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Back to the wild: does feralization impact the mandible of non-commensal house mice (*Mus musculus domesticus*)?

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Abstract

If domestication has been well studied lately with the recognition of a so-called 'domestication syndrome', the opposite process, feralization, has deserved much less interest. The commensal Western European house mouse (*Mus musculus domesticus*) lives in close contact to humans, a situation setting it between wild and domesticated animals. However, the house mouse also occurs in non-anthropogenic environments, forming feral populations and hence providing the opportunity to document how feralization may impact its morphology. In this study, three of those 'feral' populations from Orkney, Kerguelen Archipelago and Southern France are compared to Western European commensal populations. The shape and biomechanical properties of the mouse jaws were analysed to assess the impacts of 'feralization' on an organ under major environmental pressures through its feeding function. Mandible shape varied mostly with climate and phylogeny, and feral populations only slightly diverged from their geographically close relatives. In contrast, feral mice shared a biomechanical signature corresponding to a decrease in the superficial masseter/molar mechanical advantage suggesting less performance at molar biting. This is interpreted as a parallel response to a relaxation of environmental pressure, possibly due to diet shift in feral habitats.

Keywords

Adaptation; morphometrics; biomechanics; commensalism; mandible morphology; rodent evolution

Introduction

Animal and plant interactions with humans, through domestication or commensalism, have been intensively studied since Darwin. The recent recognition of a so-called ‘domestication syndrome’ (Wilkins, Wrangham & Fitch, 2014; Sánchez-Villagra, Geiger & Schneider, 2016; Geiger et al., 2017) has renewed the interest in evaluating the impact of human vicinity on the phenotypic evolution of domesticated mammals. Together with the tamed behaviour itself, the syndrome involves a suite of morphological features, as diverse as coat coloration, brain size, and osteological differences (Kruska, 2005; Albert et al., 2008; Trut, Oskina & Kharlamova, 2009; Wilkins et al., 2014). In comparison, ‘feralization’ (i.e., when domesticated animals return to living in a wild state) has received little attention (Kruska, 2005; Johnsson et al., 2016). However, by providing an alternate perspective on the selective pressures related to anthropogenic environments, it may help to evidence connections between exposure to humans and the repeated development of peculiar phenotypes.

The Western European house mouse (*Mus musculus domesticus*) adopted a commensal lifestyle as soon as human populations became sedentary before the Neolithic age (Cucchi, Vigne & Auffray, 2005; Weissbrod et al., 2017). By following human travels (Cucchi & Vigne, 2006; Gabriel et al., 2010; Bonhomme et al., 2011), the house mouse was able to colonize most of the planet, and became one of the most performant invasive species worldwide (Lowe et al., 2000). Along these travels, the house mouse colonized areas characterized by climatic and ecological conditions markedly different from its area of origin, presumably East of the Fertile Crescent (Bonhomme et al., 2011). The commensal lifestyle buffers to some extent these environmental differences providing the house mouse with shelters and more or less comparable resources in human settlements (Berry, 1970) but this is mitigated by rapid and unpredictable changes in food abundance through time and space (Hulme-Beaman et al., 2016). Because of the close proximity to humans, commensalism has been proposed to constitute one pathway towards domestication (Zeder, 2012). Nevertheless, house mice should be considered as wild animals. Direct contacts with humans constitute a stress that led to the unintentional selection for tameness in a population submitted to repeated monitoring (Geiger, Sánchez-Villagra & Lindholm, 2018). This selection for tameness was indeed associated with phenotypic changes comparable to those typically found in domesticated animals.

Conversely, the house mouse is occasionally able to establish permanent feral populations, without relying on human resources and anthropogenic environments. Such populations are rare, especially on the continent where the house mouse is outcompeted outdoors by other small mammals (Auffray et al., 1990). Three feral populations (Fig. 1, Table 1) were considered in this study. Two feral

populations were sampled on islands currently devoid of human settlements: Faray Island (Orkney Archipelago) that was deserted in the 1940s, and the sub-Antarctic Guillou Island (Kerguelen Archipelago) that never housed permanent human settlements. The third population was collected in Frontignan (Southern France) and documents a rare case of continental feral population (Cassaing & Croset, 1985). Commensal populations were sampled on the Western European continent, and on Orkney Archipelago, North of Scotland.

The morphological response of mouse mandibles to the commensal vs. feral lifestyle (Fig. 2) was investigated here. Compared to the jaw of other placental mammals, the rodent mandible displays a unique association of morphological features characterized by the presence of a large pair of incisors separated from the molar row by a large diastema. As such, incisors and molars cannot come in occlusion at the same time (Cox & Jeffery, 2011) and they are involved in different functions, biting at the incisors and chewing at the molars. The teeth are primarily moved by different masticatory muscles, the temporal and masseter muscles being mainly involved during incision and chewing respectively. Because of this direct relationship between the feeding function and the jaw geometry, the rodent mandible constitutes a relevant model to investigate adaptation to different feeding behaviours (Fabre et al., 2017).

Mandible geometry was quantified by combining landmark-based geometric morphometrics to characterize mandible shape, and the estimate of mechanical advantages to assess the functional relevance of these shape changes. The relative effect of size variations, of the phylogenetic background, of the climatic conditions being taken as a proxy for food resources available to feral mice, and commensal vs. feral lifestyle on mandible shape and biomechanics was assessed.

The following hypotheses regarding the response to feralization were investigated. (1) If the primary selective pressure associated with commensalism is on behaviour, triggering a domestication syndrome (Wilkins et al., 2014), feral mice should all share a phenotypic response to the release of this selective pressure, and not only on traits involved in the adaptation to the local environment. Convergent evolution between feral populations is expected in several traits. (2) Feralization may simply mean, for house mice, that they have to adapt to new environments, including local food resources. In that case, convergent evolution is not necessarily expected. Phenotypic changes should be important on functionally relevant traits, directly under selection in feral populations. (3) Finally, if commensalism did not trigger specific adaptation in house mice compared to outdoor lifestyle, no difference would be expected between commensal and feral mice.

Material and Methods

Phylogenetic sampling and analysis

The mitochondrial D-loop has been extensively used for phylogeographic analyses of the house mouse (Searle et al., 2009; Gabriel et al., 2010; Hardouin et al., 2010; Bonhomme et al., 2011). It is thus the most adequate marker to assess the phylogenetic backgrounds of the populations. For 44 of the mice sampled during the 1992 and 2012 field trips on the Orkney Archipelago, DNA was extracted from ethanol-preserved tissue, using the DNeasy Blood and Tissue kit (Qiagen, France) (Supplementary Table 1). The D-loop was amplified using previously described primers and protocol (Hardouin et al., 2010). The new sequences were submitted to EMBL: accession number LS398218 to LS398261.

This sampling was completed by sequences retrieved from GenBank. When possible, we used sequences from the same localities as the ones used in the morphometrical analysis. Otherwise, we used sequences from the same geographic area (Table 1, Supplementary Table 1).

