



**HAL**  
open science

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

Louise Souquet, Pascale Chevret, Guila Ganem, Jean-Christophe Auffray, Ronan Ledevin, Sylvie Agret, Lionel Hautier, Sabrina Renaud

### ► To cite this version:

Louise Souquet, Pascale Chevret, Guila Ganem, Jean-Christophe Auffray, Ronan Ledevin, et al.. Back to the wild: does feralization impact the mandible of non-commensal house mice (*Mus musculus domesticus*)?. *Biological Journal of the Linnean Society*, 2019, 126 (3), pp.471-486. 10.1093/biolinnean/bly218 . hal-02336333

**HAL Id: hal-02336333**

**<https://hal.science/hal-02336333v1>**

Submitted on 21 Nov 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3 Louise SOUQUET<sup>1,2</sup>, Pascale CHEVRET<sup>1</sup>, Guila GANEM<sup>3</sup>, Jean-Christophe AUFFRAY<sup>3</sup>, Ronan LEDEVIN<sup>1,4</sup>,  
4 Sylvie AGRET<sup>3</sup>, Lionel HAUTIER<sup>3</sup>, Sabrina RENAUD<sup>1\*</sup>

5

6

7 <sup>1</sup> Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, Université Claude Bernard Lyon 1, CNRS  
8 69100 Villeurbanne cedex, France

9 <sup>2</sup> Present address: Institut de Génomique Fonctionnelle de Lyon, UMR 5242, CNRS, Ecole Normale  
10 Supérieure de Lyon, Université Claude Bernard Lyon 1, 46 Allée d'Italie, F-69364 Lyon Cedex 07,  
11 France

12 <sup>3</sup> Institut des Sciences de l'Evolution, Université de Montpellier, UMR 5554 CNRS, IRD, EPHE, Place  
13 Eugène Bataillon, CC65, 34095 Montpellier cedex, France

14 <sup>4</sup> Present address: UMR 5199 PACEA, Université de Bordeaux, Allée Geoffroy Saint Hilaire (Bat.B8),  
15 33615 Pessac, France

16

17 \* Corresponding author: Sabrina.Renaud@univ-lyon1.fr

18

19

20 **Abstract**

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

35

36 **Keywords**

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

38

39

## 40 Introduction

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

53 The Western European house mouse (*Mus musculus domesticus*) adopted a commensal lifestyle as  
54 soon as human populations became sedentary before the Neolithic age (Cucchi, Vigne & Auffray,  
55 2005; Weissbrod et al., 2017). By following human travels (Cucchi & Vigne, 2006; Gabriel et al., 2010;  
56 Bonhomme et al., 2011), the house mouse was able to colonize most of the planet, and became one  
57 of the most performant invasive species worldwide (Lowe et al., 2000). Along these travels, the  
58 house mouse colonized areas characterized by climatic and ecological conditions markedly different  
59 from its area of origin, presumably East of the Fertile Crescent (Bonhomme et al., 2011). The  
60 commensal lifestyle buffers to some extent these environmental differences providing the house  
61 mouse with shelters and more or less comparable resources in human settlements (Berry, 1970) but  
62 this is mitigated by rapid and unpredictable changes in food abundance through time and space  
63 (Hulme-Beaman et al., 2016). Because of the close proximity to humans, commensalism has been  
64 proposed to constitute one pathway towards domestication (Zeder, 2012). Nevertheless, house mice  
65 should be considered as wild animals. Direct contacts with humans constitute a stress that led to the  
66 unintentional selection for tameness in a population submitted to repeated monitoring (Geiger,  
67 Sánchez-Villagra & Lindholm, 2018). This selection for tameness was indeed associated with  
68 phenotypic changes comparable to those typically found in domesticated animals.

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

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

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

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

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

104

## 105 **Material and Methods**

### 106 *Phylogenetic sampling and analysis*

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

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

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

122 The phylogenetic tree was reconstructed with the haplotypes alignment using Bayesian inference (BI)  
123 with MrBayes v3.2 (Ronquist et al., 2012) and Maximum Likelihood (ML) with PhyML v3.1 (Guindon  
124 et al., 2010) under the model (TN+I+G) selected with jModelTest 2 (Darriba et al., 2012) using the  
125 Akaike criterion (AIC) (Akaike, 1973). Nodes robustness was estimated using posterior probabilities  
126 (PP) in BI analyses and bootstrap percentages (BP) for ML. For BI, two Markov chain Monte Carlo  
127 (MCMC) analyses were run independently for 10 000 000 generations. As TN model was not available  
128 in Mrbayes we used Nst=mixed, which explore the different substitution models. One tree was  
129 sampled every 500 generations. The burn-in was graphically determined with Tracer v1.6 (Rambaut  
130 et al., 2014). We also checked that the effective sample sizes (ESSs) were above 200 and that the  
131 average SD of split frequencies remained <0.01 after the burn-in threshold. We discarded 50% of the  
132 trees and visualized the resulting tree under Figtree v1.4 (Rambaut, 2012). For ML, we performed  
133 1000 bootstrap replicates. Average p-distances within and between localities were estimated with  
134 MEGA 7 (Kumar, Stecher & Tamura, 2016).

