges, as well as on the Atlantic and Mediterranean islands where they occur. This allowed the characterization of the morphological variability of these two species and the investigation of their interspecific relationships on islands.

Each hemi-mandible was photographed using a Leica macroscope Z6 (× 0.5 objective, zoom × 2) coupled to a Leica digital camera (6 mega pixels). Sixty anatomical landmarks and sliding-landmarks were digitized using TPSDIG2 (Rohlf, 2010a).



**Figure 2.** Geographical range of *Crocidura russula* in grey and its overlap with the distribution of other white-toothed shrews. Black lines in Maghreb mark the eastern and southern limits of this distribution and represent the contact zones with *Crocidura ichnusae* and *Crocidura viaria*, as well as *Crocidura lusitania* and *Crocidura tarfayensis*, respectively.

**Table 1.** The origin and number of specimens used for the different species

| | | Origin | Number of specimens |
|---|---|---|---|
| *Crocidura russula* | Continental | | |
| | | Germany | 4 |
| | | France | 14 |
| | | Morocco | 32 |
| | | Portugal | 12 |
| | | Spain | 37 |
| | Insular | | |
| | | Ireland | 24 |
| | | Groix | 3 |
| | | Belle-île | 5 |
| | | Ile de Ré | 4 |
| | | Molène | 3 |
| | | Noirmoutiers | 3 |
| | | Oléron | 1 |
| | | Tomé | 5 |
| | | Ibiza | 4 |
| | | Osorio | 1 |
| *Crocidura suaveolens* | Continental | | |
| | | Bulgaria | 2 |
| | | Spain | 4 |
| | | Italy | 4 |
| | | France | 4 |
| | Insular | | |
| | | Litiri | 31 |
| | | Ouessant | 3 |
| | | Banneg | 22 |
| | | Corse | 4 |
| | | Corse Arch | 27 |
| *Crocidura leucodon* | Continental | | |
| | | France | 2 |
| | | Italy | 3 |
| | | Bulgaria | 6 |
| | Insular | | |
| | | Lesbos | 3 |
| *Crocidura ichnusae* | Continental | | |
| | | Tunisia | 4 |
| | Insular | | |
| | | Sardinia | 4 |
| *Crocidura sicula* | Insular | Sicily | 8 |
| *Crocidura lusitania* | Continental | Morocco | 26 |
| *Crocidura tarfayensis* | Continental | Morocco | 9 |
| *Crocidura viaria* | Continental | Morocco/ Senegal | 32 |
| *Crocidura whitakeri* | Continental | Morocco | 5 |
| *Suncus etruscus* | Insular | | |
| | | Sicily | 7 |
| | Continental | | |
| | | Morocco | 11 |



**Figure 3.** A, anatomical localization of landmarks (white circles) and sliding-landmarks (black circles) used to describe shape variation. B, biomechanical model showing the three measurements permitting calculation of the mechanical potential (MP): MP = $A/B$ cosine (FA).

**Table 2.** Definitions and anatomical location of landmarks

1 Intersection of the mandible and the middle of the third molar
2 Intersection of the mandible and the middle of the second molar
3 Intersection of the mandible and the middle of the first molar
4 Maximum of curvature anterior to point 5
5 Inflexion point of the mandibular body
6 Inflexion point between the angular process and the mandibular body
7 Posterior part of the mandibular foramen
8 Anterior-most corner of the coronoid fossa
9, 10, 11 Posterior-most, dorsal and ventral sides of the articular condyle

Eleven anatomical landmarks were selected (Fig. 3A; Table 2) in addition to forty-nine sliding landmarks to optimize the shape description for areas without anatomical landmarks but strong biological relevance (Bookstein, 1996; Gunz, Mitteroecker & Bookstein, 2005; Cornette, 2012; Cornette *et al*., 2013). These areas such as the coronoid process or the articular condyle not only possess species-specific, but also functional information and are therefore of interest (Cornette *et al*., 2012, 2013). The sliding step was performed with TPSRELW (Rohlf, 2010b) at the same time as minimizing the Procrustes distances (Perez, Bernal & Gonzalez, 2006; Gunz & Mitteroecker, 2013), which has been shown to be more efficient in

morphological discrimination studies (Sheets *et al.*, 2006). Sliding-landmarks are allowed to slide to minimize shape differences between each specimen and the average shape in the whole sample (Gunz & Mitteroecker, 2013). After this step, all sliding-landmarks and anatomical landmarks are rendered geometrically homologous and can be treated in the same manner.