The new Dloop sequences and the sequences retrieved from Genbank were aligned with Muscle implemented in Seaview (Gouy, Guindon & Gascuel, 2009). The final alignments comprised 377 sequences and 834 positions. Haplotypes for each locality were determined with DNAsp v 5 (Librado & Rozas, 2009).

The phylogenetic tree was reconstructed with the haplotypes alignment using Bayesian inference (BI) with MrBayes v3.2 (Ronquist et al., 2012) and Maximum Likelihood (ML) with PhyML v3.1 (Guindon et al., 2010) under the model (TN+I+G) selected with jModelTest 2 (Darriba et al., 2012) using the Akaike criterion (AIC) (Akaike, 1973). Nodes robustness was estimated using posterior probabilities (PP) in BI analyses and bootstrap percentages (BP) for ML. For BI, two Markov chain Monte Carlo (MCMC) analyses were run independently for 10 000 000 generations. As TN model was not available in Mrbayes we used Nst=mixed, which explore the different substitution models. One tree was sampled every 500 generations. The burn-in was graphically determined with Tracer v1.6 (Rambaut et al., 2014). We also checked that the effective sample sizes (ESSs) were above 200 and that the average SD of split frequencies remained <0.01 after the burn-in threshold. We discarded 50% of the trees and visualized the resulting tree under Figtree v1.4 (Rambaut, 2012). For ML, we performed 1000 bootstrap replicates. Average p-distances within and between localities were estimated with MEGA 7 (Kumar, Stecher & Tamura, 2016).

Morphometric and biomechanical sampling

Eight islands of the Orkney Archipelago (Fig. 1; Table 1), located North of Scotland, were sampled during two field trips in 1992 (Eday, Faray where house mice are feral; Papa Westray, Sanday, and Westray) (Ganem, 1998) and 2012 (Orkney Mainland, Burray, Papa Westray, and South Ronaldsay). A single mouse was trapped on Burray and pooled with those from South Ronaldsay, the closest island, for all analyses. Papa Westray was the only island sampled during two campaigns. Being trapped in slightly different environments (hay stacks in 1992 and buildings in 2012), the two samples were considered separately. All of the 1992 mice have been kept in laboratory for 3-4 months after their capture (Ganem, 1998). During the 2012 campaign, some mice from Mainland and South Ronaldsay have been sacrificed in the field while all the others, together with Papa Westray mice, were kept in laboratory. Mice maintained in the lab were fed with rodent pellets. This could cause slight morphological changes because food differences may trigger mandible shape changes through remodelling (Anderson, Renaud & Rayfield, 2014). Additionally, the mice were kept in the lab had good chances to become older than in the field. Hence, the mice maintained in the lab were considered separately from those that were sacrificed at capture. Orkney mice were obtained with authorization n° CEEA-LR-12162 from the Languedoc-Roussillon Comité d’Ethique pour l’Expérimentation Animale to JCA. The corresponding skulls are stored in the collection of the Institut des Sciences de l’Evolution (ISEM), Montpellier, France.

Six localities from Western Europe were considered: Frontignan (Southern France) where house mice are feral; and for the commensal mice: Montpellier (Southern France), and San Bernardino (Northern Italy) from the ISEM collection; Tourn (Brittany, France), and Gardouch (Southwestern France) from the collection of the Centre de Biologie et Gestion des Populations (CBGP, Baillarguet, France); and Cologne-Bonn (Germany), provided by the Max Plank Institute for Evolutionary Biology (Plön, Germany). Skulls of this latter sample are currently stored at the Laboratoire de Biométrie et Biologie Evolutive (LBBE), Lyon, France. All these mice were sacrificed at capture. The populations of Tourn and Frontignan were sampled repeatedly in different seasons, thus sampling different age structures, with younger mice in summer and autumn, towards the end of the breeding season (Renaud et al., 2017). This allowed an evaluation of the variation due to seasonal variation. The pattern of mandible shape differentiation between these populations has recently been described (Renaud et al., 2017); for authorization information, see therein.

The feral house mouse population from Guillou Island, a small island from the sub-Antarctic Kerguelen Archipelago (Southern Indian Ocean) was also considered. This sample includes mice collected over four years of trapping (Renaud et al., 2013; Renaud et al., 2015). These mice were sacrificed at capture.

All mice were collected in an anthropogenic context, corresponding to the usual commensal lifestyle for the house mouse, except for the populations from Guillou, Frontignan, and Faray. Mice were introduced on the Kerguelen Archipelago by whalers during the 19th century (Kidder, 1876; Chapuis, Frenot & Lebouvier, 2004) from a commensal Western European stock (Hardouin et al., 2010). Within the Kerguelen, the small Guillou Island was always deprived of any permanent human settlement (Chapuis et al., 2004). Mice from Frontignan correspond to a feral population found in the Aresquiers spit of land, close to Montpellier (France) (Renaud et al., 2017). Although mice can occasionally forage into garbage on the beach during summer time, they do not rely on human resources and settlement for long-term survival. The age of this feral population is unclear. Finally, Faray Island in the Orkney Archipelago used to sustain human settlements but the island was completely deserted in 1947 (Berry et al., 1992; Ganem, 1998). It is still used for pasture, with occasional transfer of sheep and food by small boats. Mice from Faray are phylogenetically nested within the rest of Orkneys (Ledevin et al., 2016) and are the descendants of commensal mice brought by human transport. Hence, in the three cases, feral populations are issued from a secondary return of commensal mice to an outdoor lifestyle without reliance on human settlements.

All specimens in this study were considered as weaned, the criterion being that the third molars were fully erupted. No sexual dimorphism has so far been documented for house mouse mandibular morphology in wild populations (Renaud et al., 2013; Renaud et al., 2017). Therefore, males and females were pooled in the subsequent analyses.

Morphometric analysis

Each hemimandible was placed flat on the lingual side and pictured using a Leica numerical camera mounted on a Leica ZM9.5 stereomicroscope (Fig. 2). The left mandible was considered. When broken, we used the mirror image of the right mandible, because directional asymmetry and antisymmetry are of limited importance in house mouse mandibles (Ginot, Agret & Claude, 2018).

Mandibular shape was quantified with a set of 15 landmarks (Fig. 3A) commonly used to describe the mouse mandible (Klingenberg, Leamy & Cheverud, 2004; Renaud, Alibert & Auffray, 2012). They were digitized using TPSDig 2.0 (Rohlf, 2010a). A Procrustes superimposition was performed using TPSRelw (Rohlf, 2010b). Using this method, the configurations of landmarks are superimposed in three steps including size scaling, translation, and rotation. The resulting aligned coordinates (Procrustes coordinates) were used as shape variables in the subsequent analyses. Mandible size was estimated by the centroid size, i.e. the square root of the sum of the squared distances from each landmark to the centroid of the landmark configuration.

