Comparative bite force in two syntopic murids (Rodentia) suggests lack of competition for food resources.
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Ginot, S., Le Noëne, C., Cassaing, J. "Comparative bite force and competition in two syntopic murids (Rodentia)."

Abstract

Closely related syntopic species have been shown to avoid competition by differentiating in the type of food they process. This can be achieved by changes in size or in the masticatory apparatus that produce modifications in bite force. The wood mouse (*Apodemus sylvaticus* L., 1758) and short-tailed mouse (*Mus spretus* Lataste, 1883) are two murid rodent species found in syntopy in the south of France. We measured bite force in wild specimens of both species to test for differences in performance. Despite its greater body mass, the wood mouse showed only slightly higher bite force than the short-tailed mouse. We found no clear sexual dimorphism in either species, however among the males of the short-tailed mouse, two groups appeared in terms of bite force. This bite force difference may correspond to a hierarchical organisation of these males. Overall, it seems that both species have similar bite forces and accordingly overlap in the resources they use. Other factors may exist that create a niche differentiation between the wood mouse and the short-tailed mouse. Another explanation may be a great abundance of food, which would cancel competition for this resource in these species.

Résumé

Il a été montré que les espèces proches vivant en syntopie évitent la competition en différenciant le type de nourriture qu'elles utilisent. Cela peut être permis par des changements de taille ou dans l'appareil masticateur qui sont à l'origine de différences dans la force de morsure. Le mulot sylvestre (*Apodemus sylvaticus* L. 1758) et la souris à queue courte (*Mus spretus* Lataste, 1883) sont deux murid rodent species found in syntopy in the south of France. We measured bite force in wild specimens of both species to test for differences in performance. Despite its greater body mass, the wood mouse showed only slightly higher bite force than the short-tailed mouse. We found no clear sexual dimorphism in either species, however among the males of the short-tailed mouse, two groups appeared in terms of bite force. This bite force difference may correspond to a hierarchical organisation of these males. Overall, it seems that both species have similar bite forces and accordingly overlap in the resources they use. Other factors may exist that create a niche differentiation between the wood mouse and the short-tailed mouse. Another explanation may be a great abundance of food, which would cancel competition for this resource in these species.
spretus Lataste 1883) sont deux espèces de rongeurs muridés trouvés en syntopie dans le sud de la France. Nous avons mesuré la force de morsure chez des spécimens sauvages des deux espèces pour tester de potentielles différences de performance. Bien que le mulot sylvestre soit plus gros, sa force de morsure n’est que légèrement plus haute que celle de la souris à queue courte. Nous n’avons pas détecté de dimorphisme sexuel marqué au sein des deux espèces, cependant parmi les souris à queue courte mâles, il apparaît deux groupes en termes de force de morsure. Ceux à la morsure plus forte pourraient représenter des mâles dominants, tandis que ceux à la morsure plus faible seraient des subordonnés. Généralement, les deux espèces ont des forces de morsures similaires, et par conséquent montrent un grand chevauchement dans les ressources qu’elles peuvent utiliser. D’autres facteurs pourraient exister qui créeraient une différenciation de niche entre le mulot sylvestre et la souris à queue courte. Une explication alternative pourrait être la présence de nourriture en abondance, qui supprimerait la compétition entre les deux espèces à ce niveau.

Keywords

Performance ; short-tailed mouse (Mus spretus) ; wood mouse (Apodemus sylvaticus) ; niche overlap ; coexistence ; sex dimorphism
Introduction