Each species was studied separately to calculate the MP and pooled to calculate the respective shape variability of each species. General Procrustes analyses (Rohlf & Slice, 1990) and principal component analyses (PCA) were performed on each of these data sets (i.e. species separately and combined). The PCA performed on all species pooled allows us to evaluate the major axis of shape variation and to calculate the shape variance of each species. PCAs performed for each species separately allowed us to visualize shape variation on axes via multivariate regressions (Monteiro, 1999) and to export the coordinates of the extreme shapes along the first axis to calculate the MP for these extremes (Cornette *et al.*, 2012).

The MP was calculated in accordance with a method developed by Carraway *et al.* (1996; see also Young, Haselkorn & Badyaev, 2007; Cornette *et al.*, 2012; Fig. 3B). This index provides an approximation of the force that can be generated by the temporalis muscle during biting (the temporalis muscle being the largest jaw closer muscle in shrews). Knowing that: MP = *A/B* cosine [force angle (FA)] and FA = 90 − α, we applied the formula:

$$C_2 = A^2 + B^2 - 2AB\cos\alpha$$

with

$$A^2 = \sqrt{[(xb^2 - xa^2)(yb^2 - ya^2)]}$$

$$B^2 = \sqrt{[(xc^2 - xa^2)(yc^2 - ya^2)]}$$

$$C^2 = \sqrt{[(xc^2 - xb^2)(yc^2 - yb^2)]}$$

Thus, we obtain α to calculate the MP value using the formula:

$$\alpha = \arccos[(A^2 + B^2 - C^2)/2AB]$$

We calculated the MP not only for each specimen, but also for the extreme configurations of the first PC axis for each species (Fig. 4). Next, we retained the highest MP for each species along the first axis and considered this as an index of performance for each species. To evaluate the influence of size on MP, we regressed the log-transformed centroid size on log-transformed MP. We also performed regressions of size and MP on shape to quantify and visualize their relationships (Monteiro, 1999).

This same approach was taken for *C. russula* and *C. suaveolens* at the population level and MP was calculated separately for each population. Box-plots were generated for the population-level MP, grouping insular, and continental populations for these two species to visualize and compare the effects of insularity and species. To investigate population shape variability, a global PCA including all individuals
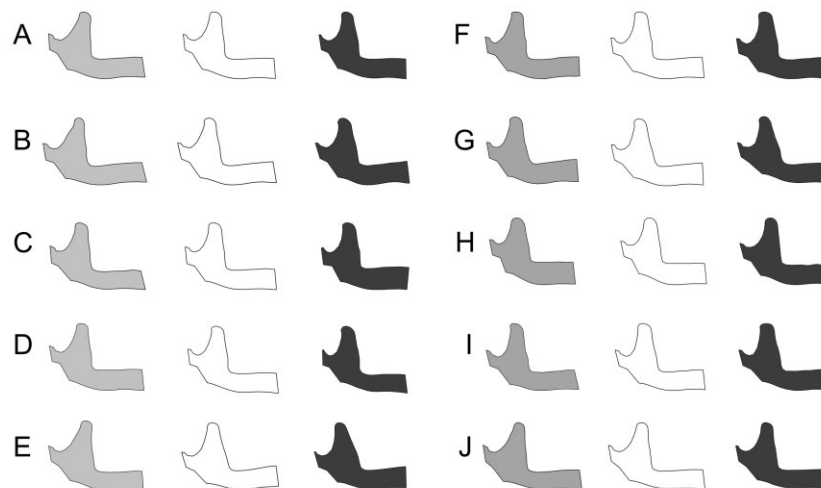


**Figure 4.** Mandible shape variation along the first principal component axis for each species. The consensus shape is illustrated in white; the shape producing the lowest mechanical potential (MP) in pale grey, and the shape producing the highest MP in dark grey. A, *Crocidura russula*. B, *Crocidura suaveolens*. C, *Crocidura leucodon*. D, *Crocidura ichnusae/*. E, *Crocidura lusitania*. F, *Crocidura sicula*. G, *Crocidura tarfayensis*. H, *Crocidura viaria*. I, *Crocidura whitakeri*. J, *Crocidura etruscus*. Shapes indicated in dark grey were been used to calculate the MP.