202 *Biomechanical analysis*

203 The mechanical advantage is a proxy of the efficiency of the mandible geometry to transmit the force
204 from the muscles to the bite point. It can be estimated as the ratio of the in-lever length (distance
205 from the articulation to the point of muscle attachment) and the out-lever length (distance from the
206 articulation to the bite point). It is used as a metric for mammalian jaw function (Anderson et al.,
207 2014; Fabre et al., 2017). An increase of the in-lever length will raise the bite strength, while an
208 increase of the out-lever length will raise its velocity.

209 Three in-lever lengths were measured (Fig. 3B, C): the temporal line of action was described by the
210 distance from the condyle to the tip of the coronoid process; the superficial masseter line of action
211 was described by the distance from the condyle to the tip of the angular process; and the deep
212 masseter line of action was described by the distance from the condyle to the anterior insertion of
213 the anterior part of the deep masseter. Two out-lever lengths were considered: the distance from
214 the condyle to the tip of the incisors, and the distance from the condyle to the first molar main cusp
215 (hypoconid). Because the incisors are primarily moved into occlusion by the action of the temporal
216 muscle, and the molars by the action of the two masseters, three mechanical advantages were
217 considered: temporal/incisor, superficial masseter/molar and deep masseter/molar. In- and out-lever
218 lengths were measured from the landmarks collected from the same pictures as those used for the
219 morphometric analyses.

220 *Statistical analyses*

221 Univariate differences between populations in mechanical advantages were tested using Kruskal-
222 Wallis tests and associated Mann-Whitney pairwise comparisons.

223 The shape variables (Procrustes coordinates) were summarized using a Principal Component Analysis
224 (PCA) performed on the variance-covariance matrix, and a between-group PCA (bgPCA). The bgPCA
225 provided the ratio of between-group to total variance, as well as axes visualizing the relationships
226 between group means.

227 Shape differences between populations were tested on the set of PC axes representing more than
228 5% of variance using a permanova (non-parametric multivariate analysis of variance based on 9999
229 permutations) and associated pairwise post-hoc tests.

230 To assess the allometric influence of size on shape, size-corrected shape variables were calculated, as
231 the residuals of a multiple regression of raw shape coordinates on centroid size.

232 Finally, linear models were used to assess the effects of phylogeny, climate, size, hosting conditions
233 and lifestyle on mandible shape and biomechanical properties.

234 Explanatory sets of variables were constructed as follows.

235 (1) Climatic data were extracted from the WorldClim database (Fick & Hijmans, 2017) with a
236 resolution of 2.5 arc-min using the raster package (Hijmans, 2014). The 19 bioclimatic
237 variables available were retrieved: Annual Mean Temperature, Mean Diurnal Range [Mean of
238 monthly (max temp - min temp)], Isothermality, Temperature Seasonality (standard
239 deviation *100), Max Temperature of Warmest Month, Min Temperature of Coldest Month,
240 Temperature Annual Range, Mean Temperature of Wettest Quarter, Mean Temperature of
241 Driest Quarter, Mean Temperature of Warmest Quarter, Mean Temperature of Coldest
242 Quarter, Annual Precipitation, Precipitation of Wettest Month, Precipitation of Driest Month,
243 Precipitation Seasonality (Coefficient of Variation), Precipitation of Wettest Quarter,
244 Precipitation of Driest Quarter, Precipitation of Warmest Quarter, Precipitation of Coldest
245 Quarter. These variables are based on average monthly climate data for minimum, mean,
246 and maximum temperature and for precipitation for the period 1960-1990. They were
247 summarized using a PCA on the correlation matrix. The set of PC axes explaining 5% of
248 variance or more were retained as explanatory variables in the model.

249 (2) The phylogenetic analysis based on mitochondrial D-loop sequences provided a matrix of p-
250 distances (proportion of nucleotide sites at which two sequences are being different)
251 assessing the relationships between the same populations as those considered in the
252 morphometric analysis. A Principal Coordinate Analysis (PCOA) was performed on this
253 distance matrix. The set of PC axes explaining more than 5% of variance were retained in the
254 linear model.

255 (3) The size of the mandible, estimated by the centroid size of the landmarks configuration.

256 (4) The hosting conditions: field vs. lab.

257 (5) Lifestyle: commensal vs. feral lifestyle of the populations.

258 The variables to be explained were (1) the set of PC axes >5% of mandible shape variance based on
259 the analysis of the Procrustes coordinates; (2) the size-corrected shape coordinates; (3) the
260 temporal/incisor mechanical advantage; (4) the superficial masseter/molar mechanical advantage
261 and (5) the deep masseter/molar mechanical advantage.

Kruskal-Wallis and Mann-Whitney tests as well as the permanova were performed using Past 3 (Hammer, Harper & Ryan, 2001). Multivariate analyses (PCA and bgPCA) were performed using the R package ade4 (Dray & Dufour, 2007). Linear models were performed using the R package ffmanova (Langsrud & Mevik, 2012).

Results

Context: Phylogenetic relationships and climatic background

All Orkney mice belong to the same clade, together with some continental mice (Fig. 4A). Mice from Guillou Island, in the Kerguelen Archipelago all displayed exactly the same haplotype (Hardouin et al., 2010). Compared to this phylogenetic homogeneity on islands, mice from Western Europe are much more diversified, and belong to different clades. This diversity reflects the long history of human travels, allowing an important gene flow all over Europe.

Regarding the climatic conditions, the 19 bioclimatic variables retrieved from WorldClim were summarized using a PCA (Fig. 4B, C). Four axes explained ~5% of variance or more (PC1: 50.7%, PC2: 31.0%, PC3: 12.3%, PC4: 4.9%). On the first principal components, all Orkney islands are characterized by a wet and relatively cold climate (Fig. 4B, C). Guillou Island (Kerguelen Archipelago) displays a stable and cold environment. In contrast, the continental localities, ranging from Germany to Italy, are characterised by variable climatic conditions.

Mandible shape

Five axes explained more than 5% of the total variance (PC1: 22.5%, PC2: 13.7%, PC3: 8.9%, PC4: 7.5%, PC5: 5.8%) in the PCA performed on the Procrustes coordinates. Based on this set of axes, significant morphological differences were evidenced between the main populations considered: commensal continent vs commensal insular (Orkney), and feral populations (Faray, Frontignan, and Guillou) vs their commensal relatives (continent and Orkney) (Table 2).

Between-group variation explained 32.9% of this total variance. On the first two axes of the between-group PCA (bgPC1: 46.7%; bgPC2: 21.6%), three groups of localities could be identified (Fig. 5A): Orkney islands, continental Western Europe, and Guillou Island. All Orkney populations tended to cluster together towards negative bgPC1 and positive bgPC2 values (upper left part of the morphospace). They were opposed along bgPC2 to the different populations of continental Western Europe. Shape differences between mean mandible shape of Western Europe vs. Orkney were subtle and distributed all over the mandible (Fig. 5B). Orkney mandibles tended to display a thinner linguo-

buccal molar alveolar region, a reduced and forwardly oriented coronoid process, and a dorso-ventrally compressed angular process. The mandibles of Orkney Mainland mice that have been kept in the lab differed from the ones sacrificed in the field (permanova, p-value= 0.0001). They display more extreme morphologies towards negative bgPC1 and positive bgPC2 (towards the upper left part of the morphospace) but still clustered with the other Orkney populations. A similar trend could be observed in the specimens from South Ronaldsay (permanova, p-value =0.0403). Mandibles from Papa Westray had a different mean shape between 1992 and 2012 (permanova, p-value=0.0062). However, both Papa Westray samples remain within the range of variation of other Orkney populations.

