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**Comparative bite force in two syntopic murids (Rodentia)
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1 **Comparative bite force in two syntopic murids (Rodentia) suggests lack of competition**
2 **for food resources.**

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10

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11 **Ginot, S., Le Noëne, C., Cassaing, J. "Comparative bite force and competition in two**
12 **syntopic murids (Rodentia)."**

13

14 **Abstract**

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

29 **Résumé**

30 Il a été montré que les espèces proches vivant en syntopie évitent la compétition en différen-
31 ciant le type de nourriture qu'elles utilisent. Cela peut être permis par des changements de
32 taille ou dans l'appareil masticateur qui sont à l'origine de différences dans la force de mor-
33 sure. Le mulot sylvestre (*Apodemus sylvaticus* L. 1758) et la souris à queue courte (*Mus*

34 *spretus* Lataste 1883) sont deux espèces de rongeurs muridés trouvés en syntopie dans le sud
35 de la France. Nous avons mesuré la force de morsure chez des spécimens sauvages des deux
36 espèces pour tester de potentielles différences de performance. Bien que le mulot sylvestre
37 soit plus gros, sa force de morsure n'est que légèrement plus haute que celle de la souris à
38 queue courte. Nous n'avons pas détecté de dimorphisme sexuel marqué au sein des deux es-
39 pèces, cependant parmi les souris à queue courte mâles, il apparaît deux groupes en termes
40 de force de morsure. Ceux à la morsure plus forte pourraient représenter des mâles domi-
41 nants, tandis que ceux à la morsure plus faible seraient des subordonnés. Généralement, les
42 deux espèces ont des forces de morsures similaires, et par conséquent montrent un grand
43 chevauchement dans les ressources qu'elles peuvent utiliser. D'autres facteurs pourraient
44 exister qui créeraient une différenciation de niche entre le mulot sylvestre et la souris à
45 queue courte. Une explication alternative pourrait être la présence de nourriture en abon-
46 dance, qui supprimerait la compétition entre les deux espèces à ce niveau.

47

48 **Keywords**

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

51 **Introduction**

52 Syntopic species (*sensu* Rivas 1964), i.e. species sharing the micro-habitats, have long
53 been known to differentiate in their ability to cope with food types and hardnesses to reduce
54 competition (e.g. Grant 1968; Grant 1972; Verwaijen et al. 2002; Yamashita et al. 2009).
55 Grant (1972) particularly highlighted that there was often significant disparities in size
56 among coexistent species with similar needs and that this was probably due to ecological and
57 evolutionary factors. His synthesis ended by the hypothesis that the advantage to the larger
58 species may be the free access to food, due to dominance, and the ability to deal with larger
59 and/or harder seeds; while the smaller species might have a greater efficiency in energy ex-
60 traction from the foods it exploits, and being better at avoiding predators. Such a dichotomy
61 can be achieved either by evolution toward a greater body size, or by changes in the mastica-
62 tory apparatus (e.g. Van Daele et al. 2009). Therefore, comparing pairs of syntopic species at
63 their natural localities can be very fruitful in highlighting ecological performance differences
64 and niche separation. Thus, Verwaijen et al. (2002) correlated bite force and prey hardness in
65 two species of lacertid lizards, and proposed that differences in bite force are an important
66 factor in prey handling efficiency and also influence prey selection in nature. In a large set of
67 turtle species, Herrel et al. (2002) demonstrated that *in vivo* bite force was correlated with
68 trophic ecology, as well as head height. Similar results were found in large Neotropical cats
69 (Kiltie et al. 1984) which differentiate from each other in terms of skull morphology, gape
70 and bite force under the influence of ecological character displacement. In Neotropical bats,
71 the amazing diversity of skull shapes among the phyllostomid radiation was also explained
72 in terms of bite force and dietary niche (Aguirre et al. 2002). Yamashita and colleagues
73 (2009) found that sympatric (living in the same national park, but not necessarily syntopic)
74 lemurs from Madagascar, all feeding on bamboo, specialized on different part of the plant

75 and accordingly segregated in their feeding behaviours. Finally, comparing two Cricetidae
76 rodent species with different sizes and diets Williams et al. (2009) highlighted the im-
77 portance of gape in the biting performance. They showed that the larger species, which is
78 also carnivorous, could maintain a large proportion of its maximal bite force at wide gape
79 angles due to a more derived and advantageous condition of the jaw muscles (notably a low-
80 er stretch factor).

