
Form and Function

Changing invaders: the evolution of alien rodents on islands

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Introduced species often adapt their behaviour, morphology, and ecological niche in response to variables that differ from those of their native range. We analysed body size and island data for 241 rodent populations belonging to 16 species on 212 islands worldwide to test whether body size of insular populations of introduced rodents is correlated with the geographical and ecological characteristics of the islands as well as time in isolation. Introduced rodents follow the predicted island rule trend, with body size shifts more pronounced for populations with greater residence times on the islands. Body size of insular populations is positively correlated with latitude, consistent with thermoregulatory predictions based on Bergmann's rule. Body size of insular populations is negatively correlated with number of co-occurring mammalian species, especially other aliens, confirming an ecological hypothesis of the island rule. Carnivory in rats and mice in the form of predation on nesting seabird colonies seems to promote 1.4- to 1.9-fold increases in body size: Henderson Island (Pitcairn Islands) and Gough Island (South Atlantic) are home to rats and mice (respectively) almost twice the size of their mainland conspecifics. The island rule is a pervasive pattern in rodents, exhibited across a broad span of geographical regions, time periods and for introduced as well as native populations. Time in isolation impacts body size evolution profoundly. All insular populations of Polynesian rats (*Rattus exulans*) and Asian house rats (*Rattus tanezumi*), both Holocene introductions, evolve larger body sizes, whereas almost all Anthropocene populations of the brown rat (*Rattus norvegicus*) evolved smaller body sizes. Individual populations, however, varied substantially in their rate of body size evolution, with some populations exhibiting significant body size change in less than 400 years, here proposed as likely coinciding with increased levels of carnivory.

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Body size and craniometry of the herb field mouse in the context of a geographical clines

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The herb field mouse (*Apodemus uralensis*) is widely but not continuously distributed across Europe and Asia, with new localities for the species being recently registered in the southern, northern, north-western and eastern parts of the species distribution range. We analyzed geographic variation of body and skull size of *A. uralensis* (over 600 individuals) across the species range, based on published sources and raw data from authors. We found the species to be characterized by high size variability, not following Bergmann's or Murphy's rules and camouflaging latitudinal and longitudinal clines in measurements. Due to wide variations in the body size across the sample, measured characters were size-adjusted using the geometric mean procedure. Distinct size differences were registered on the eastern and southern edges of the distribution range, with these populations having the largest individuals according to average body and skull size. Sex dimorphism in *A. uralensis* is weakly expressed in many populations, while juvenile and subadult individuals also differ in body weight, but not in size. Significant differences in external and cranial measurements were found in *A. uralensis* from different regions of the same country (e.g. Hungary and Slovakia). The smallest, as well as medium and highest average values of the same parameter, such as body length or upper toothrow length, were characteristic to *A. uralensis* populations from Central Europe. We can not attribute these differences to individual measurement errors or biases by different researchers, as high variability of several parameters was also shown in samples processed by a single author.

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Evolving teeth within a stable masticatory apparatus in Orkney mice

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Mice from the Orkney archipelago exhibit an important diversity regarding molar shape. While on some islands mice display a usual dental pattern, teeth from other islands display additional cusplets and unusual phenotypes that may constitute case studies for evaluating the potential functional relevance of dental changes. We developed a multifaceted approach combining 2D and 3D geometric morphometrics, dental topography, dental wear, biomechanics, estimations of masticatory muscles force, and in vivo bite force on wild-derived lab descendants exemplifying the two extreme dental morphologies. The two strains differed in the geometry of the upper and lower tooth rows, and in the topography of the upper row only. Surprisingly, the most derived tooth morphology appeared as the least complex because tooth simplification overwhelmed the signal provided by the occurrence of additional cusplets. No difference in bite force nor muscle force was evidenced, showing that the dental innovation was accommodated without changes in the rest of the masticatory apparatus. A 'non-disruptive pathway' may have facilitated the evolution of new phenotypes, together with the isolation of small populations on remote islands of the archipelago.

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A morphometric mapping analysis of mice molar morphology

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The mouse dentition has been extensively used as a model for the developmental genetic basis of dental morphology. Phenotypic change and malformation have been reported in a variety of mutant mouse strains. In the case of mutant mice showing drastic morphological change in cusp patterns, however, the conventional quantitative approaches, such as landmark-based methods, cannot be applicable due to the lack of biologically and/or geometrically homologous structures between specimens. Therefore, the phenotype–genotype relationship remains to be tested. Here, we applied a landmark-free approach, morphometric mapping (MM) to quantify mice lower first molars. The sample used in this study comprised two strains of wild type house mouse: ICR and BL6, and mice with either loss or gain of function of different developmental genes. Their lower molars were μ CT-scanned and three-dimensional surface models were reconstructed. These models were quantified by MM, using three morphometric parameters: the mean curvature on the crown surface, the height from the cervical plane, and the radius from the centroid of the cervical line. Principal Components Analysis (PCA) was performed in order to identify and visualize major patterns of shape variation in the morphospace. The MM could detect not only the morphological difference between mouse mutants, but also between two wild type strains. The MM method allowed us to quantify and visualize the complicated mice dental morphology precisely. Applying this method to various types of mice mutants that represent altered cusp patterning promises well for an elucidation of the genotype–phenotype relationship.