The Guillou mice from Kerguelen Archipelago clearly departs from all other groups mostly along bgPC1. On bgPC2, it shares positive values with most Orkney populations. The morphology of Guillou mandibles is characterized by an extended condyle, and a forwardly oriented coronoid process (Fig. 5B). Mice from Faray, the feral population from Orkney, are within the range of other Orkney populations, but the most extreme towards Guillou along the bgPC1 axis.

Continental populations display as much between-group morphological variation as those from Orkneys. Feral mice from Frontignan are within this range of variation. Seasonal variation occurs with the spring sample, dominated by old overwintered mice, being shifted along an oblique towards negative bgPC1 and positive bgPC2 values. This is the same direction of change as the one displayed between field and lab samples from Orkney. Seasonal variation was less obvious in the commensal population of Tournai. The feral population from Frontignan did not display any common trend with other feral populations.

Mechanical advantage

No clear trend emerged for the temporal/incisor mechanical advantage (Table 3; Fig. 6A) except for the Guillou sub-Antarctic population that displayed an evident increase for this biomechanical estimate, suggesting more efficient incisors biting.

Commensal populations from the continent and Orkney shared similar values of superficial masseter/molar mechanical advantage (Table 3; Fig. 6B). In contrast, the three populations sharing feral life (Frontignan, Faray, and Guillou) displayed a significant decrease of this mechanical advantage, showing lower performance for biting at the molars.

The results concerning the deep masseter/molar mechanical advantages were less distinct (Table 3; Fig. 6C). The Frontignan feral population did not differ from the commensal continental populations.

Feral mice from Faray and to a lesser extent, from Guillou, displayed lower mechanical advantage compared to other populations.

The differences observed in the above ratios are mainly explained by the in-lever length. Especially, the superficial masseter in-lever length (Supplementary Figure 1; Supplementary Table 2) is decreased in the Frontignan, Guillou and Faray, suggesting lower bite force. No clear trends arise from the out-levers lengths (Supplementary Figure 1; Supplementary Table 2).

Relationship between mandible morphology, size, phylogeny, climate, hosting conditions and lifestyle

The influence of climate, phylogeny, lifestyle (commensal vs. feral), conditions of late hosting (lab vs. field), and size on mandible shape and biomechanical properties was further investigated using linear models.

Climatic conditions were described by the first four axes of the PCA on the 19 bioclimatic variables of WorldClim. The phylogenetic relationships were described by the first four axes of a PCOA on the matrix of p-distance based on the D-loop analysis (Supplementary Table 3), all explaining more than 5% of variance (PC1: 58.8%, PC2: 22.8%, PC3: 8.7%, PC4: 5.6%).

Overall, size had a significant but small impact on the mandible shape and the three mechanical advantages (Table 4). It is the factor explaining most variance only in the case of the deep masseter/molar mechanical advantage. This limited part of size-related shape variation is confirmed by very similar results obtained on raw and size-corrected morphometric data (Table 4). The hosting conditions only slightly impacted the shape of the mandible (around 1%), and had no effect on the mechanical advantage.

The mandible shape was influenced by climate (4.7%) and phylogeny (4.8%) almost equally (Table 4). This held true when considering size-corrected shape variable. The temporal/incisor mechanical advantage was mostly explained by climate, possibly because of the important divergence of the sub-Antarctic Guillou population for this variable. The best explanatory variable for the superficial masseter/molar mechanical advantage was the feral vs. commensal lifestyle (11.4%), largely before the phylogenetic background (Table 4).

Discussion

Differentiation of mandible morphology in Orkney

Our study points out a consistent differentiation of all Orkney populations from Western Europe continental mice. This contrasts with the diversification in tooth shape occurring among the same Orkney populations, which display far more diversity than can be observed among continental populations (Ledevin et al., 2016). Two factors may promote the relative homogeneity among Orkney islands: climate and phylogenetic history. First, all Orkney islands share similar climatic conditions, departing from those prevailing on the continent. Accordingly, climate was an important explanatory factor of mandible shape, being of almost equal importance as the phylogenetic background. Orkney mice also shared a similar phylogenetic history, all belonging to the same haplogroup, whereas continental Western European populations are genetically diverse [(Ledevin et al., 2016); this study]. The genetic signature of Orkney mice has been interpreted as the consequence of their introduction by Norwegian Vikings (Searle et al., 2009; Jones et al., 2011). A founder effect shared by all Orkney mice may contribute to the idiosyncrasy of their mandible shape.

Balanced impact of climate and phylogeny on mandible shape

Phylogeny and climate almost equally explained the mandibular shape variation (around 5%). In contrast, phylogeny was the first explanatory factor when considering molar evolution among house mouse populations including insular ones (Ledevin et al., 2016) and in other rodents (Caumul & Polly, 2005; Ledevin et al., 2018). The importance of climate in the present dataset may be due to a more important influence of environmental factors on the mandible, which can remodel through life and is more prone to vary due to local food resources, compared to teeth that are only affected by wear once erupted (Renaud & Auffray, 2010; Ledevin et al., 2012). Examples of plastic shape changes are provided by the mandibles of mice maintained in the lab, and by seasonal variations in Frontignan. In both cases, ageing may be the primary driver of mandible shape differences. However, the limited influence of lifestyle and conditions of hosting on mandible shape suggests that the role of plastic remodelling remained of minor importance in driving the observed morphological differentiation compared to other sources of variation.

Does feral life trigger a convergent response?

The impact of lifestyle was tested by comparing commensal and feral mice. We purposely compared feral populations with very different environmental and phylogenetic context: (1) Frontignan, a continental population with a mixed phylogenetic composition (Renaud et al., 2017). (2) Guillou, a population of a remote sub-Antarctic island in the Kerguelen Archipelago. This population has been

shown to be highly homogeneous genetically because of initial founder effect and subsequent resilience against late invasion (Hardouin et al., 2010). (3) Faray, an Orkney population sharing with other Orkney populations a common history since introduction by the Vikings, and back to feral life since the stop of permanent human settlements in the 1940s (Berry et al., 1992). In the cases of Frontignan and Faray, the mandible shape of feral populations did not obviously diverge from their geographically close commensal relatives. Hence, the return to feral life did not constitute a homogeneous selective pressure sufficient to overwhelm the climatic and phylogenetic backgrounds shared by neighbouring feral and commensal mice. This absence of a common signature of feralization on jaw shape echoes the fact that evolution of commensalism in the different subspecies of house mice (*Mus musculus*) did not trigger a parallel evolution of jaw morphology (Siahsarvie et al., 2012). The shift from wild to commensal or from commensal to feral lifestyle seems thus to have a limited impact on mandible shape.