81 According to the various studies cited above, the measure of bite force appears to be a
82 great tool to address the evolution of food niche dimension and separation. The wood mouse
83 *Apodemus sylvaticus* (L., 1758) and the short-tailed mouse *Mus spretus* (Lataste, 1883)—two
84 murid species often found in syntopy (*i.e.* caught in the same trap lines) in southern France—
85 are good candidates to run such a study. The two species share several habitats and most
86 food items (Bauduin et al. 2013; Cassaing et al. 2013). Therefore, they may be considered to
87 be in a situation of competition for food, yet they seem to coexist at least since the Holocene
88 period. The wood mouse is about 1.5 times larger than the short-tailed mouse. In an experi-
89 mental setting in the wild, it has been shown that these rodents can carry and eat larger seeds
90 than equivalent individuals of the short-tailed mouse (Muñoz and Bonal 2008). The question
91 remains as whether it also displays differences in terms of ingestion and comminution of
92 food items. For its part, the short-tailed mouse demonstrates great skills to retrieve food
93 sources. Notably, this species appears to use inadvertent information released by others
94 (Valone 1989; Doligez et al. 2003; Danchin et al. 2004; Parejo et al. 2004), even heterospe-
95 cifics (Cassaing et al. 2013). This may be highly expensive for the wood mouse if it gets its
96 food caches used by the short-tailed mouse. To our knowledge, there has been no evidence
97 so far that the short-tailed mouse does not achieve the second part of Grant's (1972) predic-
98 tion mentioned above (*i.e.* that it is better at energy extraction and predator avoidance).

99 We will focus here on the first step of ingestion by measuring the bite force of both spe-
100 cies in the wild. This measure, which notably depends on the biomechanics of the skull and
101 associated muscles, is a good proxy of the diet- and competition-related ecological perfor-
102 mance, at the inter- and intraspecific levels (Davis et al. 2010; Santana et al. 2010). Myo-
103 morphous rodents, such as the species studied here, have been hypothesized to be "high-
104 performance generalists", according to Cox et al. (2012). If this holds true, we may expect
105 strong bite forces in the two murids studied here, compared to values reported in the litera-
106 ture for non-murid rodents. Among them, we expect bite force to correlate body size, both at
107 the interspecific (Freeman and Lemen 2008; Ginot et al. 2018), and intraspecific level
108 (Becerra et al. 2011). Within species, we may find sex dimorphism in bite force, associated
109 with intra-sex competition, as reported by Becerra and colleagues (2011) in another species
110 of rodent (*Ctenomys talarum*). Interspecifically, the wood mouse is much larger than the
111 short-tailed mouse and it should display much stronger bites. Because both species occur in
112 syntopy -and feed mostly on the same items (Bauduin et al. 2013; Cassaing et al. 2013)- the
113 difference in bite force may be expected to be large, reducing competition for food (*i.e.* by
114 giving access to harder and larger items to the largest species). On the other hand, the differ-
115 ence may be reduced if resources are widely available, therefore producing no competition
116 between both species, and if other factors (e.g. behaviour differences, intra-specific competi-
117 tion) do not influence bite force.

118

119 **Materials & methods**

120 Individuals of both species were first sampled in a garrigue near Montpellier (43° 34'
121 38" N, 03° 43' 06" W) , with a mix of custom-built multi-catch traps (described in Cassaing
122 1986) and Victor® Tin Cat® traps set up in a 7 x 7 grid. The traps were 25 m apart, so the

123 grid covered 2.25 ha. An exhaustive description of the site can be found in Cassaing et al.
124 (2013). At this site, we captured 45 specimens of wood mice and 27 short-tailed mice. Addi-
125 tional samplings (wood mouse $n = 49$; short-tailed mouse $n = 8$) were carried out at the Lu-
126 naret zoo in Montpellier in a large mixed wood (Holm oak, Aleppo pines) with dense under-
127 neath vegetation, setting the same traps every 10 meters along a 100 meter-long line. Alt-
128 hough caught within the zoo area, these specimens were wild, living in unkept spaces be-
129 tween the enclosures. Six specimens of wood mice were also captured in the Caroux moutain
130 range (Hérault, France) near the village of Douch (altitude 700m), using the same trap densi-
131 ty as for the zoo samples. Wood mice and short-tailed mice were caught in the same trap
132 lines (sometimes even in the same traps), except in the Douch locality, where only wood
133 mice were caught, probably because it is at the limits of the short-tailed mouse's range.