allowed us to reduce the dimensionality of the data set (Baylac & Frieß, 2005) at the same time as maintaining 90% of the total variability. We then used this to calculate a Neighbour-joining tree using Mahalanobis distances between populations. In this context, islands were considered as discrete populations. For continental individuals, we considered Continental Europe as a single population for both *C. russula* and *C. suaveolens*. Moreover, Moroccan individuals of *C. russula* were considered as a separate population.

All the morphometric and statistical analyses were performed using R (R Development Core Team, 2012), using the libraries 'ape' (Paradis, Claude & Strimmer, 2004), 'plotrix' (Lemon, 2006), and 'Rmorph' (Baylac, 2012).

## RESULTS

### INTERSPECIFIC ANALYSIS

An analysis of the shape variation in each species (Fig. 4) illustrates four main results: (1) the bodies of mandibles vary slightly in their relative length, curvature and robustness; (2) the coronoid processes varies widely in form and orientation; (3) these differences in shape occur both within and between species; and (4) the shape of the mandible associated with the strongest MP ($P < 0.05$, $R^2 = 0.94$) is characterized by the shortest and most robust body, the highest mandibular branch, and the greatest angle 'α' (Fig. 5A). This shape is, however, different from the shape associated with size ($P < 0.05$, $R^2 = 0.54$), especially with respect to the coronoid process (Fig. 5B).

Concerning the results of MP on first PC axis for each species, *C. russula* is ranked only just higher than *C. suaveolens* and *S. etruscus* (Fig. 6; Table 3). The highest MP is obtained for *C. viaria* and *C. whitakeri*. Given that the overall regression between size and MP is significant ($P < 0.05$, $R^2 = 0.08$), their large size may partly explain why these species also have the highest MP. However, when considering the single highest MP observed within a species (Fig. 7), *C. russula* is ranked fifth.

The variance of each species was calculated (Fig. 8; Table 3) and *C. russula* showed an average level of variance. The most variable species are *C. lusitania*, *C. leucodon*, and *C. suaveolens*, and the least variable ones in our data set are *S. etruscus*, *C. viaria*, and *C. ichnusae*. When examining both MP and variance (Figs 7, 8), the intermediate position of *C. russula* can be contrasted with the higher variance of the sympatric European species *C. suaveolens* and *C. leucodon*. Similarly, *C. lusitania* and *C. tarfayensis*, which are (or were) both in contact with *C. russula* in the Maghreb, show a higher shape variance. Two
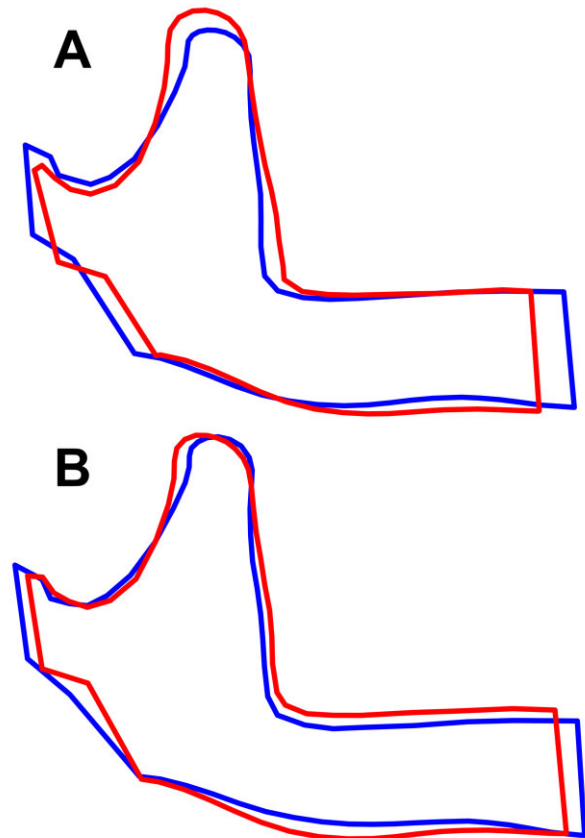


**Figure 5.** The shape changes associated with mechanical potential (MP) (A) and size (B). Red outlines represent the shape associated with highest MP and the largest specimens and blue outlines the lowest MP and small specimens.

exceptions concern the two sympatric species *S. etruscus* and *C. whitakeri*, which possess a lower variance. Moreover, *C. ichnusae* in contact with *C. russula* in Algeria also possesses a lower shape variance.

