



**Occasional intraguild predation structuring small mammal assemblages:
the marsupial *Didelphis aurita* in the Atlantic Forest of Brazil**

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Complete List of Authors:	Moura, Maira; IBAMA, Diretoria de Ecossistemas Vieira, Marcus; Universidade Federal do Rio de Janeiro, Departamento de Ecologia Cerqueira, Rui; Universidade Federal do Rio de Janeiro, Departamento de Ecologia
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4 Maíra C. Moura¹, Marcus V. Vieira² & Rui Cerqueira²

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6
7 ¹Diretoria de Ecossistemas, Edifício Sede do IBAMA, SCEN Trecho 2, Brasília DF,
8 70818-900, Brazil, maira.moura@ibama.gov.br

9 ²Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio
10 de Janeiro, CP 68020, Rio de Janeiro RJ, 21941-590, Brazil,
11 mvvieira@biologia.ufrj.br

12
13
14 Running title: Intraguild predation structuring assemblages

15
16
17 PLEASE SEND CORRESPONDENCE TO THE 2nd AUTHOR:

18 Marcus V. Vieira

19 Laboratório de Vertebrados

20 Departamento de Ecologia

21 Universidade Federal do Rio de Janeiro

22 CP 68020

23 Rio de Janeiro RJ

24 CEP 21941-590, Brazil

25 mvvieira@biologia.ufrj.br

26
27 Ph. +55-21-2562-6315 / +55-21-9681-6842

28
29

ABSTRACT

30
31 The didelphid marsupial, *Didelphis aurita*, is suggested as an intraguild predator and as
32 key-species in small mammal assemblages of the Atlantic Forest of Brazil. The field
33 experiments required to test this hypothesis are complex to implement, but the recent
34 revival of regression methods offers a viable alternative. Here in we use the dynamic
35 and static regression methods to determine the importance of *D. aurita* as a competitor
36 and intraguild predator. Capture-recapture data from two localities in the Rio de Janeiro
37 State were used, Garrafão (municipality of Guapimirim), a coastal forest of the Serra do
38 Mar, and Barra de Maricá, a costal sand dune vegetation. Population and microhabitat
39 variables were monitored from April 1997 to April 2003 in Garrafão, and from January
40 1986 to July 1990 in Barra de Maricá. Microhabitat variables were related to canopy,
41 plant, litter, and rock covers, obstruction from 0 to 1.5 m, and number of logs.
42 Exploitation competition was tested by the dynamic method, which models the effects
43 of *D. aurita* on the per capita growth rate of a species. Interference by predation or
44 competition was tested by the static method, where the abundance of *D. aurita* at trap
45 stations was regressed against the abundance of other small mammals, after removal of
46 any variation associated with microhabitat factors. Exploitation competition was not
47 detected, but the interference of *D. aurita* was pervasive, affecting all small mammals
48 studied in the two localities. The clear avoidance of *D. aurita* by all small mammals
49 tested in two localities of different physiognomies indicates that it functions as an
50 intraguild predator, even if actual predation by *D. aurita* is an occasional event.

51
52 **Keywords:** interspecific competition, interference, regression method, community
53 structure, restinga vegetation.

54

INTRODUCTION

55

56

57 The importance of interspecific competition in structuring ecological
58 communities is still an unsettled issue (Shenbrot & Krasnov 2002), but considered by
59 many to play a major role (Diamond 1975; Dickman 1984; Schoener 1992; Brown *et al.*
60 2000). One of the reasons for the controversy is the difficulty of performing field
61 experiments to detect interspecific competition. The required long-term studies to detect
62 their effects, and the practical impossibility of performing experimental studies on each
63 pair of species in an assemblage limit their applicability (Shenbrot & Krasnov 2002).
64 Intraguild predation is yet another interaction that is potentially important in structuring
65 communities (Holt 1997). Intraguild predators can have a strong effect on other species
66 of the guild because of its role both as a competitor and a predator (Holt 1997).
67 However, will the intraguild predator be equally effective as a predator and a
68 competitor? This a difficult question to address using field experiments, even more
69 difficult than in the case of plain interspecific competition because of the necessary
70 complex design.