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Functional morphology of the cochlea of the laminate-toothed rats (family: *Muridae*, subfamily: *Otomyinae*)

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Many species of desert rodents and certain subterranean rodents are known to have hypertrophied auditory bullae. A common functional explanation for this trait is that it is an adaptation to sound amplification that improves low-frequency hearing which is hypothesized to help in both prey capture and predator avoidance; thermoregulation and interspecific communication in burrows and open mostly desert environments. However, besides the hypertrophied bulla, the middle and inner ear are also important in improving low-frequency hearing. Although a plethora of hearing studies in rodents have been conducted, most of these have focused mainly on *Gerbilinae*, *Dipodomysinae*, *Meriones*, and subterranean rodents. However, no studies have looked at the hearing capabilities of *Otomyinae* subfamily in detail only vocalization has been studied on two species (*brantsii* and *littledalei*), although a vague description of *Otomys* (unknown species) malleus and incus and *Parotomys* middle ears basic data have been made. In this study, cochlea morpho-anatomical variation of seven *Otomyinae* species (*Otomys angoniensis*, *Otomys auratus*, *Otomys barbouri*, *Otomys helleri*, *Otomys sloggetti*, *Otomys unisulcatus* and *Parotomys brantsii*) from widely different environments was investigated, focusing on five cochlea features [external cochlear length (ECL), number of turns (TUR), relative length (RECL = ECL/TUR), the curvature gradient (CUR), and the oval window area (OWA)] that play a role in hearing capabilities. Micro-computed tomography and Avizo were used for skull scanning and cochlea segmentation respectively. When correcting for phylogeny and body size OWA and RECL were significantly greater in *P. brantsii*. There was no correlation between cochlea features, bulla and alpine environments.

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Torpor in dwarf hamsters, *Phodopus campbelli* and *Phodopus roborovskii*: a comparative study

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Torpor is characterized by a reduction of core body temperature (CBT) and metabolic rate, and in comparison with hibernation lasts less than one day. Comparative analysis of this phenomenon in closely related species may provide useful information to clarify its regulatory mechanisms and evolution. Species of the *Phodopus* genus provide an excellent opportunity for comparative analysis. Two of three *Phodopus* species we used in this study - desert hamsters (*Phodopus roborovskii*) (DH) and Campbell's hamsters (*Phodopus campbelli*) (CH) originated from different parts of the range. Adult males provided with temperature transponders implanted intraperitoneally to record CBT from September to May were kept in an outdoor enclosure under natural light and temperature. Substantial within- an intraspecific difference in torpor expression were observed. Some hamsters never demonstrated torpor as others had multiple regular torpor bouts. In CH the torpor incidents were timed to the beginning of the photophase, as DH demonstrated multiple bouts of torpor during the whole day. The lowest CBT in CH was 11.5 °C as in DH it did not drop below 23 °C. At that, in DH CBT at the majority (about 90%) of torpor incidents was in the range of 30-32 °C. The results indicate that there are remarkable differences in response to low ambient temperatures between CH and DH. DH demonstrated a shallow torpor with CBT that is much higher not only than that in CH, but also in other daily heterotherms. We may assume that such differences in response to winter conditions reflect species-specific physiological adaptations to the different environment. Supported in part by RFBR-GFEN: #17-54-53206.

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Seasonal features of humoral immune response to T-cell dependent antigen in palaeartic hamsters (*Rodentia, Cricetinae*)