### POPULATION LEVEL ANALYSIS

The global shape analysis summarized in the Neighbour-joining tree offers a remarkable specific and geographical consistency (Fig. 9). When comparing the MP of insular and continental populations for each species (Fig. 10), it becomes clear that the MP of continental populations is markedly higher than that of insular ones for *C. russula* but does not differ for *C. suaveolens*. When considering insular populations only, *C. suaveolens* shows a marginally higher average MP, although this remains within the range of *C. russula*.
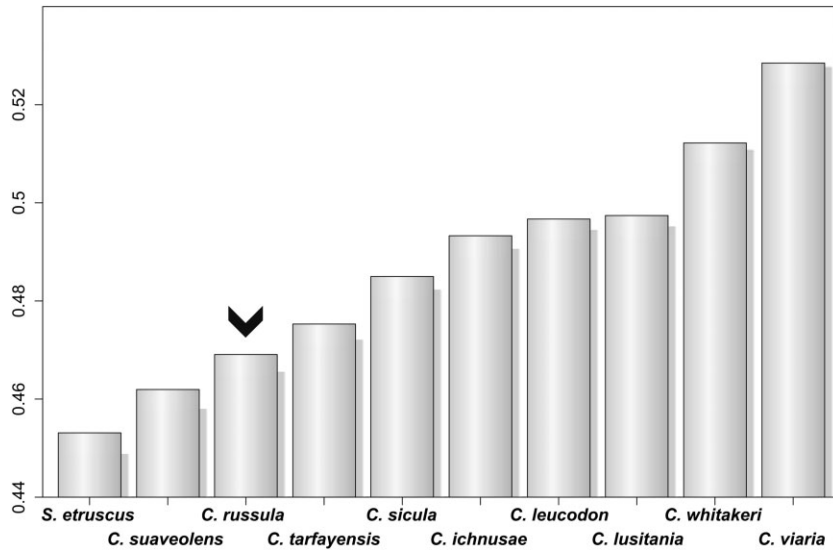
**Figure 6.** The highest mechanical potential (MP) on the first principal component axis for each species. The arrowhead indicates *Crocidura russula*.

**Table 3.** Table summarizing the mechanical potential (MP) on the first principal component axis, the maximum MP observed by species, and the shape variance for each species

| Species | MP on the first axis | Maximum MP | Variance |
|---|---|---|---|
| *Suncus etruscus* | 0.453 | 0.474 | $7.84 \times 10^{-5}$ |
| *Crocidura viaria* | 0.528 | 0.542 | $9.79 \times 10^{-5}$ |
| *Crocidura ichnusae* | 0.493 | 0.491 | $1.03 \times 10^{-4}$ |
| *Crocidura whitakeri* | 0.512 | 0.519 | $1.15 \times 10^{-4}$ |
| *Crocidura sícula* | 0.485 | 0.488 | $1.17 \times 10^{-4}$ |
| *Crocidura russula* | 0.469 | 0.494 | $1.41 \times 10^{-4}$ |
| *Crocidura tarfayensis* | 0.475 | 0.486 | $1.42 \times 10^{-4}$ |
| *Crocidura suaveolens* | 0.461 | 0.484 | $1.50 \times 10^{-4}$ |
| *Crocidura leucodon* | 0.494 | 0.494 | $1.62 \times 10^{-4}$ |
| *Crocidura lusitania* | 0.497 | 0.519 | $2.24 \times 10^{-4}$ |