In contrast, when considering functionally relevant mechanical advantages, mice from the three feral populations share a decrease in the superficial masseter/molar mechanical advantage, that is further shared by other feral sub-Antarctic populations (Renaud et al., 2018). The masseter/molar mechanical advantage is associated with chewing (Baverstock, Jeffery & Cobb, 2013), a high value being associated with the consumption of hard or resistant food items. A strong bite force at molars should be important for commensal mice feeding mostly on grains in agricultural settings. Out of the commensal habitat, mice from Frontignan and Faray may rely more on diversified outdoor resources, as do mice from Guillou, which incorporated an increased fraction of invertebrates to their diet (Le Roux et al., 2002). The decrease in the masseter/molar mechanical advantages may thus be due to a relaxation on molar biting shared by the three populations of feral mice.

A biomechanical signature of feralization, but no convergent evolution of mandible shape

In sub-Antarctic mice, the decrease in the masseter/molar mechanical advantages is associated with an increase in the temporal/incisor mechanical advantage, solicited for the capture and consumption of macro-invertebrate preys (Renaud et al., 2015; Renaud et al., 2018). A shorter coronoid process leads to an increased in-lever arm for the temporalis, which may allow a stronger jaw closure at the incisor tip, although at the expense of speed. A longer out-lever arm at the incisors may however allow to maintain speed biting (Renaud et al., 2018). Overall, sub-Antarctic mice display a convergent adaptive evolution that is only partly shared by other feral mice. Possibly, the food resources available to Frontignan and Faray feral mice are more diverse than those on which sub-Antarctic mice feed, leading to different fine-tuning of the jaw 'toolkit' in the different populations.

Not mutually exclusive, the time span since mice from Faray returned to feral life may be too short to observe a morphological evolution as pronounced as that on sub-Antarctic islands, where the colonization by the mouse dates back to the 19th century (Kidder, 1876). As for the Frontignan population, its genetic diversity suggests that this population could function as a sink population regularly fuelled by migration from neighbour commensal populations (Renaud et al., 2017). Such gene flow may be a factor impeding local adaption to the feral habitat (Lenormand, 2002). Finally, other factors such as genetic isolation, levels of predation and competition, may be different in the three feral populations, further contributing to the differentiation of each feral population in another morphological direction.

The 'domestication syndrome' suggests that selection for tameness is accompanied by a cohort of phenotypic changes, all being integrated consequences of reduced neural crest cell input (Wilkins et al., 2014). Some of these traits involve head shape, with a shortening of the head documented in various domestic mammals (O'Regan & Kitchener, 2005). Such traits were not directly measured here, but the incisor in-lever length, roughly corresponding to mandible length, would likely vary with snout length. Our results evidence no trend towards longer mandibles in feral mice, as could be expected if commensal mice were displaying, due to their habituation to human presence, a first step towards a domestication syndrome. This contrasts with other studies (Slábová & Frynta, 2007; Geiger et al., 2018) showing that house mice strongly associated with humans (commensal vs. feral or tamed vs. commensal) displayed shorter heads, possibly because brain size rather than snout length may be involved in this response, as it is in the response to domestication (Smith et al., 2017). Additional data on commensal and feral populations would be required to tease apart the indirect effects of a possible 'commensal' syndrome, from direct effects related to specific selective pressures as those related to food resources, that have also been documented in domestic breeds (O'Regan & Kitchener, 2005). Since commensalism also affects emotivity in house mice, by changing the social structure of the populations (Ganem, 1991), aggressiveness levels may be affected as well. Aggressive behavior has been shown to influence mandible shape due to its functional importance during biting (Corti & Rohlf, 2001).

Conclusions

Based on our analysis of mandible shape, a convergent feral evolution was not detected. Feral mice populations shared, however, a similar biomechanical signature showing decreased performance for molar biting. A shift toward a more diverse diet, including invertebrates, may be responsible for this morphological change, but it is not accompanied by adaptive changes in the incisor/temporalis

functional complex, as expected based on carnivorous rodents (Fabre et al., 2017) and sub-Antarctic mice (including Guillou) relying on an invertebrate-enriched diet (Renaud et al., 2018). Hence, only the relaxation of the functional demand on molar biting was shared by the non-commensal mice, due to the decreased availability of grain stocks, and is responsible for this discrete morphological signature of ‘feralization’.

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Group	Country	Code	Lifestyle	Locality _{morpho}	Hosting conditions	N _{morpho}	Locality _{genetic}	N _{genetic}	N _{haplo}
Continental Europe	Germany	CB	Commensal	Cologne-Bonn	Field	14	Cologne-Bonn	59	35
	France	FR (AUT/SP)	Feral	Frontignan	Field	20/7	Frontignan	22	11
		GA	Commensal	Gardouch	Field	68	Toulouse, Severac-le-Chateau	38	21
		MP	Commensal	Montpellier	Field	19	Montpeyrroux, St Georges d'Orques, Montpellier, Gigean, Severac-le-Chateau	41	24
		TO (SP/SU/WI)	Commensal	Tourch	Field	20/21/28	Tourch	26	3
	Italy	SB	Commensal	San Bernardino	Field	14	Northern Italy (34 localities)	47	27
Kerguelen Archipelago	France	GU	Feral	Guillou Island	Field	79	Guillou Island	79	1
Orkney Archipelago	United Kingdom	ED	Commensal	Eday	Lab	27	Eday	12	3
		FA	Feral	Faray	Lab	9	Faray	6	1
		ML (L/F)	Commensal	Mainland	Lab/Field	109/61	Mainland	7	5
		PW1992	Commensal	Papa Westray 1992	Lab	8	Papa Westray	4	1
		PW2012 (L)	Commensal	Papa Westray 2012	Lab	12	Papa Westray	8	2
		PW	Commensal	-	-	-	Papa Westray	4	2
		SA	Commensal	Sanday	Lab	13	Sanday	7	1
		SR (L/F)	Commensal	South Ronaldsay	Lab/Field	20/6	South Ronaldsay	10	2
		SR	Commensal	Burray	Field	1			
		WE	Commensal	Westray	Lab	9	Westray	7	3

Table 1. Details on the origin and characteristics of samples used in this study. Localities of trapping and countries are indicated with number of specimens for the morphometric (Locality_{morpho}, N_{morpho}) and the genetic analysis (Locality_{genetic}, N_{genetic}). For each locality, abbreviation code, lifestyle, conditions of hosting (field vs. lab, i.e. sacrificed on the field, or brought back to the lab) and number of haplotypes (N_{haplo}) are also indicated. Some groups were split in the morphometric analyses according to season (Frontignan and Tourch; SP = spring, SU = summer, AUT = autumn, WI = winter) or to hosting conditions (L = lab, F = field).