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It is well documented that immune function varies substantially on a seasonal basis. The autumn–winter season is the most critical period for animals. Non-tropical animals have evolved specific adaptations to cope with winter energy shortages. Animals can overcome periods of unfavorable environmental conditions by physiological hypothermia (daily torpor/ hibernation), characterized by strongly reduced metabolic rate and body temperature. Studies from mammals indicate that hibernation affects both the innate and adaptive immune systems. During winter representatives of subfamily *Cricetinae* demonstrate different types of hypothermia: (a) long-term hibernation (e.g. *Cricetus cricetus*); (b) nonstandard short hibernation with irregular bouts of normothermia (*Allocricetulus* sp.); and (c) daily torpor (*Phodopus* sp.). It is the first attempt to compare humoral immunity of the animals with different overwintering strategies. We analyzed seasonal changes in humoral adaptive immune response to a T-cell dependent antigen (KLH) in hamsters with different types of hypothermia. The animals were housed individually under natural light and temperature conditions (outdoor enclosures). The group of ten males of each hamster species was immunized in each season with KLH. Blood samples were taken on day 10. To assess humoral immunity, serum anti-KLH IgG concentrations were assayed using an ELISA according to the method of Drazen et al. with our modifications. The humoral immunity declined during the autumn-winter season and rose in spring (termination of hibernation and onset of reproduction) in hibernating hamster species. Whereas species with daily torpor demonstrated the highest level of specific antibody in autumn, but it decreased in winter and spring. Thus we suggest that humoral immunity is compromised during hibernation in *C. cricetus* and *Allocricetulus curtatus*, but not in breeding season (as trade-off hypothesis predicted), while torpid species (*Phodopus sungorus*, *Phodopus roborovskii*) enhanced their immune function (in autumn) in order to counteract the immunosuppressive effects of stressors that occur in winter (low ambient temperatures and reduced food availability). Supported by a RFBR grant № 17-04-01061.

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Penial and bacular morphology of mammals - what it can reveal about their owner?

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The reproductive organs exhibit an extraordinary morphological variability, both external (shape of phallus, lappets, papillas, surface ornamentation, spinosity, etc.) and also internal (os penis, os clitoridis). In general, a positive allometry and a high degree of phenotypic variability have been described for the characters associated with the reproduction apparatus, which is probably caused by the sexual selection. This topic was intensively studied during 1960s - 1970s, then the interest declined rapidly, but recently its popularity is rising again. New studies have revealed that morphological traits can fit well into phylogeny and they are also distinguishable in closely related species. The penis of some mammalian groups contains a penis bone (os penis) called baculum, that also displays an astonishing morphological diversity. And it's assumed that the baculum was lost and gained several times during the evolution of mammals. There is also increasing evidence of interdependence of the penial and bacular morphology with life history parameters (i.e. mating system, ovulation type, seasonality of reproduction, degree of sociality). For example, it was found that the increasing level of sociality is associated with a decreasing complexity of penile morphology or that the complexity of genital structure is generally higher in multi-male/multi-female groups as compared to monogamous species. Seasonality of reproduction, unpredictable mating opportunities, high degree of sperm competition, risk of multiple-mating or ovulation induction could be the driving force for the diverse and complex morphology of reproductive organs. Our research is focused on the description of genital morphology, the detection of correlations the penial-bacular morphology with life-history parameters and application of morphological traits to the phylogeny with the particular emphasis on several groups of rodents. And this contribution presents our first results.

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Body weight regulation in small rodents a matter between predation risk and starvation?

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Genetic and environmental factors have been linked on several models that, in the recent years, have discussed the evolutionary background of body weight regulation. Small wild mammals are known to have a strong body weight regulation system. The risk of predation is among the factors suggested to explain the non-prevalence of overweight animals within natural populations, as the ability to escape predators, can be highly compromised if the animals are carrying large fat reserves. Such risk needs to be balanced with the risk of starvation due to the absence of fat stores, when food resources are scarce. We experimentally investigated the predications of the predation-starvation model using wood mice (*Apodemus sylvaticus*) and C57BL/6 mice by manipulating the risks of starvation and predation. We analysed the physiological and behavioural responses by simulating stochastic starvation events and manipulating the predation risk through broadcasting of owl calls. Results showed reductions in body weight, and body weight gain, induced by the increased risk of predation. Such variations were mostly explained by reduction of food intake, and increase in energy expenditure through alteration of physical activity and behaviour. Resting metabolic rate and thermogenic capacity were not affected. Starvation periods were compensated by overfeeding and reduction in activity during the recovery period, however fat storages did not increase over the limits of the pre-starvation period. These observations showed the influence of environmental components setting the body weight regulation limits and support the hypothesis of the predation risk being a factor modulating small rodents body weight.

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Molecular evolutionary inferences of recent biological innovations in mice and rats

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The releases and analyses of the genome sequences of the house mouse and of the Norway rat provided new insights into the biological differences between *Mus* and *Rattus*. However, technically these differences could not be mapped specifically onto either the mouse or the rat lineage. We added map-based assemblies of the genomes of the Roof rat (*Rattus rattus* "S") and of the Algerian mouse (*Mus spretus*) and conducted comparative molecular evolutionary analyses of the protein coding portions of the two species of mouse and rat followed by bioinformatics inferences of the biology encoded by the emerged sets of genes. We were able to specifically map protein encoding differences and inferred biological differences onto the *Mus* and *Rattus* lineages. Thus, we were able to compare and contrast some of the most recent evolutionary innovations in the rat and mouse lineages.