Syntopic species (*sensu* Rivas 1964), i.e. species sharing the micro-habitats, have long been known to differentiate in their ability to cope with food types and hardnesses to reduce competition (e.g. Grant 1968; Grant 1972; Verwaijen et al. 2002; Yamashita et al. 2009). Grant (1972) particularly highlighted that there was often significant disparities in size among coexistent species with similar needs and that this was probably due to ecological and evolutionary factors. His synthesis ended by the hypothesis that the advantage to the larger species may be the free access to food, due to dominance, and the ability to deal with larger and/or harder seeds; while the smaller species might have a greater efficiency in energy extraction from the foods it exploits, and being better at avoiding predators. Such a dichotomy can be achieved either by evolution toward a greater body size, or by changes in the masticatory apparatus (e.g. Van Daele et al. 2009). Therefore, comparing pairs of syntopic species at their natural localities can be very fruitful in highlighting ecological performance differences and niche separation. Thus, Verwaijen et al. (2002) correlated bite force and prey hardness in two species of lacertid lizards, and proposed that differences in bite force are an important factor in prey handling efficiency and also influence prey selection in nature. In a large set of turtle species, Herrel et al. (2002) demonstrated that *in vivo* bite force was correlated with trophic ecology, as well as head height. Similar results were found in large Neotropical cats (Kiltie et al. 1984) which differenciate from each other in terms of skull morphology, gape and bite force under the influence of ecological character displacement. In Neotropical bats, the amazing diversity of skull shapes among the phyllostomid radiation was also explained in terms of bite force and dietary niche (Aguirre et al. 2002). Yamashita and colleagues (2009) found that sympatric (living in the same national park, but not necessarily syntopic) lemurs from Madagascar, all feeding on bamboo, specialized on different part of the plant...
and accordingly segregated in their feeding behaviours. Finally, comparing two Cricetidae rodent species with different sizes and diets Williams et al. (2009) highlighted the importance of gape in the biting performance. They showed that the larger species, which is also carnivorous, could maintain a large proportion of its maximal bite force at wide gape angles due to a more derived and advantageous condition of the jaw muscles (notably a lower stretch factor).

According to the various studies cited above, the measure of bite force appears to be a great tool to address the evolution of food niche dimension and separation. The wood mouse *Apodemus sylvaticus* (L., 1758) and the short-tailed mouse *Mus spretus* (Lataste, 1883)–two murid species often found in syntopy (i.e. caught in the same trap lines) in southern France– are good candidates to run such a study. The two species share several habitats and most food items (Bauduin et al. 2013; Cassaing et al. 2013). Therefore, they may be considered to be in a situation of competition for food, yet they seem to coexist at least since the Holocene period. The wood mouse is about 1.5 times larger than the short-tailed mouse. In an experimental setting in the wild, it has been shown that these rodents can carry and eat larger seeds than equivalent individuals of the short-tailed mouse (Muñoz and Bonal 2008). The question remains as whether it also displays differences in terms of ingestion and comminution of food items. For its part, the short-tailed mouse demonstrates great skills to retrieve food sources. Notably, this species appears to use inadvertent information released by others (Valone 1989; Doligez et al. 2003; Danchin et al. 2004; Parejo et al. 2004), even heterospecifics (Cassaing et al. 2013). This may be highly expensive for the wood mouse if it gets its food caches used by the short-tailed mouse. To our knowledge, there has been no evidence so far that the short-tailed mouse does not achieve the second part of Grant’s (1972) prediction mentioned above (i.e. that it is better at energy extraction and predator avoidance).
We will focus here on the first step of ingestion by measuring the bite force of both species in the wild. This measure, which notably depends on the biomechanics of the skull and associated muscles, is a good proxy of the diet- and competition-related ecological performance, at the inter- and intraspecific levels (Davis et al. 2010; Santana et al. 2010). Myomorphous rodents, such as the species studied here, have been hypothesized to be "high-performance generalists", according to Cox et al. (2012). If this holds true, we may expect strong bite forces in the two murids studied here, compared to values reported in the literature for non-murid rodents. Among them, we expect bite force to correlate body size, both at the interspecific (Freeman and Lemen 2008; Ginot et al. 2018), and intraspecific level (Becerra et al. 2011). Within species, we may find sex dimorphism in bite force, associated with intra-sex competition, as reported by Becerra and colleagues (2011) in another species of rodent (Ctenomys talarum). Interspecifically, the wood mouse is much larger than the short-tailed mouse and it should display much stronger bites. Because both species occur in syntopy—and feed mostly on the same items (Bauduin et al. 2013; Cassaing et al. 2013)—the difference in bite force may be expected to be large, reducing competition for food (i.e. by giving access to harder and larger items to the largest species). On the other hand, the difference may be reduced if resources are widely available, therefore producing no competition between both species, and if other factors (e.g. behaviour differences, intra-specific competition) do not influence bite force.

