



Original investigation

Morphometric variations at an ecological scale: Seasonal and local variations in feral and commensal house mice

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ABSTRACT

The time scales of evolutionary and ecological studies tend to converge, as shown by evidences that contemporary evolution can occur as fast as ecological processes. This opens new questions regarding variation of characters usually considered to change mostly along an evolutionary time scale, such as morphometric traits, including osteological and dental features such as mandibles and teeth of mammals. Using two-dimensional geometric morphometric approach, we questioned whether such features can change on a seasonal and local basis, in relation to the ecological dynamics of the populations. Our model comprised populations of house mice (*Mus musculus domesticus*) in two contrasted situations in mainland Western Europe: a feral population vs. two close commensal populations. Mitochondrial DNA (D-loop) provided insight into the diversity and dynamics of the populations.

The feral population appeared as genetically highly diversified, suggesting a possible functioning as a sink in relation to the surrounding commensal populations. In contrast, commensal populations were highly homogeneous from a genetic point of view, suggesting each population to be isolated. This triggered morphological differentiation between neighboring farms. Seasonal differences in morphometric traits (mandible size and shape and molar size and shape) were significant in both settings, although seasonal variations were greater in the feral than in the commensal population. Seasonal variations in molar size and shape could be attributed to differential wear in young or overwintered populations. Differences in mandible shape could be related to aging in overwintered animals, but also possibly to differing growth conditions depending on the season. The impact of these ecological processes on morphometric traits is moderate compared to divergence over a large biogeographic scale, but their significance nevertheless underlines that even morphological characters may trace populations dynamics at small scale in time and space.

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Introduction

Issues of important current concern, such as adaptation of invasive species to their new environments, response of local species to invasions and/or climate change, deliver growing evidence that evolution can take place at time scales usually considered to be characteristic of ecological processes (Kinnison and Hairston, 2007; Lambrinos, 2004). Morphological characters were traditionally thought to vary at evolutionary timescales. Nevertheless, due to plasticity but also to microevolutionary changes, they can also vary

at fast rates and be involved in contemporary evolution (Collyer et al., 2007; Ghalambor et al., 2007). This growing body of evidence may also be due to the development of geometric morphometric methods, allowing the quantification of such fine-scale variation. To provide a background for such fine-scale processes, reference studies to assess the amount of variation expected for morphological traits due to background ecological processes, such as seasonal variations in populations, are often lacking because sampling designed for ecology, such as mark-recapture, are not designed for delivering osteological material for morphometric studies.

The aim of this study is to provide a hint into morphometric variations related to small-scale processes such as seasonal variation and local differentiation. The model is the Western house mouse (*Mus musculus domesticus*). It is known for its great adaptability

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and behavioral flexibility, thus exposing it to contrasted ecological conditions even at small scale in time and space. We investigated two features well studied in mice, having different developmental characteristics and hence potentially responding differently to processes at an ecological scale. The mandible is an osteological structure that grows postnatally, reaching ~95% of its final adult shape shortly after weaning (Swiderski and Zelditch, 2013). Bone remodeling occurs nevertheless during the whole animal's life, and this can trigger plastic differences in response to food resources even during adult, post-weaning life (Anderson et al., 2014). In contrast, the first upper molar is mineralized during pre-natal life and once erupted, it is only affected by wear. This may make the mandible more prone to respond to short term processes.

The size and shape of both features were quantified using a 2D outline analysis (Renaud et al., 2013). Several small-scale sources of variations were investigated: (1) Seasonal variations in two populations sampled successively in time. (2) Way of life, by considering feral and commensal populations. Way of life may interfere with seasonal variation. Commensal mice may reproduce all year round when food of sufficient quality and quantity is available (Berry, 1981; Pocock et al., 2004; Pryor and Bronson, 1981; Rowe et al., 1983). In contrast, feral populations are more exposed to seasonal variations in climate and food supply, and consequently, they should display seasonal breeding (Berry, 1981; Efford et al., 1988; Matthewson et al., 1994; Triggs, 1991). (3) Local differences between neighboring farms.

Wear stage based on the upper molar row has been proposed to be the best estimate of age for wild populations of mice (Lidicker, 1966). It was used to assess age structure in the different populations. Body size measurements were further used to evaluate body condition of the animals, and to compare the overall growth to the size of the osteological trait (mandible). Genetics (mitochondrial DNA) was assessed for a subset of mice, to describe the phylogenetic background of the investigated populations. Altogether, these informations provided the background to investigate morphometric variations of the mandible and molar through seasons and across populations. Finally, the variations due to seasonality and local differentiation were compared to a set of mainland localities, in order to assess the importance of the small-scale processes compared to larger scale differentiation.