Groups	Frontignan	Guillou	Commensal Orkney	Faray
Lifestyle	Feral	Feral	Commensal	Feral
Commensal continent	0.0001	0.0001	0.0001	0.0001
Frontignan (feral)		0.0001	0.0001	0.0001
Guillou (feral)			0.0001	0.0001
Commensal Orkney				0.0001

Table 2. Differentiation in mandible shape between groups of commensal and feral house mice. P-values of a permanova on the first five axes of a PCA on the Procrustes coordinates are provided. In bold: significant probabilities ($P < 0.05$).

Groups		Frontignan		Guillou		Commensal	Faray
Lifestyle		Feral		Feral		Commensal	Feral
		Mean	sd	P-values			
Temp/Inc	Commensal continent	0.23	0.02	0.188	6.9E-20	0.001	0.723
	Frontignan (feral)	0.19	0.02		1.5E-09	0.008	0.201
	Guillou (feral)	0.27	0.02			4.6E-13	0.000
	Commensal Orkney	0.24	0.02				0.560
	Faray (feral)	0.20	0.01				
Sup Mass /Mol	Commensal continent	0.53	0.02	2.5E-09	4.5E-20	0.371	5.0E-06
	Frontignan (feral)	0.49	0.02		0.272	2.5E-08	0.001
	Guillou (feral)	0.49	0.02			3.0E-21	0.003
	Commensal Orkney	0.52	0.03				3.5E-06
	Faray (feral)	0.46	0.02				
Deep Mass/Mol	Commensal continent	0.97	0.02	0.153	0.000	8.1E-7	0.001
	Frontignan (feral)	0.96	0.02		0.528	0.000	0.021
	Guillou (feral)	0.96	0.02			8.3E-12	0.056
	Commensal Orkney	0.98	0.02				3.1E-5
	Faray (feral)	0.94	0.01				

Table 3. Biomechanical differentiation of the mandible between commensal and feral groups of house mice. Upper panel: temporal/incisor mechanical advantage; middle panel: superficial masseter/molar mechanical advantage; lower panel: deep masseter/molar mechanical advantage. First columns: mean and standard deviation (sd) of the mechanical advantages for each group. Next columns: P-values of pairwise Mann-Whitney tests. In bold: significant probabilities ($P < 0.05$).

	Climate		Phylogeny		Lifestyle		Hosting		Size	
	P	%	P	%	P	%	P	%	P	%
Shape	< 0.0001	4.7%	< 0.0001	4.8%	< 0.0001	2.2%	< 0.0001	1.7%	< 0.0001	3.7%
Size-corrected shape	< 0.0001	4.6%	< 0.0001	5.1%	< 0.0001	2.0%	< 0.0001	1.1%		
Temp/Inc	< 0.0001	8.9%	0.0837	0.1%	0.7354	0.0%	0.5632	0.0%	0.0136	0.08%
Sup Mass /Mol	< 0.0001	5.3%	< 0.0001	7.1%	< 0.0001	11.4%	0.504	0.0%	< 0.0001	2.2%
Deep Mass/Mol	< 0.0001	2.3%	0.1	0.8	< 0.0001	2.3%	0.06	0.4%	< 0.0001	4.8%

Table 4. Influence of climate, phylogeny, lifestyle (commensal vs. feral), conditions of hosting (field vs. laboratory), and size on mandible shape (raw and size-corrected shape variables), and biomechanical properties (temporal/incisor, superficial masseter/molar and deep masseter/molar mechanical advantages). Results of a linear model are given, with p-values (P) and percentage (%) of variance explained by the variables.

Figure Captions

Figure 1. Localization of sampling sites. (A) General map presenting the three main origins; (B) Continental Western Europe; (C) Orkney Archipelago (North Scotland); (D) Kerguelen Archipelago (Southern Indian Ocean). Color code throughout the paper: blue, Western European continent; green: Orkney; red: Guillou, Kerguelen. Colored names in bold and italics: feral populations.

Figure 2. Mandibles illustrating each population (all at the same scale). a-f: Continental Western Europe. g: Guillou, Kerguelen. h-q: Orkney. f,g,h: feral populations. F: sacrificed in the field. L: kept in laboratory. For each population, the illustrative mandible has been chosen as the closest to the group mean in the morphospace of the PCA on the aligned coordinates.

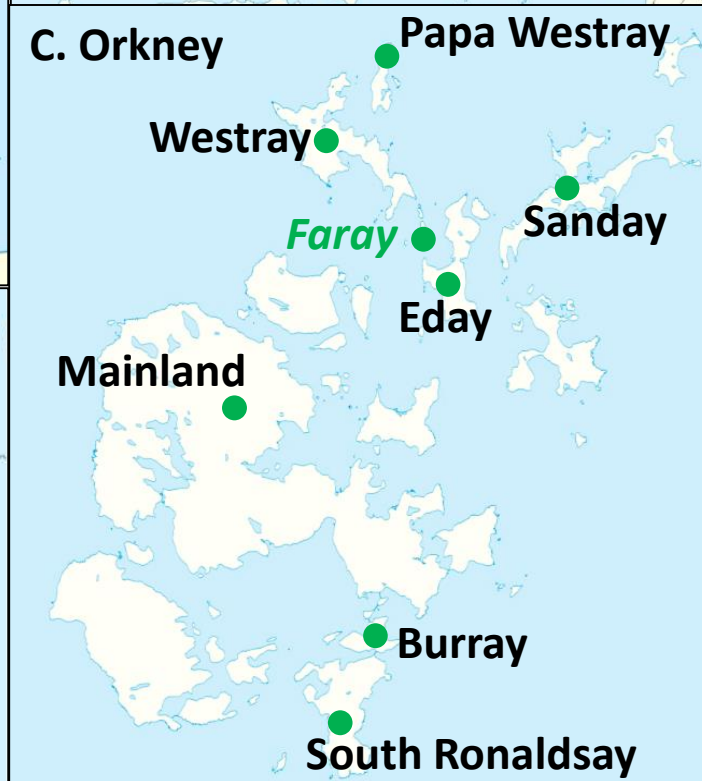
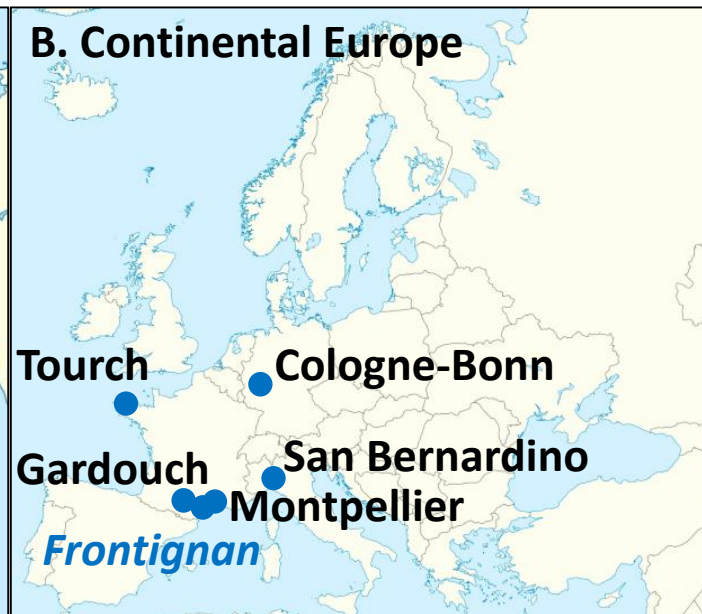
Figure 3. Morphometric and biomechanical measurements on a house mouse left mandible. (A) The 15 landmarks used in the morphometric analysis. (B) In- and out-lever for the temporal/incisor complex, with delineation of the insertion of the temporal muscle. (C) In- and out-levers for the two masseter (deep and superficial)/molar complexes, with delineation of the insertion of the masseter muscles. Out-levers (first molar and incisor) in orange, temporal in-lever in red, masseter in-levers in blue.