71 The revival of regression methods (Fox & Luo 1996; Shenbrot & Krasnov 2002)
72 offers an alternative to infer the relative importance of interspecific competition, and the
73 type of competition involved: exploitation or interference competition. These methods
74 are based on census data and the estimation of competitive coefficients by regression
75 models (Abramsky *et al.* 1986). Two regression methods were proposed, the dynamic
76 and the static methods (Schoener 1974; Crowell & Pimm 1976; Seifert & Seifert 1976;
77 Shenbrot & Krasnov 2002). The dynamic method measures exploitation competition
78 through associations in the temporal dynamics of two species, whereas the static method

79 measures spatial associations between species at specific moments in time (Shenbrot &
80 Krasnov 2002). As the name suggests, the static method excludes temporal variation.

81 The dynamic method was proposed by Seifert & Seifert (1976) and relies on a
82 time series of species abundance data to examine whether per capita changes in one
83 species are associated with changes in the abundance of other species. The static method
84 was proposed by Schoener (1974) and Crowell & Pimm (1976). It uses census data of a
85 species at one point in time over many independent sites, assuming equilibrium
86 conditions (Rosenzweig et al. 1984; Pfister 1995). Contrary to the static approach, the
87 dynamic method does not assume equilibrium conditions (Seifert & Seifert 1976; Pfister
88 1995; Shenbrot & Krasnov 2002). Both methods are based on Lotka-Volterra equations,
89 but differ in the incorporation of temporal or spatial dynamics between two competing
90 species.

91 The combination of the dynamic and regression methods may also be used to
92 infer the occurrence of intraguild predation. Species that are exclusively competitors or
93 are predator and prey should have contrasting dynamics: competitors negatively
94 associated, whereas predator positively associated with the abundance of prey.
95 Intraguild predators, however, may have more complex dynamics and interactions,
96 alternating periods of positive and negative associations depending on the productivity
97 of the system, and reducing the potential exploitative competition (Polis et al. 1989).
98 Thus, the dynamic method may fail to detect such mixed dynamics, but interference of
99 an intraguild predator on other species should be strong, and detected by the static
100 method. Negative spatial associations were interpreted as interference competition in
101 previous applications of the static method (Schoener 1974; Crowell & Pimm 1976;
102 Pfister 1995), but predation or simply the presence of a potential predator could produce

103 the same result. Thus, the combination of the two methods allows the inference of
104 exploitation competition, and if interference between species occurs by competition or
105 by intraguild predation.

106 The static model was discredited for some time because estimated competition
107 coefficients were inconsistent with the results of removal experiments (Rosenzweig *et*
108 *al.* 1985). However, there was a statistical artifact between competitive ability and
109 census variance (Luo *et al.* 1998; Shenbrot & Krasnov 2002). Fox & Luo (1996)
110 demonstrated that after standardization of the census data the competition coefficients
111 estimated by the static method were consistent with the values observed in removal
112 experiments. Competitive coefficients estimated by the dynamic method also agreed
113 with the results of removal experiments (Seifert & Seifert 1976; Pfister 1995; Shanbrot
114 & Krasnov 2002). These results revitalized the regression technique as a method to
115 evaluate community structure (Fox & Luo 1996; Luo *et al.* 1998).

116 Small mammals have been used as a model for studying interspecific
117 competition in terrestrial systems (Dickman & Woodside 1983; Eccard & Ylonen 2002;
118 2003; Ziv *et al.* 2003). However, to date most studies have focused on competition
119 between species in rodent assemblages (Brown & Munger 1985; Lacher & Alho 1989;
120 Fox & Brown 1993; Eccard & Ylonen 2002), whereas interspecific competition between
121 marsupials is less studied, especially in the neotropics (Dickman & Woodside 1983, but
122 see Lacher & Alho 1989; Vieira 2002). An exception is the study of Fonseca &
123 Robinson (1990) in Brazil, who observed reduced richness of small mammal species in
124 Atlantic Forest remnants with high abundance and biomass of the marsupial *Didelphis*
125 *aurita* Wied-Neuwied 1826. It was suggested that *D. aurita* could be negatively
126 affecting the occurrence of the other species. This process could occur either by

127 exploitation competition, resulting from the overlap in resource use, or by interference
128 competition and intraguild predation, resulting from agonistic and predatory behaviors
129 of *D. aurita*.