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

141 Shortly after capture we measured the animals' voluntary bite force at the incisors using
142 a piezoelectric force transducer (Kistler, type 9203, range 0-500 N, accuracy 0.01–0.1 N;
143 Amherst, NY, USA ; calibrated by the constructor at 25 °C and 36% humidity) attached to a
144 handheld charge amplifier (Kistler, type 5995, Amherst, NY, USA ; Herrel et al. 1999). The
145 force transducer was mounted between two steel bite plates as described in Herrel et al.
146 (1999). We adjusted the distance between the bite plates by measuring it with a caliper, and

147 by increasing or decreasing it via the micrometer head, so that each individual had a gape
148 angle of approximately 30° (Dumont and Herrel 2003), at which we found the rodents bit
149 most consistently. All animals bit directly onto steel at the same spot on the plates (*i.e.* at the
150 tip), to ensure a consistent out-lever length. We recorded three trials in a row for each indi-
151 vidual, and the maximal score was used in the analyses. Body mass (g) was recorded using a
152 Pesola® LightLine tubular weighing scale. Bite force over body weight ratios were also
153 computed (Bite Force Quotient, or BFQ, Table 1), after converting mass (g) to weight (N),
154 by dividing it by 1000 g/kg and multiplying by 9.8 m/s^2 .

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

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

167

168 **Results**

169 Both species have a similar bite force, barely higher for the wood mouse than for the
170 short-tailed mouse (mean=9.08, max=12.66, min=3.50 for the wood mouse; mean=8.31,

171 max=11.20, min=5.13 for the short-tailed mouse, Table 1). Although apparently negligible,
172 the difference between mean absolute bite force values was significant (Student's t-test:
173 $t=2.13$, $df=64$, $p<0.05$). When comparing only adult specimens with sexes pooled between
174 both species (mean= 9.73 ± 2.01 for adult wood mouse ; mean= 8.93 ± 1.75 for adult short-
175 tailed mouse), the difference was not significant (Student's t-test: $t=1.59$, $df=30$, $p=0.123$).
176 On the other hand, interspecific differences of mean body mass (g) values were significant
177 either when looking at the whole dataset (Student's t-test: $t=10.60$, $df=81$, $p<0.01$) or only at
178 adults (Student's t-test: $t=11.30$, $df=33$, $p<0.01$). In accordance with the literature, the wood
179 mouse was almost 1.5 times bigger than the short-tailed mouse (20.42 g and 13.72 g respec-
180 tively on average). Therefore, BFQ mean value was significantly higher for the short-tailed
181 mouse than the wood mouse (Student's t-test: $t=5.70$, $df=43$, $p<0.01$).

182 When body mass was plotted against bite force (Fig. 1), both species showed similar
183 ranges in bite force and body mass. Both linear regressions showed a significant relationship,
184 however with fairly low coefficients of determination (short-tailed mouse: $R^2=0.14$, $df=32$,
185 $p<0.05$; wood mouse: $R^2=0.24$, $df=99$, $p<0.01$). The ANCOVA run on both species showed
186 that as a whole, body mass had a significant effect on bite force ($F=39.22$, $df=1$, $p<0.$
187 001) and that the slopes were almost exactly identical to each other ($F=0.00$, $df=1$, $p=0.988$,
188 *i.e.* the relationship between bite force and body mass is the same for both species). Further-
189 more, the intercepts were not significantly different between both species ($F=2.90$, $df=1$,
190 $p=0.091$), although the regression line for the short-tailed mouse was slightly higher than
191 that of the wood mouse. Tests of the slopes of log bite force against log body mass showed
192 no significant deviation from isometry ($p=0.096$ for the wood mouse, $p=0.202$ for the short-
193 tailed mouse).

194 Looking at adults within species, we found that the female short-tailed mice did not bite
195 significantly harder than males (Student's t-test: $t=1.96$, $df=14$, $p=0.069$). No sex dimor-
196 phism was found in terms of body mass (Student's t-test: $t=0.66$, $df=7.37$, $p=0.526$). Like-
197 wise, in the wood mouse there was no difference in either bite force (Student's t-test: $t=-$
198 0.35 , $df=36.67$, $p=0.725$), or body mass (Student's t-test: $t=-1.38$, $df=30.10$, $p=0.176$) be-
199 tween sexes.