Figure 4. Phylogenetic and climatic background. (A) Bayesian phylogenetic tree based on D-loop sequences. For each node posterior probabilities (MrBayes) and bootstrap support (Phyml) are indicated. In blue, continental Western Europe; green: Orkney; red: Guillou, Kerguelen. (B, C) Climatic variations among localities. (B) Scores of the localities on the first two axes of a PCA on the 19 Bioclim climatic variables. (C) Circle of correlation, showing the contribution of the climatic variables on the first two PC axes. The projection of each arrow on an axis shows its contribution to this axis. If the arrow is shorter than 1 (arrow length = 1 materialized by the circle), the corresponding variable contributes to other axes out of the first principal plane.

BIO1 = Annual Mean Temperature; BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)); BIO3 = Isothermality (BIO2/BIO7) (* 100); BIO4 = Temperature Seasonality (standard deviation * 100); BIO5 = Max Temperature of Warmest Month; BIO6 = Min Temperature of Coldest Month; BIO7 = Temperature Annual Range (BIO5-BIO6); BIO8 = Mean Temperature of Wettest Quarter; BIO9 = Mean Temperature of Driest Quarter; BIO10 = Mean Temperature of Warmest Quarter; BIO11 = Mean Temperature of Coldest Quarter; BIO12 = Annual Precipitation; BIO13 = Precipitation of Wettest Month; BIO14 = Precipitation of Driest Month; BIO15 = Precipitation Seasonality (Coefficient of Variation); BIO16 = Precipitation of Wettest Quarter; BIO17 = Precipitation of Driest Quarter; BIO18 = Precipitation of Warmest Quarter; BIO19 = Precipitation of Coldest Quarter.

Figure 5. Mandible shape differentiation. (A) Differentiation between populations. The first two principal axes of the between-group PCA on the Procrustes coordinates characterizing mandible shape are displayed. Each abbreviation stands for the mean shape of the population. Thick boxes with bold names: feral populations. (B) Visualization of the shape changes between mean mandible shape of Western Europe vs. Orkney, and Western Europe vs. Kerguelen (Guillou). In blue continental Western Europe, in green Orkney, in red Guillou. Abbreviation codes in Table 1. Splitting by season (SP = spring, SU = summer, AUT = autumn, WI = winter) or by hosting conditions (L = lab, F = field) are indicated after the high dash in the group name.

Figure 6: Biomechanical variations between localities. (A) Mechanical advantages for the temporal/incisor complex. (B) Mechanical advantages for the superficial masseter/molar complex. (C) Mechanical advantages for the deep masseter/molar complex. In blue Continental Western Europe, in green Orkney, in red Guillou. Abbreviation in bold: feral populations.



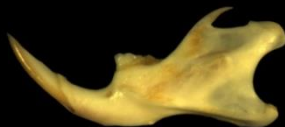
5 mm



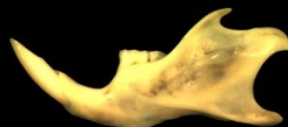
a. Cologne-Bonn



b. Gardouch



c. Montpellier

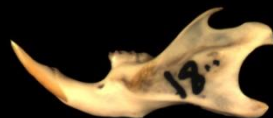


d. San Bernardino

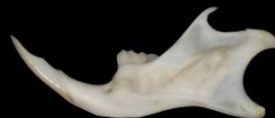


e. Tournai

Continent commensal



f. Frontignan



g. Guillo



h. Faray

Feral



i. Eday



j. Mainland F



k. Mainland L



l. Papa Westray 1992



m. Papa Westray 2012



n. Sanday



o. South Ronaldsay F

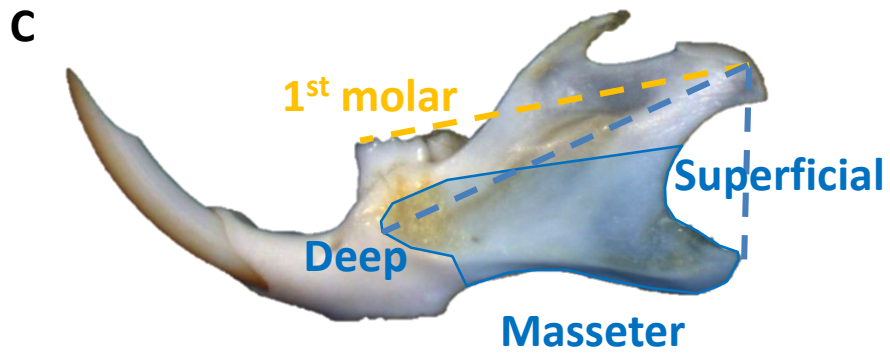
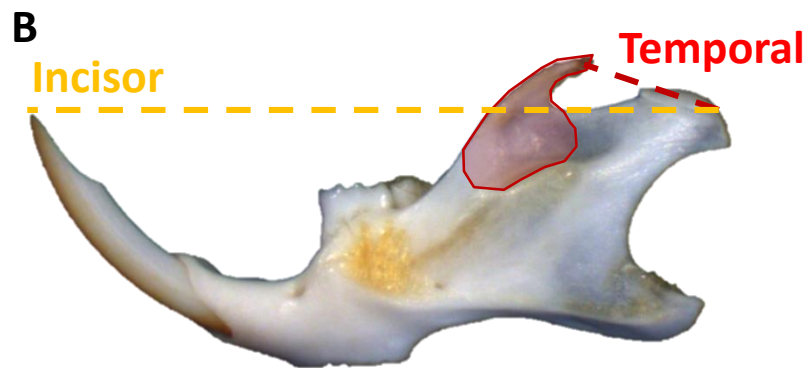
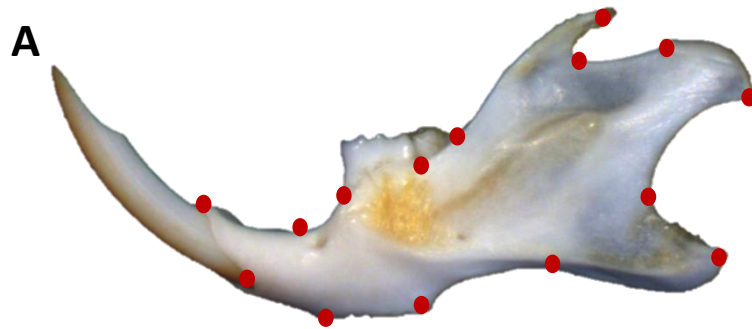