130 Marsupials of the genus *Didelphis* (Didelphimorphia, Didelphidae) are the
131 largest and most generalist among Neotropical small mammals (Astúa de Moraes *et al.*
132 2003), with reports of aggressive and predatory behavior towards other small mammals
133 (Wilson 1970) and vertebrates (Oliveira & Santori 1999). Although mostly terrestrial,
134 they can use all strata of the forest (Charles-Dominique *et al.* 1981; Leite *et al.* 1996;
135 Cunha & Vieira 2002; Grelle 2003), and have a broad diet, overlapping with the diet of
136 other small mammals (Astúa de Moraes *et al.* 2003). Species of *Didelphis* also consume
137 small vertebrates, which are present in the stomach or faecal material of up to 30% of
138 the individuals in natural populations of *Didelphis aurita* (Santori *et al.* 1995; Freitas *et*
139 *al.* 1997; Cáceres & Monteiro-Filho 2001).

140 Here in we use the static and the dynamic regression methods to determine if *D.*
141 *aurita* affects other small mammals in two local communities of the neotropics, and
142 which mechanism is involved, exploitation competition or interference. Small mammal
143 populations and microhabitat use were monitored for more than four years in these two
144 communities, providing a unique opportunity to determine the importance of *D. aurita*
145 as a intraguild predator, and its effect on small mammal communities of the Atlantic
146 Forest.

147

METHODS

148

149 **Study areas**

150 We used data from two localities in the Rio de Janeiro State, Brazil: Garrafão
151 and Barra de Maricá. The two areas are part of the Atlantic Forest Biome, but Garrafão
152 is a neotropical forest, whereas Barra de Maricá is a “restinga”, a sand dune
153 physiognomy composed of a patchwork vegetation of shrubs and low trees, distributed
154 upon sand barrier beaches and coastal sand plains. The physiognomy of the restinga in
155 Barra de Maricá is not of a continuous forest, but floristically it is a subset of the
156 Atlantic forest flora (Araújo & Henriques 1984; Araújo 1992). The two localities are
157 less than 200 km apart, with subtle differences in climate. In Garrafão climate is mild-
158 humid-mesothermic, whereas Barra de Maricá is classified as warm superhumid tropical
159 (Nimer 1989). In Garrafão, mean minimum and maximum monthly temperatures were
160 10.7°C and 30.5°C, respectively, and total annual rainfall between 1300 and 1700 mm
161 (Macedo *et al.* 2007). In Barra de Maricá, mean minimum and maximum monthly
162 temperatures were 20°C and 27°C, respectively, and total annual rainfall between 1250
163 and 1600 mm (Cerqueira *et al.* 1993).

164 Garrafão is located at the edge of Serra dos Órgãos National Park in the
165 municipality of Guapimirim (22°28'28"S, 42° 59' 86"W). The area is in the Coastal
166 Forest of the Serra do Mar, a subdivision of the Atlantic Forest Biome (Dinerstein *et al.*
167 1995). The soil is shallow, clayey, and rocky (Rizzini 1979). Weekend houses are
168 common in Garrafão, but the canopy of the forest remains continuous in most of its
169 range. Barra de Maricá is part of the Atlantic Coast Restingas ecoregion (Dinerstein *et*
170 *al.* 1995). In Barra de Maricá two sand dunes formed by marine deposits enclose a
171 lagoon, the Maricá Lagoon. The study area was located between Maricá Lagoon and the

172 Atlantic Ocean, in the restinga scrubs of the first sand dune. This is the most species-
173 rich of the two sand dunes (Cerqueira *et al.* 1993).

174 Fifteen species of small mammals were captured in the two localities, eight
175 marsupials and seven rodents (Cerqueira *et al.* 1993; Gentile *et al.* 2004; Macedo *et al.*
176 2007). The marsupial and rodents are all potentially consumed by *Didelphis aurita*
177 because of their smaller size, all weighting less than 600g as adults. The marsupial
178 *Didelphis aurita* was among the most abundant species captured in the two study sites
179 (472 captures of 223 individuals in Garrafão, 67 captures of 26 individuals in Barra de
180 Marica), followed by the marsupials *Philander frenatus* (166 captures of 69 individuals
181 in Garrafão, 167 captures of 91 individuals in Barra de Maricá), and *Metachirus*
182 *nudicaudatus* (180 captures of 82 individuals in Garrafão, 36 captures of 15 individuals
183 in Barra de Maricá). Other species were abundant but only in one site: in Garrafão, the
184 marsupials *Marmosops incanus* (367 captures of 151 individuals) and *Micoureus*
185 *travassossi* (69 captures of 22 individuals); in Barra de Maricá, the rodents *Akodon*
186 *cursor* (178 captures of 96 individuals) and *Trinomys eliasi* (79 captures of 42
187 individuals). Sample size of the other small mammals did not allow their inclusion in
188 the analyses. Details of the two localities and their assemblages are in Cerqueira *et al.*
189 (1993) and Macedo *et al.* (2007).