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

209

210 Discussion

211 The two murids we studied showed a consistent bite force compared with published data
212 on murid rodents. Cox et al. (2012) for example, reported an average *in vivo* bite force of
213 31.1 ± 10.75 N in laboratory *R. norvegicus*, which is much bigger than the species studied
214 here. Between our species, the difference in bite force appeared to be small compared to the
215 difference in body mass, and was not significant in adults. As shown by its greater average
216 BFQ (Table 1), the short-tailed mouse *M. spretus* had a greater bite force relative to its size,
217 compared to the wood mouse *A. sylvaticus*. Within species, a significant positive relationship

218 was found between bite force and size (represented here by body mass), as was found other
219 vertebrates (Herrel and Gibb 2006). Indeed, the lightest individuals, likely the youngest,
220 showed an absolute bite force lower than that of the heavier ones (Fig. 1). Furthermore, we
221 found that bite force scaled isometrically with body mass in both our species, showing that,
222 relative to their mass, the lighter individuals do not have lower bite force than heavier indi-
223 viduals.

224 Short-tailed mouse adult females bit on average harder than males, although not signifi-
225 cantly. Furthermore, adult males in this species appeared to be split in two groups in terms of
226 bite force (Fig. 2). However, the distribution was not significantly different from unimodal-
227 ity, perhaps due to small sample size. Still, this result is in line with those of staged dyadic
228 encounters reported by Cassaing (1984). That study suggested some behavioural differences
229 in males due to social hierarchy, and this may influence bite force as well. The adult males
230 with the weaker bite forces could be the subordinate ones, while the other group would com-
231 prise the more dominant males. The mean bite force of the latter group is significantly higher
232 than the one of subadult and adult females. So the potentially more dominant males appear to
233 bite harder than the females, in accord with to previous results on rodents (e.g. Becerra et al.
234 2011). Although our data may fit with Cassaing's (1984) and Hurst's (1994) hypotheses that
235 male short-tailed mice display hierarchical relationships (with dominant or subordinate sta-
236 tus), it is not sufficient to explain or quantify them, and it was not the goal of this study. One
237 way to assess how bite force and social status may be linked to each other in the short-tailed
238 mouse would be by measuring bite force in dominant and defeated individuals of male-male
239 encounters (e.g. Husak et al. 2006).

240 Our results show a surprisingly close bite force for the two syntopic murines studied
241 here. As far as bite force is concerned, their abilities to break down hard seeds seem to be

242 similar. Even if the wood mouse could handle larger acorns thanks to its greater body size -
243 as showed by Muñoz and Bonal (2008) in Central Spain- it should be noted that the higher
244 range of acorns occurring in Spain is missing in garrigues in southern France where animals
245 were captured. It seems that in our case both species eat the same seeds (Bauduin et al. 2013)
246 and share the same habitat (Cassaing et al. 2013), therefore displaying a great niche overlap,
247 despite their important size differences. This would suggest that, in the areas we studied, the
248 competition for food is not a limiting factor. This may partially explain why the wood mouse
249 seems to show no attempt of pushing the short-tailed mouse aside, despite being used by the
250 latter as a cue to resource abundance.

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

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365 TABLES

366 **Table 1** : Bite force, body mass, and bite force quotient (bite force/weight ratio) measured in
 367 two syntopic species of murine rodents, the short-tailed mouse *Mus spretus* and the
 368 woodmouse *Apodemus sylvaticus*. Values shown in the table represent the mean \pm
 369 standard deviation for each subset. Sex was recorded based on the presence of testi-
 370 cles or nipples, age class is based on body mass (for *M. spretus* : juveniles < 10g ;
 371 10g < subadults < 13g ; > 13g adults. For *A. sylvaticus* : juveniles < 15g ; 15g <
 372 subadults < 20g ; > 20g adults).