135

### 136 *Morphometric and biomechanical sampling*

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

154 Six localities from Western Europe were considered: Frontignan (Southern France) where house mice  
155 are feral; and for the commensal mice: Montpellier (Southern France), and San Bernardino (Northern  
156 Italy) from the ISEM collection; Tournay (Brittany, France), and Gardouch (Southwestern France) from  
157 the collection of the Centre de Biologie et Gestion des Populations (CBGP, Baillarguet, France); and  
158 Cologne-Bonn (Germany), provided by the Max Plank Institute for Evolutionary Biology (Plön,  
159 Germany). Skulls of this latter sample are currently stored at the Laboratoire de Biométrie et Biologie  
160 Evolutive (LBBE), Lyon, France. All these mice were sacrificed at capture. The populations of Tournay  
161 and Frontignan were sampled repeatedly in different seasons, thus sampling different age structures,  
162 with younger mice in summer and autumn, towards the end of the breeding season (Renaud et al.,  
163 2017). This allowed an evaluation of the variation due to seasonal variation. The pattern of mandible  
164 shape differentiation between these populations has recently been described (Renaud et al., 2017);  
165 for authorization information, see therein.

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

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

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

### 189 *Morphometric analysis*

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

194 Mandibular shape was quantified with a set of 15 landmarks (Fig. 3A) commonly used to describe the  
195 mouse mandible (Klingenberg, Leamy & Cheverud, 2004; Renaud, Alibert & Auffray, 2012). They  
196 were digitized using TPSDig 2.0 (Rohlf, 2010a). A Procrustes superimposition was performed using  
197 TPSRelw (Rohlf, 2010b). Using this method, the configurations of landmarks are superimposed in  
198 three steps including size scaling, translation, and rotation. The resulting aligned coordinates  
199 (Procrustes coordinates) were used as shape variables in the subsequent analyses. Mandible size was  
200 estimated by the centroid size, i.e. the square root of the sum of the squared distances from each  
201 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.

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

266

## 267 **Results**

### 268 *Context: Phylogenetic relationships and climatic background*

269 All Orkney mice belong to the same clade, together with some continental mice (Fig. 4A). Mice from  
270 Guillo Island, in the Kerguelen Archipelago all displayed exactly the same haplotype (Hardouin et al.,  
271 2010). Compared to this phylogenetic homogeneity on islands, mice from Western Europe are much  
272 more diversified, and belong to different clades. This diversity reflects the long history of human  
273 travels, allowing an important gene flow all over Europe.

274 Regarding the climatic conditions, the 19 bioclimatic variables retrieved from WorldClim were  
275 summarized using a PCA (Fig. 4B, C). Four axes explained ~5% of variance or more (PC1: 50.7%, PC2:  
276 31.0%, PC3: 12.3%, PC4: 4.9%). On the first principal components, all Orkney islands are  
277 characterized by a wet and relatively cold climate (Fig. 4B, C). Guillo Island (Kerguelen Archipelago)  
278 displays a stable and cold environment. In contrast, the continental localities, ranging from Germany  
279 to Italy, are characterised by variable climatic conditions.

### 280 *Mandible shape*

281 Five axes explained more than 5% of the total variance (PC1: 22.5%, PC2: 13.7%, PC3: 8.9%, PC4:  
282 7.5%, PC5: 5.8%) in the PCA performed on the Procrustes coordinates. Based on this set of axes,  
283 significant morphological differences were evidenced between the main populations considered:  
284 commensal continent vs commensal insular (Orkney), and feral populations (Faray, Frontignan, and  
285 Guillo) vs their commensal relatives (continent and Orkney) (Table 2).

286 Between-group variation explained 32.9% of this total variance. On the first two axes of the  
287 between-group PCA (bgPC1: 46.7%; bgPC2: 21.6%), three groups of localities could be identified (Fig.  
288 5A): Orkney islands, continental Western Europe, and Guillo Island. All Orkney populations tended  
289 to cluster together towards negative bgPC1 and positive bgPC2 values (upper left part of the  
290 morphospace). They were opposed along bgPC2 to the different populations of continental Western  
291 Europe. Shape differences between mean mandible shape of Western Europe vs. Orkney were subtle  
292 and distributed all over the mandible (Fig. 5B). Orkney mandibles tended to display a thinner linguo-

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

302 The Guillou mice from Kerguelen Archipelago clearly departs from all other groups mostly along  
303 bgPC1. On bgPC2, it shares positive values with most Orkney populations. The morphology of Guillou  
304 mandibles is characterized by an extended condyle, and a forwardly oriented coronoid process (Fig.  
305 5B). Mice from Faray, the feral population from Orkney, are within the range of other Orkney  
306 populations, but the most extreme towards Guillou along the bgPC1 axis.

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

#### 314 *Mechanical advantage*

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

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

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

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

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

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

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

334 Climatic conditions were described by the first four axes of the PCA on the 19 bioclimatic variables of  
335 WorldClim. The phylogenetic relationships were described by the first four axes of a PCOA on the  
336 matrix of p-distance based on the D-loop analysis (Supplementary Table 3), all explaining more than  
337 5% of variance (PC1: 58.8%, PC2: 22.8%, PC3: 8.7%, PC4: 5.6%).

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

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

350

## 351 **Discussion**

352 *Differentiation of mandible morphology in Orkney*

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

365

#### 366 *Balanced impact of climate and phylogeny on mandible shape*

367 Phylogeny and climate almost equally explained the mandibular shape variation (around 5%). In  
368 contrast, phylogeny was the first explanatory factor when considering molar evolution among house  
369 mouse populations including insular ones (Ledevin et al., 2016) and in other rodents (Caumul & Polly,  
370 2005; Ledevin et al., 2018). The importance of climate in the present dataset may be due to a more  
371 important influence of environmental factors on the mandible, which can remodel through life and is  
372 more prone to vary due to local food resources, compared to teeth that are only affected by wear  
373 once erupted (Renaud & Auffray, 2010; Ledevin et al., 2012). Examples of plastic shape changes are  
374 provided by the mandibles of mice maintained in the lab, and by seasonal variations in Frontignan. In  
375 both cases, ageing may be the primary driver of mandible shape differences. However, the limited  
376 influence of lifestyle and conditions of hosting on mandible shape suggests that the role of plastic  
377 remodelling remained of minor importance in driving the observed morphological differentiation  
378 compared to other sources of variation.