190

191 **Field methods - Garrafão**

192 Animals were captured in bimonthly trapping sessions of five consecutive nights
193 each, from April 1998 to April 2003, as part of a capture-recapture study of small-
194 mammal populations (trapping started in April 1997, but habitat measurements only in
195 April 1998). Trapping sessions were conducted in three 0.64 ha grids (A, B, and C)

196 established at three elevations (748, 652, and 522 m) along the Iconha river, hence all in
197 the same drainage basin. Distance between grids A and B was 853 m, and between grids
198 B and C was 573 m. Each grid had 25 trap stations, 20 m apart, distributed in five
199 parallel lines. At each station, two traps were placed on the ground: one Tomahawk
200 model 201 (41 x 14 x 14 cm), and one Sherman model XLK (30.5 x 9.8 x 8 cm).
201 Thirteen of the 25 trap stations of a grid received one extra trap of each model on
202 above-ground platforms varying from 5 to 13 m high.

203 Each trap station was marked with a central stake and four additional stakes
204 were placed 3 m away in the four cardinal directions. Thus, each point was the center of
205 a 6 x 6 m quadrat of 36 m² where the measurements were done. Microhabitat structure
206 was characterized by eight variables (Table 1), measured 3 m from the center of this
207 quadrat, in each direction, using a 0.25-m² square wooden frame (0.50 x 0.50 m) with a
208 wire mesh divided in to 100 open squares, based on Freitas *et al.* (2002). Each
209 measurement consisted of the frequency of squares more than 50% obstructed.
210 Microhabitat measurements were taken concurrently with the capture-recapture
211 sessions, from April 1998 to April 2003.

212 Data from the three grids in Garrafão were pooled because population
213 parameters of *D. aurita* are synchronized and similar between them, indicating that the
214 three grids are part of the same population (Gentile *et al.* 2004; Rademaker &
215 Cerqueira 2006), and because the distance between trapping grids is similar to linear
216 distances moved by individuals of species studied (Loretto & Vieira 2005; Moraes
217 Junior & Chiarello 2008). Population size at every trapping session was estimated by
218 the minimum number of individuals known alive, MNKA, which is the number of
219 individuals captured in a trapping session plus the number of individuals that skipped

220 capture (captured in previously and recaptured latter but not captured in a current
221 trapping session) (Krebs 1966).

222

223 **Field methods - Barra de Maricá**

224 Animals were captured every three months, from January 1986 to July 1987, and
225 from July 1998 to June 2000, as part of a capture-recapture study of small mammals in
226 restinga (Cerqueira *et al.* 1993). Trapping sessions lasted six consecutive nights each in
227 a 4 ha fragment of restinga vegetation in the first sand dune. Initially, trapping sessions
228 were conducted in one 1 ha grid with 100 trap stations, 10 m apart, from January 1986
229 to October 1987. After that, the trapping grid was enlarged and from July 1988 to July
230 1990 trapping was conducted in 4 ha grid with 100 trap stations, 20 m apart, covering
231 the whole patch. At each station, one Young trap was placed on the ground (size 40 x 20
232 x 21cm or 31 x 16 x 16cm).

233 Eight variables were measured at each trap station (Table 2), every trapping
234 session. The variables Herbaceous density, Wood species density, and Obstruction 1 to
235 3 were measured within a circle of 1.0 m diameter centered at the trap station, whereas
236 Number of logs was measured within a circle of 2.5 m diameter. The variables Litter
237 density and Canopy height were measured at the center of the trap station.

238

239 **Exploitation competition between *D. aurita* and other small mammals**

240 The occurrence of exploitation competition was tested by the dynamic method,
241 based on a sample size of 36 for Garrafão and 15 for Restinga de Maricá. Each datum
242 consisted of the ratio between the population size at time $t + 1$ and at time t . The MNKA
243 for each trapping session was used as a measure of population size.