Apodemus sylvaticus (n=103)							
		Females (n=42)			Males (n=61)		
		Juveniles (n=4)	Subadults (n=22)	Adults (n=16)	Juveniles (n=3)	Subadults (n=19)	Adults (n=39)
Bite force (N)	Sex (Age class) mean	7.63 \pm 0.91	8.57 \pm 1.83	9.6 \pm 1.65	6.67 \pm 1.05	8.28 \pm 1.26	9.79 \pm 2.17
	Sex mean	8.87 \pm 1.78			9.24 \pm 2.10		
	Species mean	9.09 \pm 1.97					
Body mass (g)	Sex(Age class) mean	12.88 \pm 1.65	17.18 \pm 1.25	22.63 \pm 2.47	11.25 \pm 2.88	18.61 \pm 0.99	23.67 \pm 2.67
	Sex mean	18.85 \pm 3.71			21.50 \pm 3.99		
	Species mean	20.42 \pm 4.07					
BFQ (Bite force/weight)	Sex(Age class) mean	61.11 \pm 11.00	50.72 \pm 9.02	43.34 \pm 6.26	62.45 \pm 13.80	46.25 \pm 8.34	42.40 \pm 9.75
	Sex mean	48.90 \pm 9.66			44.53 \pm 10.42		
	Species mean	46.35 \pm 10.29					
Mus spretus (n=35)							
		Females (n=13)			Males (n=22)		

		Juveniles (n=0)	Subadults (n=6)	Adults (n=7)	Juveniles (n=1)	Subadults (n=10)	Adults (n=10)
Bite force (N)	Sex(Age class) mean	NA	7.81 ± 0.44	9.83 ± 0.61	10.38 ± NA	7.13 ± 1.80	8.30 ± 2.03
	Sex mean	8.89 ± 1.17			7.97 ± 2.074		
	Species mean	8.31 ± 1.80					
Body mass (g)	Sex(Age class) mean	NA	12.00 ± 1.22	16.29 ± 3.90	9 ± NA	11.90 ± 0.66	15.25 ± 1.57
	Sex mean	13.16 ± 3.61			13.36 ± 2.26		
	Species mean	13.72 ± 2.85					
BFQ (Bite force/weight)	Sex(Age class) mean	NA	66.97 ± 7.85	63.88 ± 11.91	117.72 ± NA	61.44 ± 16.12	55.12 ± 9.75
	Sex mean	65.31 ± 9.96			61.11 ± 18.38		
	Species mean	62.72 ± 15.66					

373

374 **FIGURE LEGENDS**

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

380 **Figure 2** : Histogram of bite force in adult and subadult males of *Mus spretus*, representing
381 the two groups of potentially dominant and subordinate individuals.

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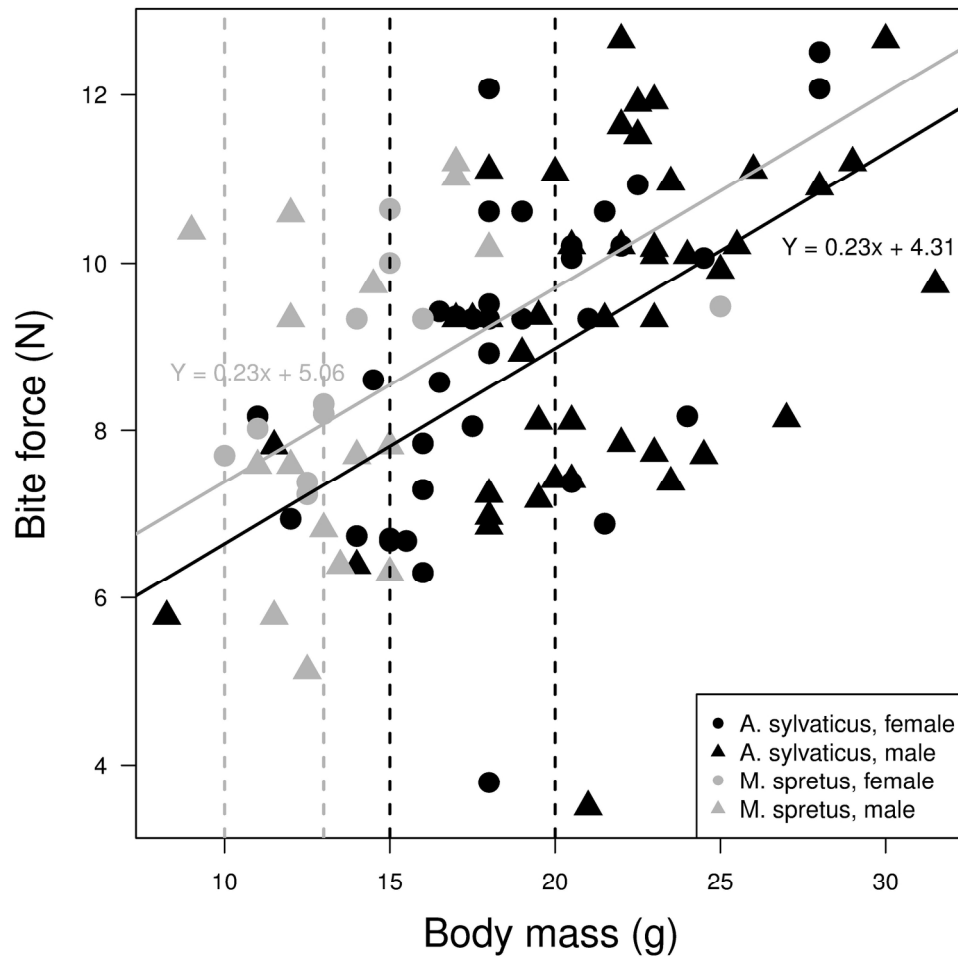