379

#### 380 *Does feral life trigger a convergent response?*

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

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

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

407

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

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

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

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

445

#### 446 *Conclusions*

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



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

456

## 457 **Acknowledgments**

458 We thank Annie Orth and Josette Catalan for their participation to the 2012 field campaign, as well as  
459 Jean-Pierre Quéré for facilitated access and many discussions about the material from the CBGP. We  
460 also thank Julien Claude, Anthony Herrel, Samuel Ginot, and Anne Beatrice Dufour for support and  
461 constructive discussions on different aspects of this study, as well as Anne Tresset and two  
462 anonymous reviewers for their constructive comments. This study was supported by the ANR  
463 Bigtooth (ANR-11-BSV7-008). This is publication ISEM 2018-296.

464

## 465 **References**

- 466 **Akaike H. 1973.** Maximum likelihood identification of Gaussian autoregressive moving average  
467 models. *Biometrika* **60**: 255-265.
- 468 **Albert FW, Shchepina O, Winter C, Römler H, Teupser D, Palme R, Ceglarek U, Kratzsch J, Sohr R,  
469 Trut LN, Thiery J, Morgenstern R, Plyusnina IZ, Schöneberg T, Pääbo S. 2008.** Phenotypic  
470 differences in behavior, physiology and neurochemistry between rats selected for tameness  
471 and for defensive aggression towards humans. *Hormones and Behavior* **53**: 413-421.
- 472 **Anderson PSL, Renaud S, Rayfield EJ. 2014.** Adaptive plasticity in the mouse mandible. *BMC*  
473 *Evolutionary Biology* **14**: 85.
- 474 **Auffray J-C, Tchernov E, Bonhomme F, Heth G, Simson S, Nevo E. 1990.** Presence and ecological  
475 distribution of *Mus "spretoides"* and *Mus musculus domesticus* in Israel. Circum-  
476 Mediterranean vicariance in the genus *Mus*. *Zeitschrift für Säugetierkunde* **55**: 1-10.
- 477 **Baverstock H, Jeffery N, Cobb SN. 2013.** The morphology of the mouse masticatory musculature.  
478 *Journal of Anatomy* **223**: 46-60.
- 479 **Berry RJ. 1970.** The natural history of the house mouse. *Field Studies* **3**: 219-269.
- 480 **Berry RJ, A.J. B, Anderson TJC, Scriven P. 1992.** The house mice of Faray, Orkney. *Journal of Zoology*  
481 **228**: 233-246.
- 482 **Bonhomme F, Orth A, Cucchi T, Rajabi-Maham H, Catalan J, Boursot P, Auffray J-C, Britton-Davidian  
483 J. 2011.** Genetic differentiation of the house mouse around the Mediterranean basin:  
484 matrilineal footprints of early and late colonization. *Proceedings of the Royal Society of  
485 London, Biological Sciences (serie B)* **278**: 1034-1043.
- 486 **Cassaing J, Croset H. 1985.** Organisation spatiale, compétition et dynamique des populations  
487 sauvages de Souris (*Mus spretus* Lataste et *Mus musculus domesticus* Ruddy) du Midi de la  
488 France. *Zeitschrift für Säugetierkunde* **50**: 271-284.
- 489 **Caumul R, Polly PD. 2005.** Phylogenetic and environmental components of morphological variation:  
490 skull, mandible, and molar shape in marmots (*Marmota*, Rodentia). *Evolution* **59**: 2460-2472.

491 **Chapuis J-L, Frenot Y, Lebouvier M. 2004.** Recovery of native plant communities after eradication of  
492 rabbits from the subantarctic Kerguelen Islands, and influence of climate change. *Biological*  
493 *Conservation* **117**: 167-179.

494 **Corti M, Rohlf FJ. 2001.** Chromosomal speciation and phenotypic evolution in the house mouse.  
495 *Biological Journal of the Linnean Society* **73**: 99-112.

496 **Cox PG, Jeffery N. 2011.** Reviewing the morphology of the jaw-closing musculature in squirrels, rats,  
497 and guinea pigs with contrast-enhanced microCT. *The Anatomical Record* **294**: 915-928.

498 **Cucchi T, Vigne J-D. 2006.** Origin and diffusion of the house mouse in the Mediterranean. *Human*  
499 *Evolution* **21**: 95-106.

500 **Cucchi T, Vigne J-D, Auffray J-C. 2005.** First occurrence of the house mouse (*Mus musculus*  
501 *domesticus* Schwarz & Schwarz, 1943) in the Western Mediterranean: a zooarchaeological  
502 revision of subfossil occurrences. *Biological Journal of the Linnean Society* **84**: 429-445.

503 **Darriba D, Taboada GL, Doallo R, Posada D. 2012.** jModelTest 2: more models, new heuristics and  
504 parallel computing. *Nature Methods* **9**: 772.

505 **Dray S, Dufour A-B. 2007.** The ade4 package: implementing the duality diagram for ecologists.  
506 *Journal of Statistical Software* **22**: 1-20.