## DISCUSSION

### SHAPE VARIABILITY

*Crocidura russula* is considered to be both genetically and morphologically stable throughout its range. This feature has been suggested to be the result of the small number of individuals that colonized Western Europe after crossing the Strait of Gibraltar to the Iberian Peninsula (Cosson *et al.*, 2005). The northern front of this colonization is currently located in the north of Germany, although a new colonization front has recently been established in Ireland (Tosh *et al.*, 2008; McDevitt *et al.*, 2014). One consequence of this uniform morphology is that the number of subspecies described for *C. russula* (17) is low compared to *C. suaveolens* (33) (Wilson & Reeder, 2005). The latter species, in contrast, is considered to be morphologically variable (Dubey *et al.*, 2006). However, the accuracy of geometric morphometric techniques allows us to highlight significant morphological differences among different species of white-toothed shrews, including those considered to be not very variable. Moreover, we also show that different populations of *C. russula* are well identified and classified, showing population-specific shapes. This is of interest in an insular context where *C. russula* and *C. suaveolens* are frequently misidentified based on morphology (Poitevin *et al.*, 1986; Dubey *et al.*, 2006). We also demonstrate that *C. russula* is intermediate in shape variability on the major axis of shape variation compared to the other species examined. In addition, we find that some of its direct competitors have a greater morphological variability. Interestingly, this morphological variability does not appear to have direct selective advantages because *C. russula* appears to be dominant in the majority of cases of interspecific competition. Moreover, the observed variability in shape in other species does not systematically produce a higher mechanical potential. By contrast, the morphological stability provides *C. russula* with a possible advantage because it allows this species to preserve the capacity to produce specimens with high mechanical potential. Thus, stabilizing selection on this trait may have occurred and subsequently resulted in the maintenance of the overall shape of the mandible of *C. russula*, maintaining its competitive advantage over closely-related species with similar ecologies.