244 In the dynamic approach, the effects of a potential competitor on the per capita
245 growth rate of a species are modeled as

246

$$247 \quad \ln [N_1 (t + 1) / N_1 (t)] = r [K_1 - N_1 (t) - \alpha_{12}N_2(t)] / K_1$$

248

249 where N_1 is the population size of species 1, N_2 is the population size of the potential
250 competitor N_2 (in this case *D. aurita*), K_1 is the carrying capacity of species 1, and α_{12} is
251 the competition coefficient estimating the effect of species 2 on species 1.

252 The parameters of this model can be estimated by a multiple regression of the
253 form

254

$$255 \quad Z = a - bx - cy$$

256

257 where $Z = \ln [N_1 (t + 1) / N_1 (t)]$, $x = N_1 (t)$, $y = N_2(t)$, $a = r$, $b = r / K_1$, and $c = r\alpha_{12} /$
258 K_1 . Cases where $N_i (t) = N_i (t + 1) = 0$ were discarded following the suggestion of Pfister
259 (1995) and Shenbrot & Krasnov (2002). Values of the ratio c/b in cases of c
260 significantly negative are considered estimates of competitive interactions.

261

262 **Interference by *D. aurita* on other small mammals**

263 The occurrence of spatial association was tested by the static method using
264 residuals (Fox & Luo 1996), which requires species abundances and microhabitat
265 measurements per trap station and sampling period. For each species, the total number
266 of individuals captured in a trap station during a field session was a measure of its local
267 abundance, and a result of its microhabitat preference and interaction with other

268 individuals (Rozenzweig *et al.* 1984; Fox & Luo 1996; Shenbrot & Krasnov 2002). In
 269 regressions involving the abundance of two species, one as dependent and the other as
 270 independent variables, trap stations with no capture of either species are excluded from
 271 the analyses to avoid false zeros (Fox & Luo 1996; Luo *et al.* 1998; Shenbrot &
 272 Krasnov 2002). Thus, sample size differed for each regression model depending on the
 273 species pair.

274 The effect of the abundance of other species and microhabitat variables can be
 275 estimated by the multiple regression

$$276 \quad N_1 = K_1 + b_1 X_1 + b_2 X_2 + \dots + b_n X_n + \alpha_{12} N_2$$

277
 278 where N_1 is the population size of species 1, N_2 is the population size of species 2, K_1 is
 279 the carrying capacity of species 1, X_1, \dots, X_n are environmental variables, b_1, \dots, b_n are
 280 regression coefficients, and α_{12} is the competition coefficient estimating the effect of
 281 species 2 on species 1. In the static method using residuals, this regression is broken in
 282 two sets. In a first set, the local abundance of each species is regressed against habitat
 283 factors and the residuals saved; in the second set, the residuals are regressed against the
 284 local abundance of the potential predator/competitor. The residual method is a variation
 285 of the static method that assures that only spatial variation in the abundance of each
 286 species unexplained by habitat factors is tested for the effects of the potential
 287 predator/competitor.

288 Species abundances were standardized by the mean and standard deviation
 289 following Fox & Luo (1996). Principal components were extracted from the correlation
 290 matrix of microhabitat variables and used as independent variables in the first set of
 291 regressions. Principal components were used to obtain a reduced number of orthogonal,

292 independent variables. Only components with eigenvalues greater than one were
293 considered in the analysis (Shenbrot & Krasnov 2002).

294

295

296

RESULTS

297 Garrafão

298 The dynamic method did not detect significant effects of *D. aurita* on any of the
299 other species in Garrafão, and no apparent trend was observed. The intraspecific
300 coefficient of the model [$N_{\text{intra}}(t)$], was significantly negative for all species (Table 3).

301 The first three principal components explained 66.2% of the variance of
302 microhabitat variables in Garrafão, and summarize the effect of five of the eight original
303 variables. The first component was negatively correlated with the three measures of
304 obstruction, representing openness of vegetation from 0.00 m to 1.50 m height; the
305 second component was negatively associated with litter cover, hence represents the
306 proportion of bare soil; the third component was a contrast between absence of rocks
307 and plant cover. Loadings of microhabitat variables on the components, eigenvalues and
308 variance explained are in Appendix 1.