507 **Fabre P-H, Herrel A, Fitriana Y, Meslin L, Hautier L. 2017.** Masticatory muscle architecture in a  
508 water-rat from Australasian (Murinae, *Hydromys*) and its implication for the evolution of  
509 carnivory in rodents. *Journal of Anatomy* **231**: 380-397.

510 **Fick SE, Hijmans RJ. 2017.** WorldClim 2: new 1-km spatial resolution climate surfaces for global land  
511 areas. *International Journal of Climatology* **37**: 4302-4315.

512 **Gabriel SI, Jóhannesdóttir F, Jones EP, Searle JB. 2010.** Colonization, mouse-style. *BMC Biology* **8**:  
513 131.

514 **Ganem G. 1991.** A comparative study of different populations of *Mus musculus domesticus*:  
515 emotivity as an index of adaptation to commensalism. *Comparative Biochemistry and*  
516 *Physiology* **99A**: 531-536.

517 **Ganem G. 1998.** Behavioural and physiological characteristics of standard and chromosomally  
518 divergent populations of house mice from the Orkney archipelago (Scotland). *Acta*  
519 *Theriologicala* **43**: 23-38.

520 **Geiger M, Evin A, Sánchez-Villagra MR, Gascho D, Mainini C, Zollikofer CPE. 2017.** Neomorphosis  
521 and heterochrony of skull shape in dog domestication. *Scientific Reports* **7**: 13443.

522 **Geiger M, Sánchez-Villagra MR, Lindholm AK. 2018.** A longitudinal study of phenotypic changes in  
523 early domestication of house mice. *Royal Society Open Science* **5**: 172099.

524 **Ginot S, Agret S, Claude J. 2018.** Bite force performance, fluctuating asymmetry and antisymmetry in  
525 the mandible of inbred and outbred wild-derived strains of mice (*Mus musculus domesticus*).  
526 *Evolutionary Biology* **45**: 287-302.

527 **Gouy M, Guindon S, Gascuel O. 2009.** SeaView version 4: a multiplatform graphical user interface for  
528 sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* **27**: 221-  
529 224.

530 **Guindon S, Dufayard J-F, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010.** New algorithms and  
531 methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML  
532 3.0. *Systematic Biology* **59**: 307-321.

533 **Hammer Ø, Harper DAT, Ryan PD. 2001.** PAST: Paleontological Statistics software package for  
534 education and data analysis. *Palaeontological Electronica* **4**: 1-9.

535 **Hardouin E, Chapuis J-L, Stevens MI, van Vuuren JB, Quillfeldt P, Scavetta RJ, Teschke M, Tautz D.**  
536 **2010.** House mouse colonization patterns on the sub-Antarctic Kerguelen Archipelago  
537 suggest singular primary invasions and resilience against re-invasion. *BMC Evolutionary*  
538 *Biology* **10**: 325.

539 **Hijmans RJ. 2014.** raster: Geographic data analysis and modelling. R package.

540 **Hulme-Beaman A, Dobney KM, Cucchi T, Searle JB. 2016.** An ecological and evolutionary framework  
541 for commensalism in anthropogenic environments. *Trends in Ecology and Evolution* **31**: 633-  
542 645.

543 **Johnsson M, Gering E, Willis P, Lopez S, Van Dorp L, Hellenthal G, Henriksen R, Friberg U, Wright D.**  
544 **2016.** Feralization targets different genomic loci to domestication in the chicken. *Nature*  
545 *Communications* **7**: 12950.

546 **Jones EP, Jóhannesdóttir F, Gündüz I, Richards MB, Searle JB. 2011.** The expansion of the house  
547 mouse into north-western Europe. *Journal of Zoology* **283**: 257-268.

548 **Kidder JH. 1876.** The natural history of the Kerguelen Island. *The American Naturalist* **10**: 481-484.

549 **Klingenberg CP, Leamy LJ, Cheverud JM. 2004.** Integration and modularity of quantitative trait locus  
550 effects on geometric shape in the mouse mandible. *Genetics* **166**: 1909-1921.

551 **Kruska DCT. 2005.** On the evolutionary significance of encephalization in some eutherian mammals:  
552 effects of adaptive radiation, domestication and feralization. *Brain, Behavior and Evolution*  
553 **65**: 73-108.

554 **Kumar S, Stecher G, Tamura K. 2016.** MEGA7: Molecular Evolutionary Genetics Analysis version 7.0  
555 for bigger datasets. *Molecular Biology and Evolution* **33**: 1870-1874.

556 **Langsrud Ø, Mevik B-H. 2012.** ffmanova: Fifty-fifty MANOVA. [https://CRAN.R-](https://CRAN.R-project.org/package=ffmanova)  
557 [project.org/package=ffmanova](https://CRAN.R-project.org/package=ffmanova).

558 **Le Roux V, Chapuis J-L, Frenot Y, Vernon P. 2002.** Diet of the house mouse (*Mus musculus*) on  
559 Guillou Island, Kerguelen archipelago, Subantarctic. *Polar Biology* **25**: 49-57.

560 **Ledevin R, Chevret P, Ganem G, Britton-Davidian J, Hardouin EA, Chapuis J-L, Pisanu B, Mathias**  
561 **MdL, Schlager S, Auffray J-C, Renaud S. 2016.** Phylogeny and adaptation shape the teeth of  
562 insular mice. *Proceedings of the Royal Society of London, Biological Sciences (serie B)* **283**:  
563 20152820.