A



B
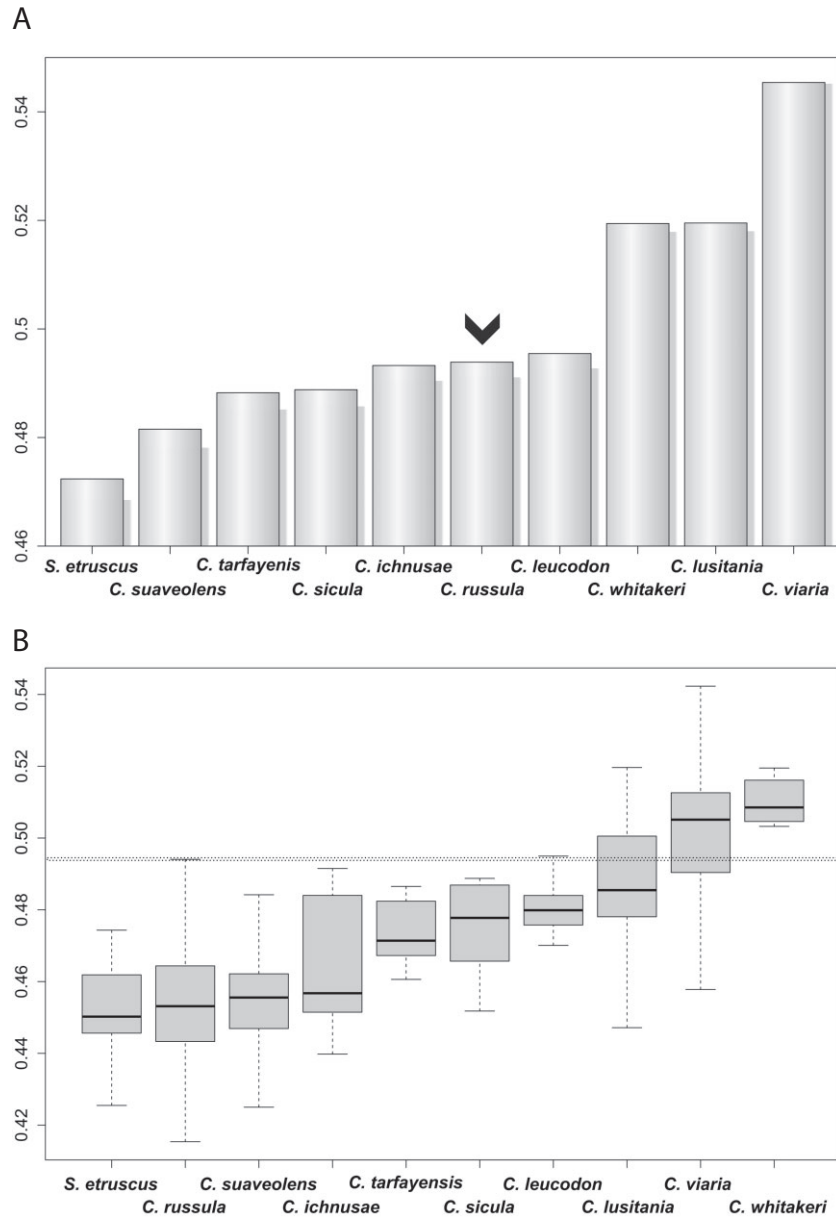


**Figure 7.** A, the single highest mechanical potential (MP) by species. The arrowhead indicates *Crocidura russula*. B, boxplot illustrating the mean MP by species. *Crocidura russula* shows a rather low mean mechanical potential but contains individuals that have a relatively high mechanical potential (black line).

MECHANICAL POTENTIAL

The greater white-toothed shrew presents a medium potential to generate bite force compared to other species in our data set. In this context, it is ranked fifth among species when considering the highest MP observed within a species. This ability offers directly, or indirectly, two selective advantages compared to other white-toothed shrews at contact zones or in sympatry. First, a high mechanical potential is commonly associated with the ability to eat harder or larger prey (Young *et al*., 2007), suggesting a distinct selective advantage. Indeed, this may allow *C. russula* to occupy an otherwise empty niche, or to shift its niche to one that is previously unexploited. Our calculation of mechanical potential focuses principally on the temporalis muscle, which is the biggest jaw adductor muscle in shrews (Gasc, 1963; Cornette, 2012; Cornette *et al*., 2013). Because the temporalis muscle is optimally situated to generate high bite force at wide gape, this likely provides a specific
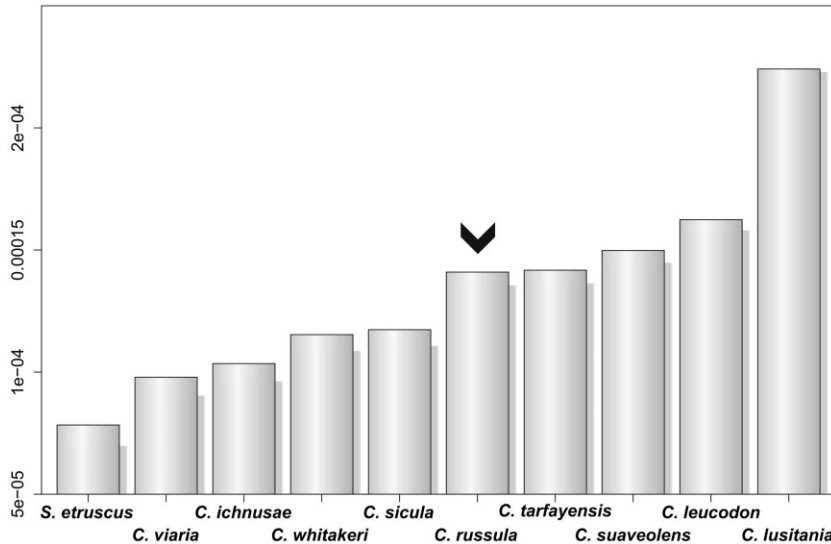
**Figure 8.** The shape variance of the mandible on the first principal component axis for each species.
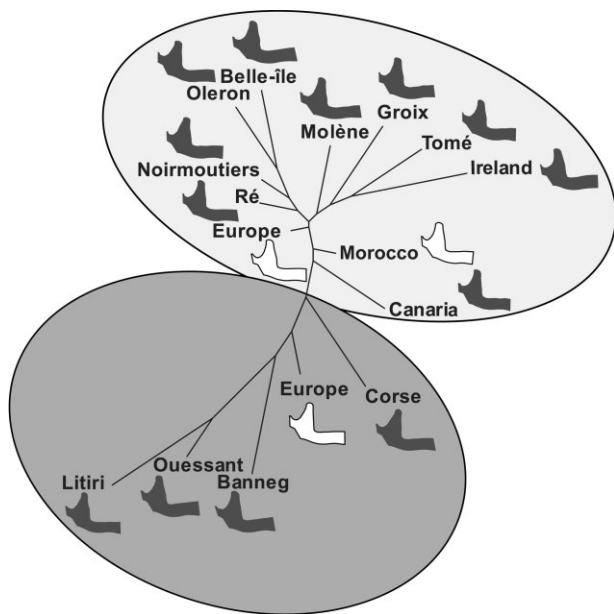