Material

Commensal mice were sampled from two farms in Tourn (Brittany, France). Most mice were trapped in a large pigsty in Kerloyou, in August 2011, November 2011 and May 2012 (Table 1, Fig. 1F). A farm in the nearby place Kerc'hoaler, 1.8 km away, was further sampled in June 2012.

Mice from Frontignan corresponded to an outdoor, feral population found in the Aresquiers spit of land between the Mediterranean Sea and the Étang de Vic, close to Montpellier (France). Mice were trapped in April 2009, October 2009 and March 2010 over less than 1 km (Table 1). Despite the uneven sample size (7, 20 and 4 specimens respectively), the trapping effort was similar for the three seasons. One additional mouse was captured in March 2013.

The commensal population of Gardouch, near Toulouse, was further documented (Renaud et al., 2015a). It was trapped in a roe deer enclosure from November 2003 to April 2004 (68 specimens). This context of roe deer breeding provided the mice with food ad libitum, as in the Kerloyou pigsty.

In Frontignan, Tourn and Gardouch, animals were live trapped, weighed and measured for head + body length (HBL) by the same operator (JPQ). Wear stage was evaluated on the upper molar row for all animals, using classes from one (juvenile, third molar not erupted) up to seven (heavily worn molars with all cusps associated

on the three molars of the row) (Avenant and Smith, 2004). Each molar row was scored twice, and the average of the two scorings was used as proxy for the age of the animals. Although wear pattern may vary from one population to the other, depending on tooth morphology and food processed, it provided a proxy for assessing the age structure of the populations.

All these specimens are housed at the collection of the Centre de Biologie et Gestion des Populations (Baillarguet, France). The animals were sacrificed by cervical dislocation according to the 2010/63/UE directive with an official authorization held by JPQ (permit 34–107 from the Préfecture de l'Hérault).

All mice were considered in the morphometric analysis, except for the only mouse from March 2013 in Frontignan (Table 1; Fig. 1F). Adults and sub-adults animals with their third molars erupted were considered for morphometric analyses. This excluded one juvenile specimen from November 2011 in Kerloyou, Tourn. It was represented on the size plots but discarded from all tests.

Mandible and tooth shape in Tourn, Frontignan and Gardouch was compared to the geographic variation among a set of commensal populations in mainland Western Europe: Montpellier (Southern France), Cologne-Bonn (Germany), Reggio, San Bernardino and Lombardy (Northern Italy) (Renaud et al., 2015a; Renaud et al., 2015b).

Phylogenetics

The morphometric study was complemented by a genetic analysis of the D-loop (mtDNA) sequences. Twenty-six mice were sequenced in Tourn, corresponding to six randomly sampled specimens for each of the three seasons at the Kerloyou pigsty and eight at the Kerc'hoaler farm (Table 1). Twenty-two mice were sequenced in Frontignan, most of them (14) trapped in October 2009 and the other ones trapped in April 2009 (5), March 2010 (2), and March 2013 (1) (Table 1).

For these samples, DNA was extracted from ethanol-preserved tissue, using the DNeasy Blood and Tissue kit (Qiagen, France). The D-loop was amplified using previously described primers and protocol (Hardouin et al., 2010). The sequences generated were visualized using MEGA6 (Tamura et al., 2013). The new sequences were deposited in GenBank under accession numbers LT718851 to LT718898 (Supplementary Table 1).

This sampling was completed by sequences of various mainland Western Europe locations retrieved from GenBank (Supplementary Table 2).

Methods

Phylogenetic analyses

Haplotypes and genetic diversity indices for Frontignan and Tourn sequences were determined with DNAsp v 5 (Librado and Rozas, 2009). The haplotypes were combined with sequences retrieved from GenBank and aligned with MUSCLE implemented in SeaView (Gouy et al., 2010). The final alignments comprised 313 sequences and 833 positions. The phylogenetic tree was reconstructed using Bayesian inference (BI) with MrBayes v3.2 (Ronquist et al., 2012). The best model (TrN+I+G) was determined with jModelTest (Darriba et al., 2012) using the Akaike criterion (AIC) (Akaike, 1973). As TrN model was not available in MrBayes we used Nst = mixed, which sampled across substitution models. Node robustness were estimated using posterior probabilities (PP) in BI analyses. For BI, two Markov chain Monte Carlo (MCMC) analyses were run independently for 20 000 000 generations. One tree was sampled every 500 generations. The burn-in was graphically determined with Tracer v1.6 (Rambaut et al., 2014). We also checked

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