564 **Ledevin R, Chevret P, Helvaci Z, Michaux JR, Renaud S. 2018.** Bank voles in Southern Eurasia:  
565 Vicariance and adaptation. *Journal of Mammalian Evolution* **25**: 119-129.

566 **Ledevin R, Quéré J-P, Michaux JR, Renaud S. 2012.** Can tooth differentiation help to understand  
567 species coexistence? The case of wood mice in China. *Journal of Zoological Systematics and*  
568 *Evolutionary Research* **50**: 315-327.

569 **Lenormand T. 2002.** Gene flow and the limits to natural selection. *Trends in Ecology and Evolution*  
570 **17**: 183-189.

571 **Librado P, Rozas J. 2009.** DnaSP v5: a software for comprehensive analysis of DNA polymorphism  
572 data. *Bioinformatics* **25**: 1451-1452.

573 **Lowe S, Browne M, Boudjelas S, De Poorter M. 2000.** 100 of the World's Worst Invasive Alien  
574 Species. A selection from the Global Invasive Species Database.: The Invasive Species  
575 Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the  
576 World Conservation Union (IUCN). 1-12.

577 **O'Regan H, Kitchener A. 2005.** The effects of captivity on the morphology of captive, domesticated,  
578 and feral mammals. *Mammal Review* **35**: 215-230.

579 **Rambaut A. 2012.** Figtree v1.4. <http://tree.bio.ed.ac.uk/software/figtree/>.

580 **Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014.** Tracer v1.6.

581 **Renaud S, Alibert P, Auffray J-C. 2012.** Modularity as a source of new morphological variation in the  
582 mandible of hybrid mice. *BMC Evolutionary Biology* **12**: 141.

583 **Renaud S, Auffray J-C. 2010.** Adaptation and plasticity in insular evolution of the house mouse  
584 mandible. *Journal of Zoological Systematics and Evolutionary Research* **48**: 138-150.

585 **Renaud S, Gomes Rodrigues H, Ledevin R, Pisanu B, Chapuis J-L, Hardouin EA. 2015.** Fast  
586 morphological response of house mice to anthropogenic disturbances on a Sub-Antarctic  
587 island. *Biological Journal of the Linnean Society* **114**: 513-526.

588 **Renaud S, Hardouin EA, Pisanu B, Chapuis J-L. 2013.** Invasive house mice facing a changing  
589 environment on the Sub-Antarctic Guillou Island (Kerguelen Archipelago). *Journal of*  
590 *Evolutionary Biology* **26**: 612-624.

591 **Renaud S, Hardouin EA, Quéré J-P, Chevret P. 2017.** Morphometric variations at an ecological scale:  
592 Seasonal and local variations in feral and commensal house mice. *Mammalian Biology* **87**: 1-  
593 12.

594 **Renaud S, Ledevin R, Pisanu B, Chapuis J-L, Quillfeldt P, Hardouin EA. 2018.** Divergent in shape and  
595 convergent in function: adaptive evolution of the mandible in Sub-Antarctic mice. *Evolution*  
596 **72:** 878-892.

597 **Rohlf FJ. 2010a.** TPSdig v.2. 2.16 ed: Ecology and Evolution, SUNY at Stony Brook.

598 **Rohlf FJ. 2010b.** TPSRelw, relative warps analysis.: Department of Ecology and Evolution, State  
599 University of New York at Stony Brook, Stony Brook, NY.

600 **Ronquist F, Teslenko M, Mark Pvd, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA,  
601 Huelsenbeck JP. 2012.** MrBayes 3.2: Efficient Bayesian phylogenetic inference and model  
602 choice across a large model space. *Systematic Biology* **61:** 539-542.

603 **Sánchez-Villagra MR, Geiger M, Schneider RA. 2016.** The taming of the neural crest: a  
604 developmental perspective on the origins of morphological covariation in domesticated  
605 mammals. *Royal Society Open Science* **3:** 160107.

606 **Searle JB, Jones CS, Gündüz İ, Scascitelli M, Jones EP, Herman JS, Victor RR, Noble LR, Berry RJ,  
607 Giménez MD, Jóhannesdóttir F. 2009.** Of mice and (Viking?) men: phylogeography of British  
608 and Irish house mice. *Proceedings of the Royal Society of London, Biological Sciences (serie B)*  
609 **276:** 201-207.

610 **Siahsarvie R, Auffray J-C, Darvish J, Rajabi-Maham H, Yu H-T, Agret S, Bonhomme F, Claude J. 2012.**  
611 Patterns of morphological evolution in the mandible of the house mouse *Mus musculus*  
612 (Rodentia: Muridae). *Biological Journal of the Linnean Society* **105:** 635-647.

613 **Slábová M, Frynta D. 2007.** Morphometric variation in nearly unstudied populations of the most  
614 studied mammals: The non-commensal house mouse (*Mus musculus domesticus*) in the Near  
615 East and Northern Africa. *Zoologischer Anzeiger* **246:** 91-101.

616 **Smith BP, Lucas TA, Norris RM, Henneberg M. 2017.** Brain size/body weight in the dingo (*Canis*  
617 *dingo*): comparisons with domestic and wild canids. *Australian Journal of Zoology* **65:** 292-  
618 301.

619 **Trut L, Oskina I, Kharlamova A. 2009.** Animal evolution during domestication: the domesticated fox  
620 as a model. *Bioessays* **31:** 349-360.