p. South Ronaldsay L

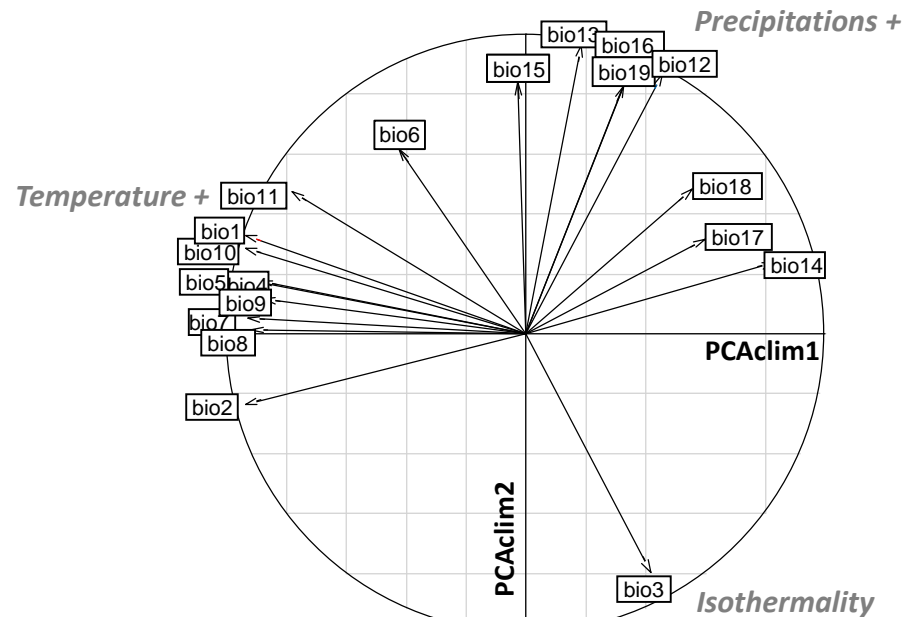


q. Westray

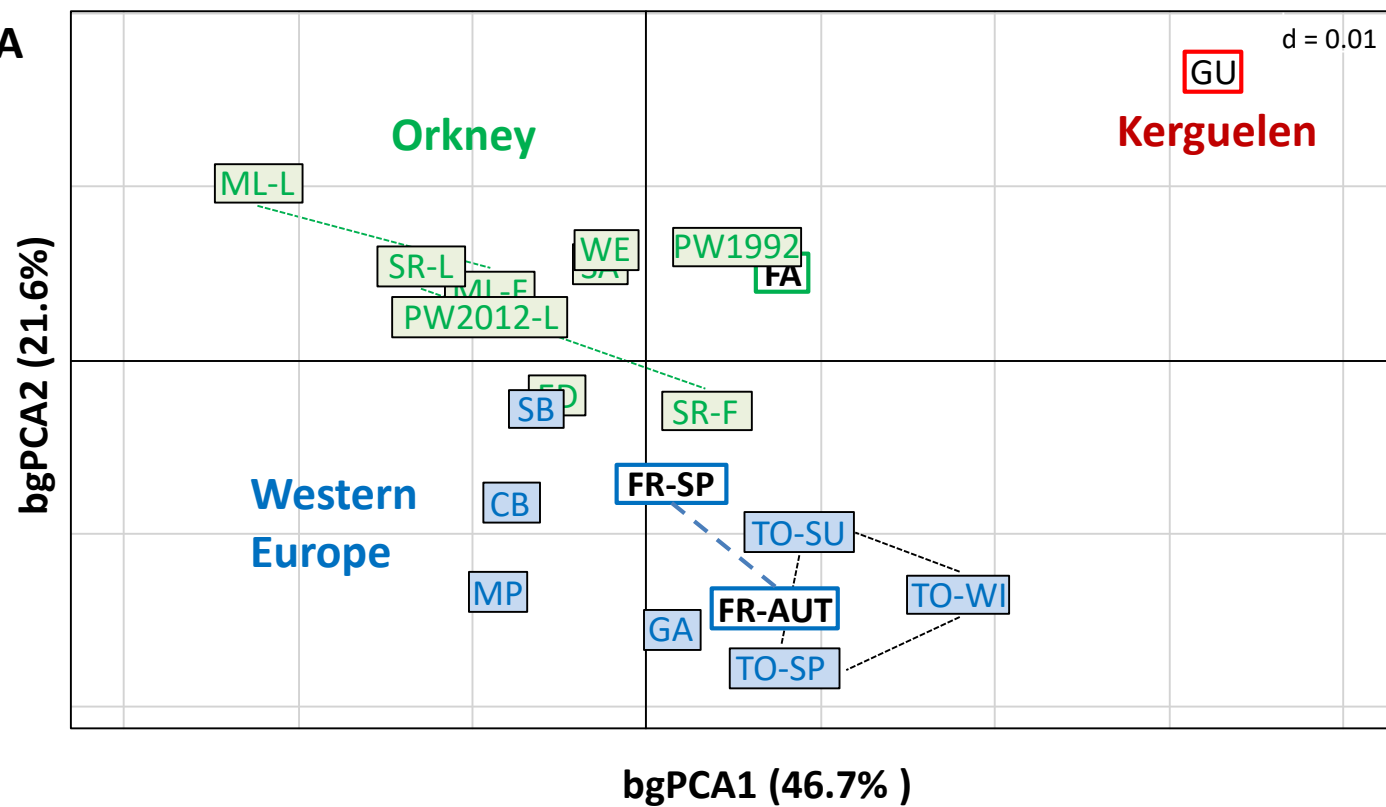
Orkney commensal



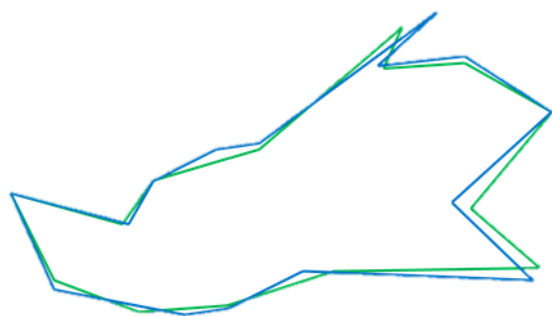
B. Climatic variation among localities



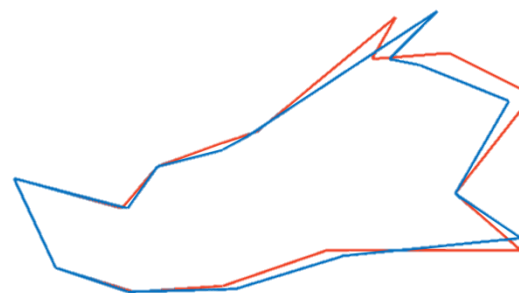
A



B



Western Europe vs Orkney



Western Europe vs Kerguelen