**Materials & methods**

Individuals of both species were first sampled in a garrigue near Montpellier (43° 34’ 38” N, 03° 43’ 06” W), with a mix of custom-built multi-catch traps (described in Cassaing 1986) and Victor® Tin Cat® traps set up in a 7 x 7 grid. The traps were 25 m apart, so the
grid covered 2.25 ha. An exhaustive description of the site can be found in Cassaing et al. (2013). At this site, we captured 45 specimens of wood mice and 27 short-tailed mice. Additional samplings (wood mouse $n = 49$; short-tailed mouse $n = 8$) were carried out at the Lunaret zoo in Montpellier in a large mixed wood (Holm oak, Aleppo pines) with dense underneath vegetation, setting the same traps every 10 meters along a 100 meter-long line. Although caught within the zoo area, these specimens were wild, living in unkept spaces between the enclosures. Six specimens of wood mice were also captured in the Caroux mountain range (Hérault, France) near the village of Douch (altitude 700m), using the same trap density as for the zoo samples. Wood mice and short-tailed mice were caught in the same trap lines (sometimes even in the same traps), except in the Douch locality, where only wood mice were caught, probably because it is at the limits of the short-tailed mouse's range.

We determined the rodents’ age on the basis of their weight, which is known to have a good correlation with genuine age (Pearson's correlation: male $R^2=0.88$, female $R^2=0.79$, with $p<0.05$ for both sexes according to Frynta and Zižková 1992). Broad age categories were defined as follows: for the short-tailed mouse, juveniles $<10g$; subadults 10 to 13g; adults $>13g$; for the wood mouse, juveniles $<15g$; subadults 15 to 20g; adults $>20g$. We recorded their sex and their apparent reproductive status by morphological features (e.g. testis position, opening of the vagina, nipple condition, suspected gestation).

Shortly after capture we measured the animals' voluntary bite force at the incisors using a piezoelectric force transducer (Kistler, type 9203, range 0-500 N, accuracy 0.01–0.1 N; Amherst, NY, USA; calibrated by the constructor at 25 °C and 36% humidity) attached to a handheld charge amplifier (Kistler, type 5995, Amherst, NY, USA; Herrel et al. 1999). The force transducer was mounted between two steel bite plates as described in Herrel et al. (1999). We adjusted the distance between the bite plates by measuring it with a caliper, and
by increasing or decreasing it via the micrometer head, so that each individual had a gape angle of approximately 30° (Dumont and Herrel 2003), at which we found the rodents bit most consistently. All animals bit directly onto steel at the same spot on the plates (i.e. at the tip), to ensure a consistent out-lever length. We recorded three trials in a row for each individual, and the maximal score was used in the analyses. Body mass (g) was recorded using a Pesola® LightLine tubular weighing scale. Bite force over body weight ratios were also computed (Bite Force Quotient, or BFQ, Table 1), after converting mass (g) to weight (N), by dividing it by 1000 g/kg and multiplying by 9.8 m/s².

All field procedures were under the Approval No. A34-172-042 (Hérault Prefecture). The animals were gently handled, and when necessary, marked by toe-tattooing (e.g. Leclercq and Rozenfeld 2001) to avoid duplicated measurements. All individuals were released at the location of their capture after manipulations.

Difference in mean bite forces, mass and BFQ between species, as well as differences in bite force between sexes were tested using two-tailed Student's t-tests. Correlations between bite force and weight were assessed by fitting least-squares linear regressions, and differences between the slopes and intercepts were tested using an ANCOVA. Allometric trajectories of log bite force against log body mass were tested against the expected slope of 2/3 for isometric scaling by linear regressions. Distribution of bite forces within sexes were visually inspected and tested for multimodality using Hartigan's dip test. All analyses were run in R (R Core Team 2017).