621 **Weissbrod L, Marshall FB, Valla FR, Khalaily H, Bar-Oz G, Auffray J-C, Vigne J-D, Cucchi T. 2017.**  
622 Origins of house mice in ecological niches created by settled hunter-gatherers in the Levant  
623 15,000 y ago. *Proceedings of the National Academy of Sciences, USA* **114:** 4099-4104.

624 **Wilkins AS, Wrangham RW, Fitch WT. 2014.** The "domestication syndrome" in mammals: a unified  
625 explanation based on neural crest cell behavior and genetics. *Genetics* **197:** 795-808.

626 **Zeder MA. 2012.** Pathways to animal domestication. In: Gepts P, Famula TR, Bettinger RL, Brush SB,  
627 Damania AB, McGuire PE and Qualset CO, eds. *Biodiversity in agriculture: Domestication,  
628 evolution and sustainability*. Cambridge: Cambridge University Press. 227-259.

629

630

Group	Country	Code	Lifestyle	Locality <sub>morpho</sub>	Hosting conditions	N <sub>morpho</sub>	Locality <sub>genetic</sub>	N <sub>genetic</sub>	N <sub>haplo</sub>
<b>Continental Europe</b>	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
<b>Kerguelen Archipelago</b>	France	GU	Feral	Guillou Island	Field	79	Guillou Island	79	1
<b>Orkney Archipelago</b>	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<sub>morpho</sub>, N<sub>morpho</sub>) and the genetic analysis (Locality<sub>genetic</sub>, N<sub>genetic</sub>). 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<sub>haplo</sub>) 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	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>
Frontignan (feral)		<b>0.0001</b>	<b>0.0001</b>	<b>0.0001</b>
Guillou (feral)			<b>0.0001</b>	<b>0.0001</b>
Commensal Orkney				<b>0.0001</b>

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



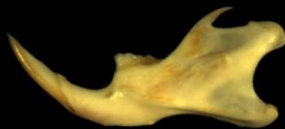
5 mm



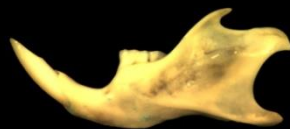
a. Cologne-Bonn



b. Gardouch



c. Montpellier

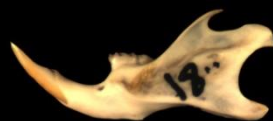


d. San Bernardino

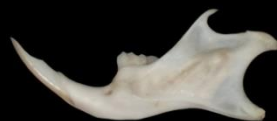


e. Tournai

*Continent commensal*



f. Frontignan

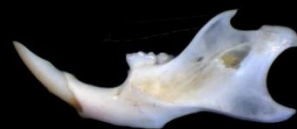


g. Guillou



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

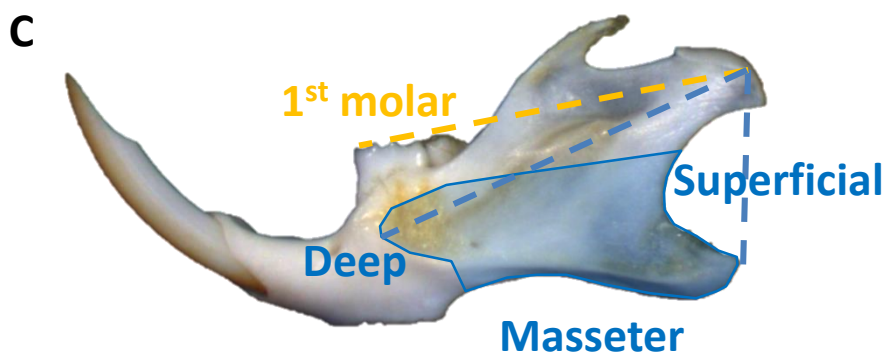
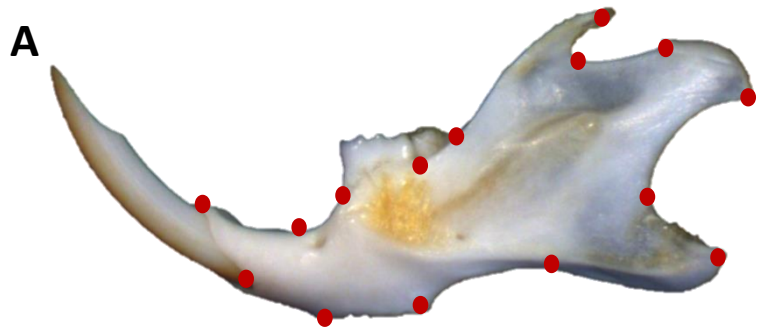