**Figure 9.** Neighbour-joining tree constructed using the Mahalanobis distances of the principal component analysis explaining 90% of the overall variability in shape. The different populations of *Crocidura russula* (pale grey ellipses) and *Crocidura suaveolens* (dark grey ellipses) are shown. In addition, the mandibular shape producing the highest mechanical potential on the first principal component axis is mapped for each population (white for continental populations; dark grey for insular populations).

advantage in the consumption of large and hard prey. The present study demonstrates that the greater white-toothed shrew is, at least in some cases, theoretically able to exploit a wider ecological niche than

its competitors (e.g. *C. suaveolens* or *C. tarfayensis*). *Crocidura russula* is known to be a generalist predator that is able to eat a wide variety of prey (Churchfield, 1990) from collembolla to snails (Fig. 1) and even small vertebrates, such as lizards or small mammals (Churchfield, 1990). Being able to bite hard might thus explain, at least partly, the wide choice of prey and its success in consuming novel prey during colonization events.

Second, shrews are known to be territorial and aggressive, and are known to fight and bite each other in competitive interactions, both within and between species (Churchfield, 1990; Kirkland, 1991; Zuri & Rado, 2000). Thus, direct interspecific aggression, especially among different shrew species, may play an important role in structuring ecological niches (Churchfield, 1991). Most of the time, *C. russula* appears to be the winner in competitive interactions with other shrews (McDevitt *et al.*, 2014) and our results suggest that, in some cases, its high bite force potential could explain a part of this competitive superiority. Moreover, the two beneficial consequences linked to a high bite force (diet and interspecific aggression) are cumulative and clearly in favour of *C. russula* compared to *C. suaveolens*, for example. Direct consequences of this interspecific competition can be seen in the insular distribution patterns of the greater white-toothed shrew.

In the Maghreb, the eastern and meridional zones of its distribution form the northern and western limits of the distribution of *C. viaria*, *C. lusitania*, *C. tarfayensis*, and *C. ichnusae*. In this zone, *C. russula* is not considered as an invasive species but appears to limit the expansion of other white-toothed shrews and *vice versa*. The sympatric species *C. whitakeri*
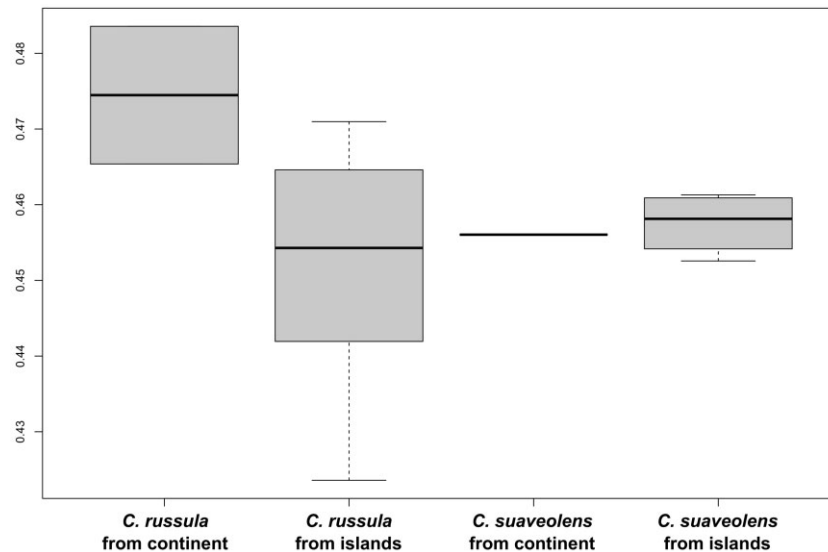
**Figure 10.** Boxplot illustrating the variation in mechanical potential (MP) of continental and insular populations for both *Crocidura russula* and *Crocidura suaveolens*. Note that all individuals of Continental Europe were considered as a single population for both *C. russula* and *C. suaveolens*.