Results

Both species have a similar bite force, barely higher for the wood mouse than for the short-tailed mouse (mean=9.08, max=12.66, min=3.50 for the wood mouse; mean=8.31,
max=11.20, min=5.13 for the short-tailed mouse, Table 1). Although apparently negligible, the difference between mean absolute bite force values was significant (Student's t-test: $t=2.13$, $df=64$, $p<0.05$). When comparing only adult specimens with sexes pooled between both species (mean=9.73 ± 2.01 for adult wood mouse; mean=8.93 ± 1.75 for adult short-tailed mouse), the difference was not significant (Student's t-test: $t=1.59$, $df=30$, $p=0.123$). On the other hand, interspecific differences of mean body mass (g) values were significant either when looking at the whole dataset (Student's t-test: $t=10.60$, $df=81$, $p<0.01$) or only at adults (Student's t-test: $t=11.30$, $df=33$, $p<0.01$). In accordance with the literature, the wood mouse was almost 1.5 times bigger than the short-tailed mouse (20.42 g and 13.72 g respectively on average). Therefore, BFQ mean value was significantly higher for the short-tailed mouse than the wood mouse (Student's t-test: $t=5.70$, $df=43$, $p<0.01$).

When body mass was plotted against bite force (Fig. 1), both species showed similar ranges in bite force and body mass. Both linear regressions showed a significant relationship, however with fairly low coefficients of determination (short-tailed mouse: $R^2=0.14$, $df=32$, $p<0.05$; wood mouse: $R^2=0.24$, $df=99$, $p<0.01$). The ANCOVA run on both species showed that as a whole, body mass had a significant effect on bite force ($F=39.22$, $df=1$, $p<0.001$) and that the slopes were almost exactly identical to each other ($F=0.00$, $df=1$, $p=0.988$, i.e. the relationship between bite force and body mass is the same for both species). Furthermore, the intercepts were not significantly different between both species ($F=2.90$, $df=1$, $p=0.091$), although the regression line for the short-tailed mouse was slightly higher than that of the wood mouse. Tests of the slopes of log bite force against log body mass showed no significant deviation from isometry ($p=0.096$ for the wood mouse, $p=0.202$ for the short-tailed mouse).
Looking at adults within species, we found that the female short-tailed mice did not bite significantly harder than males (Student's t-test: \( t=1.96, \ df=14, \ p=0.069 \)). No sex dimorphism was found in terms of body mass (Student's t-test: \( t=0.66, \ df=7.37, \ p=0.526 \)). Likewise, in the wood mouse there was no difference in either bite force (Student's t-test: \( t=-0.35, \ df=36.67, \ p=0.725 \)), or body mass (Student's t-test: \( t=-1.38, \ df=30.10, \ p=0.176 \)) between sexes.

Visual inspection (Fig. 2) of the distribution of bite forces in short-tailed subadult and adult males reveals two groups, the first one with 14 individuals (11 subadults and 3 adults), had a mean of 6.59 N, and a range from 5.13 N to 7.82 N. The other group, with 7 individuals (2 subadults and 5 adults), had a mean of 10.38 N, with a range from 9.33 N to 11.20 N. Despite the large gap between both groups, Hartigan's dip test for multimodality showed that the distribution was not significantly different from unimodality (\( D=0.10, \ p=0.33 \)). Comparing short-tailed mouse adult and subadult males with the higher bite forces to conspecific adult and subadult females, we found a significant difference in mean bite force (Student's t-test: \( t=3.61, \ df=18, \ p<0.01 \)).

Discussion

The two murids we studied showed a consistent bite force compared with published data on murid rodents. Cox et al. (2012) for example, reported an average \textit{in vivo} bite force of \( 31.1 \pm 10.75 \) N in laboratory \textit{R. norvegicus}, which is much bigger than the species studied here. Between our species, the difference in bite force appeared to be small compared to the difference in body mass, and was not significant in adults. As shown by its greater average BFQ (Table 1), the short-tailed mouse \textit{M. spretus} had a greater bite force relative to its size, compared to the wood mouse \textit{A. sylvaticus}. Within species, a significant positive relationship
was found between bite force and size (represented here by body mass), as was found other vertebrates (Herrel and Gibb 2006). Indeed, the lightest individuals, likely the youngest, showed an absolute bite force lower than that of the heavier ones (Fig. 1). Furthermore, we found that bite force scaled isometrically with body mass in both our species, showing that, relative to their mass, the lighter individuals do not have lower bite force than heavier individuals.