p. South Ronaldsay L

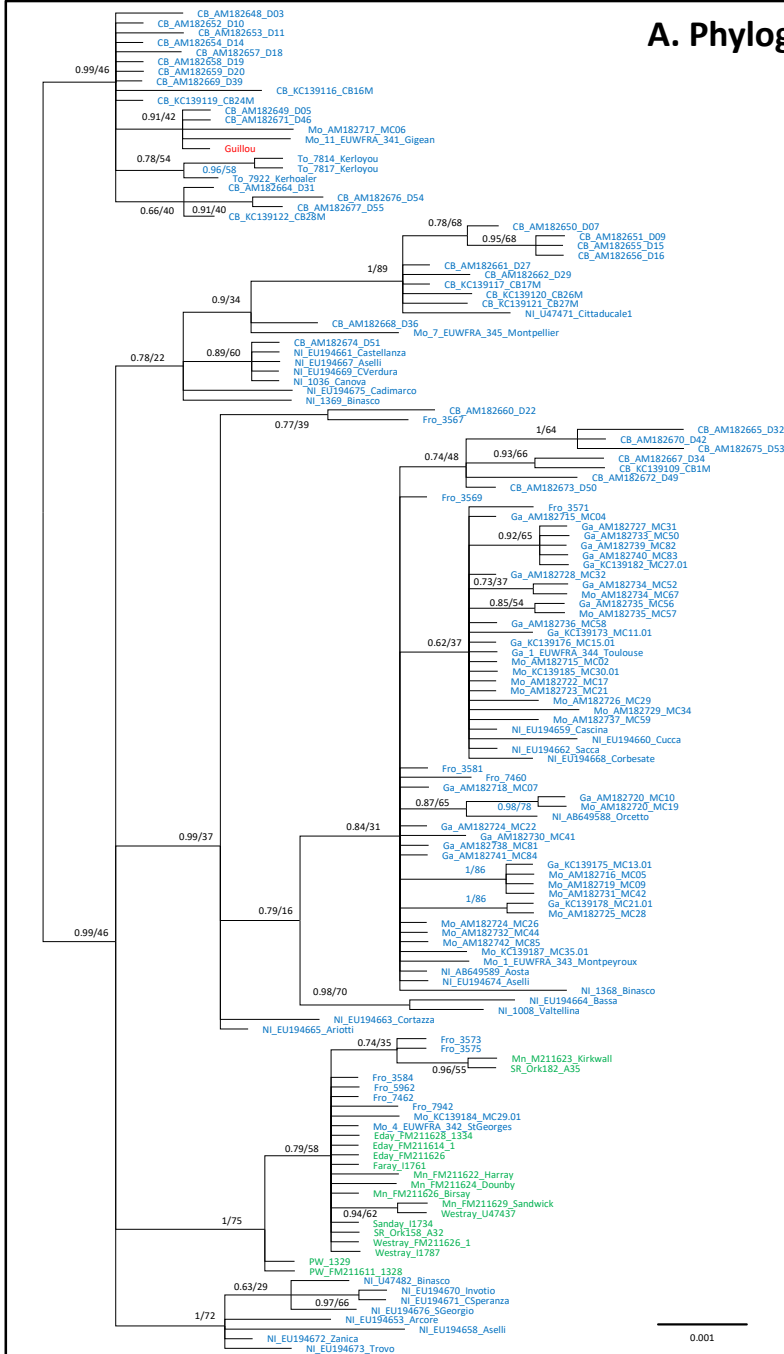


q. Westray

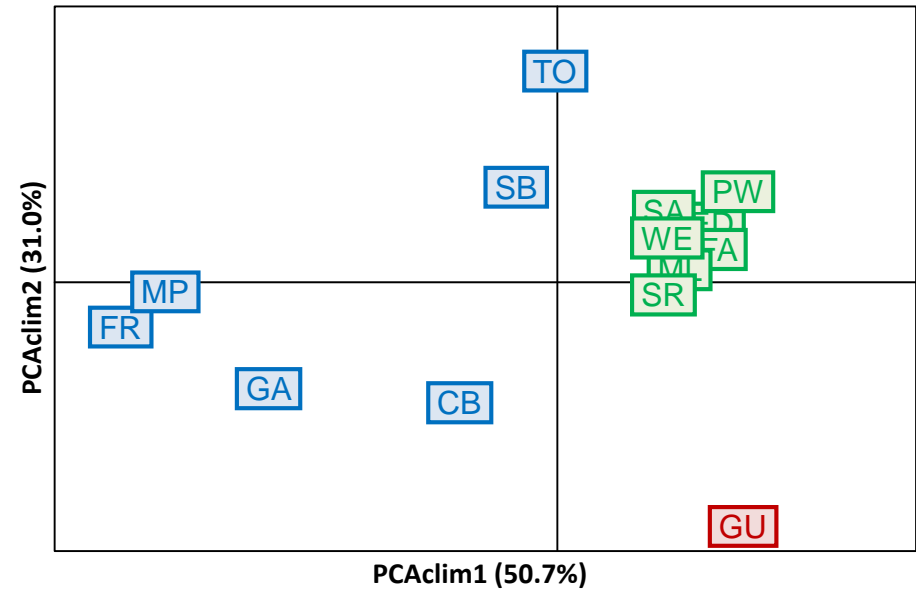
*Orkney commensal*



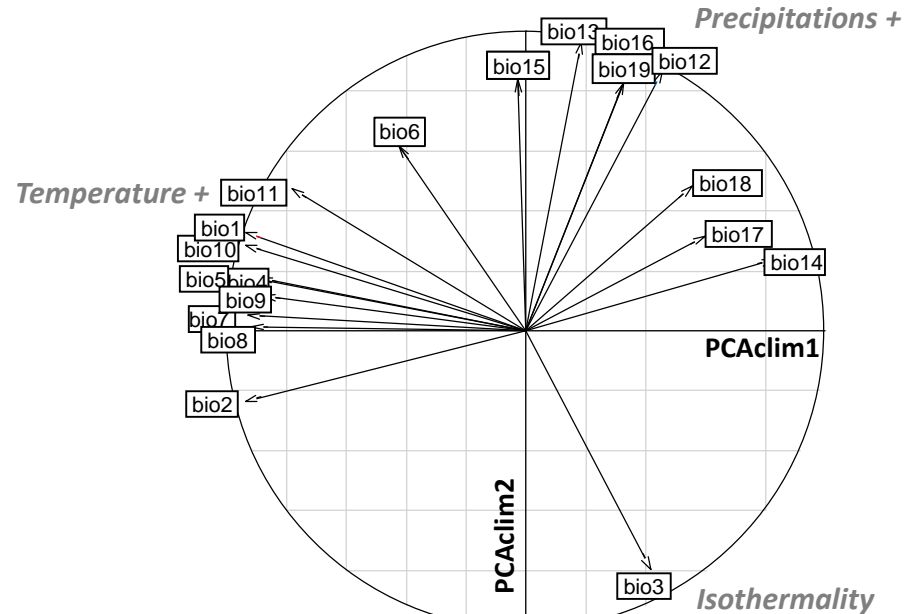
## A. Phylogeny

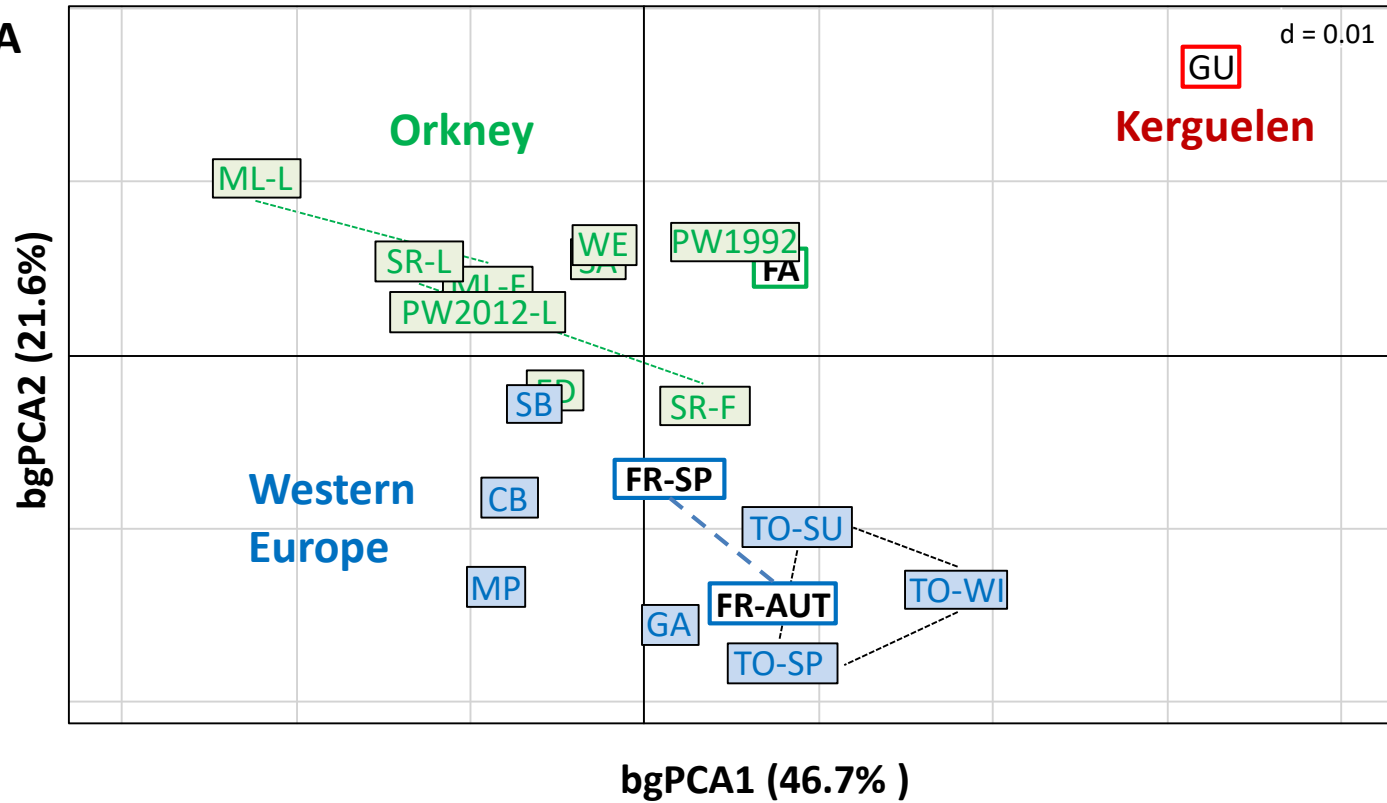