Figure 1 : Bite force plotted against body mass in two syntopic murids of the south of France, *Apodemus sylvaticus* and *Mus spretus*. Solid lines are the least-square regression lines for each species. Dashed lines represent the limits of the age categories based on body mass for each species (to the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

177x177mm (300 x 300 DPI)

Bite force in adult and subadult male short-tailed mice

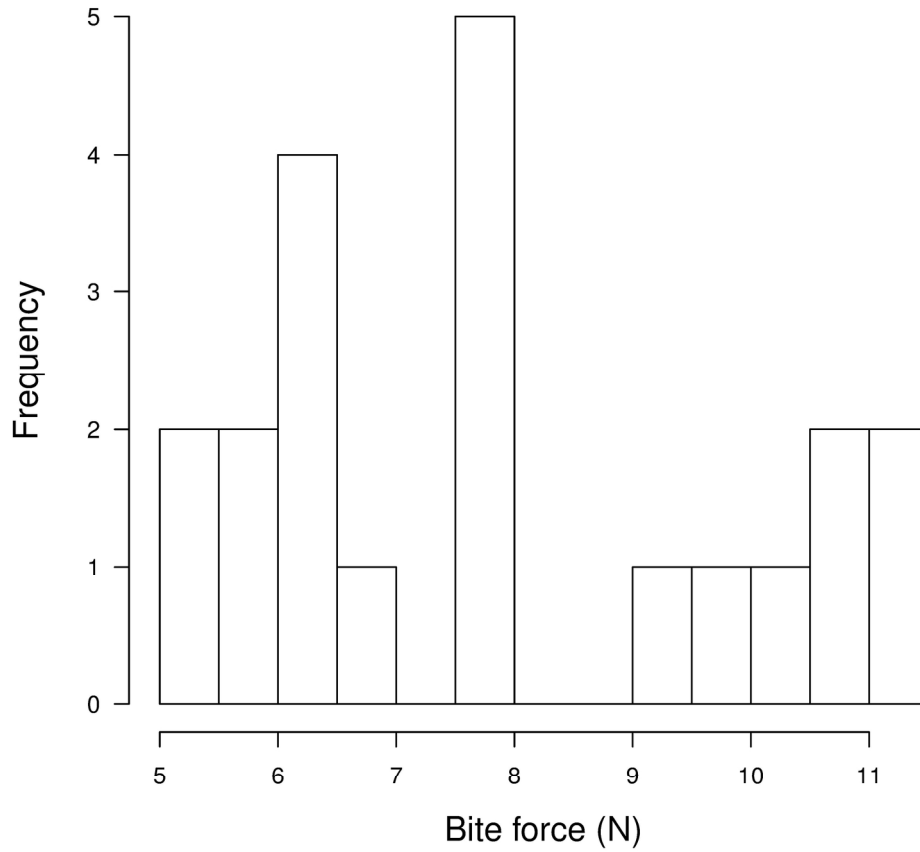


Figure 2 : Histogram of bite force in adult and subadult males of *Mus spretus*, representing the two groups of potentially dominant and subordinate individuals.

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