**Table 4.** Summary table describing the mechanical potential (MP) on the first principal component axis for the different populations of *Crocidura russula* and *Crocidura suaveolens* sampled

| Species | Population | Origins | MP |
| --- | --- | --- | --- |
| *Crocidura russula* | Osorio | insular | 0.469 |
| *Crocidura russula* | Groix | insular | 0.464 |
| *Crocidura russula* | Belle-Île | insular | 0.441 |
| *Crocidura russula* | Oléron | insular | 0.423 |
| *Crocidura russula* | Ré | insular | 0.454 |
| *Crocidura russula* | Noirmoutiers | insular | 0.454 |
| *Crocidura suaveolens* | Corse | insular | 0.455 |
| *Crocidura suaveolens* | Banneg | insular | 0.460 |
| *Crocidura suaveolens* | Litiri | insular | 0.461 |
| *Crocidura russula* | Europe | continental | 0.465 |
| *Crocidura russula* | Molène | insular | 0.447 |
| *Crocidura suaveolens* | Ouessant | insular | 0.452 |
| *Crocidura russula* | Irlande | insular | 0.470 |
| *Crocidura suaveolens* | Europe | continental | 0.456 |
| *Crocidura russula* | Tomé | insular | 0.439 |
| *Crocidura russula* | Maroc | continental | 0.483 |

which is the most directly in competition with *C. russula*, is very rare, as has been demonstrated by recent field work in Morocco (C. Denys, pers. comm.). Interestingly, Moroccan populations of *C. russula* possess the highest MP score of all populations (Table 4). In Europe, the two sympatric species, *C. suaveolens* and *C. leucodon*, possess a lower and a higher MP, respectively, compared to *C. russula*, which might explain the outcome of competitive interactions with the lesser white-toothed shrew (*C. suaveolens*). Indeed, if *C. russula* crossed the strait of Gibraltar from Morocco with a relatively high mechanical potential, then it would have been directly competitively superior to other species present in South-Western Europe, such as *C. suaveolens* and *S. etruscus*.

### ISLAND COLONIZATION

When examining the relationships between the greater and the lesser white-toothed shrew, our work suggests a potential explanatory framework for the invasive success of *C. russula* and, together with pre-existing data of diverse sources (molecular and zooarchaeological), it offers a potential scenario of its invasion in France and, more precisely, on the French Atlantic islands: (1) few specimens arrived in the Iberian peninsula from Morocco (Cosson *et al*., 2005) with a high mechanical potential and a low shape variability (this study). (2) These specimens expanded in continental France sometime between 8000 and 6000 years BP (Poitevin *et al*., 1986) and encountered species with a lower MP, such as *S. etruscus* or *C. suaveolens* (present study). (3) A few millennia later, they reached Atlantic islands (where *C. suaveolens* was already present before the isolation of these islands from the continent, approximately 10 000 to 4000 years BP) through human-mediated transport. Moreover, island populations of *C. suaveolens* have a markedly lower MP than continental populations including continental *C. russula* (present study). (4) *Crocidura russula* from continental populations

outcompeted *C. suaveolens* (Pascal *et al.*, 2006). (5) The different selective pressures on islands produced insular populations of *C. russula* with a different shape and lower mechanical potential (present study) likely adapted to the changes in resource availability. The scenario sketched here with the relaxation of MP after competitive exclusion on islands suggests that the higher MP of *C. russula* might be related more strongly to interspecific competition than ecological niche expansion, although this remains to be tested.

## CONCLUSIONS

To conclude, the present study shows that the mechanical potential of *C. russula* is intermediate compared to its potential competitors. This mechanical potential is also linked to an intermediate level of shape variability, suggesting potential stabilizing selection on morphology. The superior mechanical potential of this species compared to *C. suaveolens* provides possible insights into colonization events, both when arriving in mainland Europe, as well as during the colonization of Atlantic islands. This approach could be applied to other biological models to test the generality of the observed link between mechanical potential and competitive success, as suggested by our data.

## ACKNOWLEDGEMENTS

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table S1.** List of the materials examined in this study including location and specimen numbers.