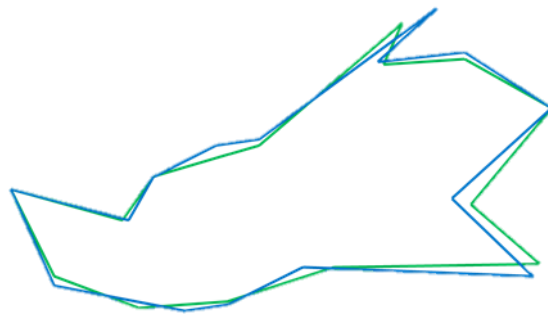


## B. Climatic variation among localities

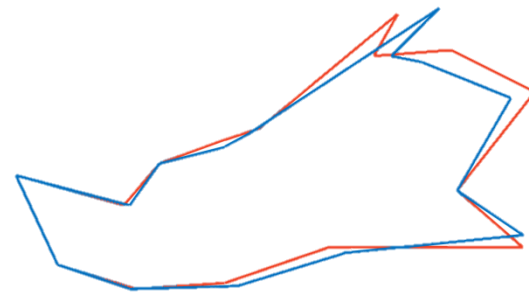


## C. Contribution of the climatic variables to the axes



**A****B**

Western Europe vs Orkney



Western Europe vs Kerguelen