Short-tailed mouse adult females bit on average harder than males, although not significantly. Furthermore, adult males in this species appeared to be split in two groups in terms of bite force (Fig. 2). However, the distribution was not significantly different from unimodality, perhaps due to small sample size. Still, this result is in line with those of staged dyadic encounters reported by Cassaing (1984). That study suggested some behavioural differences in males due to social hierarchy, and this may influence bite force as well. The adult males with the weaker bite forces could be the subordinate ones, while the other group would comprise the more dominant males. The mean bite force of the latter group is significantly higher than the one of subadult and adult females. So the potentially more dominant males appear to bite harder than the females, in accord with to previous results on rodents (e.g. Becerra et al. 2011). Although our data may fit with Cassaing's (1984) and Hurst's (1994) hypotheses that male short-tailed mice display hierarchical relationships (with dominant or subordinate status), it is not sufficient to explain or quantify them, and it was not the goal of this study. One way to assess how bite force and social status may be linked to each other in the short-tailed mouse would be by measuring bite force in dominant and defeated individuals of male-male encounters (e.g. Husak et al. 2006).

Our results show a suprisingly close bite force for the two syntopic murines studied here. As far as bite force is concerned, their abilities to break down hard seeds seem to be
similar. Even if the wood mouse could handle larger acorns thanks to its greater body size -
as showed by Muñoz and Bonal (2008) in Central Spain- it should be noted that the higher
range of acorns occurring in Spain is missing in garrigues in southern France where animals
were captured. It seems that in our case both species eat the same seeds (Bauduin et al. 2013)
and share the same habitat (Cassaing et al. 2013), therefore displaying a great niche overlap,
despite their important size differences. This would suggest that, in the areas we studied, the
competition for food is not a limiting factor. This may partially explain why the wood mouse
seems to show no attempt of pushing the short-tailed mouse aside, despite being used by the
latter as a cue to resource abundance.

It seems that niche partitioning between our species, if any, does not occur through a
qualitative difference in the access to harder foods. Resource partitioning may be produced
by other factors such as the level of the habitat being exploited (strictly on the ground, or at
least partially above and partially below it), the proportion of the animal parts in the diet, and
the metabolic assimilation rate of both species. However, our data, as well as those of
Bauduin and colleagues (2013) seem to point toward a lack of competition for resources,
perhaps due to a great abundance of food in the localities studied rather than toward.
Acknowledgements

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**Table 1**: Bite force, body mass, and bite force quotient (bite force/weight ratio) measured in two syntopic species of murine rodents, the short-tailed mouse *Mus spretus* and the woodmouse *Apodemus sylvaticus*. Values shown in the table represent the mean ± standard deviation for each subset. Sex was recorded based on the presence of testicles or nipples, age class is based on body mass (for *M. spretus*: juveniles < 10g; 10g < subadults < 13g; > 13g adults. For *A. sylvaticus*: juveniles < 15g; 15g < subadults < 20g; > 20g adults).

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FIGURE LEGENDS

Figure 1: Bite force plotted against body mass in two syntopic murids of the south of France, *Apodemus sylvaticus* and *Mus spretus*. Solid lines are the least-square regression lines for each species. Dashed lines represent the limits of the age categories based on body mass for each species (to the left of the line are juveniles, in the middle are subadults, and to the right are adults).

Figure 2: Histogram of bite force in adult and subadult males of *Mus spretus*, representing the two groups of potentially dominant and subordinate individuals.
Figure 1: Bite force plotted against body mass in two syntopic murids of the south of France, Apodemus sylvaticus and Mus spretus. Solid lines are the least-square regression lines for each species. Dashed lines represent the limits of the age categories based on body mass for each species (to the left of the line are juveniles, in the middle are subadults, and to the right are adults).

Y = 0.23x + 4.31
Y = 0.23x + 5.06

177x177mm (300 x 300 DPI)
Figure 2: Histogram of bite force in adult and subadult males of Mus spretus, representing the two groups of potentially dominant and subordinate individuals.

177x177mm (300 x 300 DPI)