309 In the first set of regression analyses, of the effects of habitat factors on species
310 abundances, the spatial occurrence of *M. nudicaudatus* was positively associated with
311 openness of the understory (PC1) ($t = 2.014$; $P = 0.045$; $R^2 = 0.014$; $N = 474$). The
312 spatial occurrence of *M. travassossi* was negatively associated with openness of the
313 understory (PC1) and with the proportion of bare soil (PC2) ($t = -3.033$, $P = 0.030$, and
314 $t = -2.196$, $P = 0.029$ respectively, with $R^2 = 0.039$; $N = 402$). The other species were
315 not significantly affected by the habitat factors.

316 In the second set of regressions, using the residuals of the first set, *D. aurita* had
317 a significantly negative effect on all other species (Table 4).

318

319 **Barra de Maricá**

320 Similarly as in Garrafão, the dynamic method did not detect significant
321 associations between *D. aurita* and any of the other species (Table 5). The intraspecific
322 term of the model [$N_{intra}(t)$] was negative for all species, but significant only for *P.*
323 *frenatus* and *T. eliasi* (Table 5).

324 The first four components explained 67.62% of the variance of microhabitat
325 variables in Barra de Maricá, and summarize the effect of six of the eight original
326 variables. Loadings of microhabitat variables on the components, eigenvalues and
327 variance explained are in Appendix 1. Only the local abundance of *Philander frenatus*
328 in the grids was negatively associated with obstruction of vegetation (PC1) ($t = -2.303$,
329 $P = 0.022$, $R^2 = 0.073$, $N = 325$). The other species did not show significant correlations
330 with any component.

331 As in Garrafão, in the second set of regressions *D. aurita* had significantly
332 negative correlations with all other species (Table 6).

333

334

335 **DISCUSSION**

336

337 The contrasting results of the dynamic and static methods suggest *D. aurita* as a
338 truly intraguild predator rather than simply a potential competitor. The interference of
339 *D. aurita* on all small mammals in the two assemblages studied was impressive, and
340 indicates that it should be considered key-species in the community structure of small

341 mammals. However, the dynamic method did not detect any significant negative
342 competition coefficient, hence exploitation competition between *D. aurita* and the other
343 species was not detected. This was to be expected if *D. aurita* alternates its major effect
344 on other small mammals, sometimes as a competitor, others as a predator (Polis *et al.*
345 1989).

346 Interference competition was identified as more important than exploitation
347 competition in some small mammal communities (Terman 1974; Dickman & Woodside
348 1983; Kincaid & Cameron 1989). Other studies that demonstrated behaviors of
349 dominance and aggression between small mammal species indicate that interference
350 competition can be common among sympatric small mammal species (Ziv *et al.* 1993;
351 Eccard & Ylonen 2003). A strong interference of individuals of *Didelphis* on other
352 small mammals also explains the results of Fonseca & Robinson (1990), which
353 observed a low capture success of small mammals in Atlantic Forest fragments where
354 *D. aurita* was abundant. Hypotheses to explain its high abundance in some assemblages
355 include local extinction of large predators (Fonseca & Robinson 1990; Terborgh 1992),
356 the mesopredator release hypothesis (Soulé *et al.* 1988), and additional food resources
357 provided by garbage of the local human population (Harmon *et al.* 2005 for *D.*
358 *virginiana*).

359 Regardless of the reason for the high abundance of *D. aurita* in some
360 assemblages, the magnitude of its effect is indeed strong. It was highly significant for all
361 species in two assemblages that differ in habitat and species composition. Although the
362 two assemblages are in the Atlantic Forest biome, Garrafão is part of a large, continuous
363 area of tropical rainforest, whereas Barra de Maricá is a fragment of restinga vegetation.
364 The strong effect of *D. aurita* on other small mammals could result from the

365 opportunistic feeding habits and large body size of species of *Didelphis*, making them
366 occasional predators of small mammals (Wilson 1970). Because of the large overlap in
367 feeding habits of didelphid marsupials and small mammals in general (Astúa de Moraes
368 et al. 2003), they are likely to convey in food patches, increasing the chance of
369 aggressive interactions between them.

370 It is possible that the observed spatial segregation results from scent marks left
371 by individuals of *D. aurita*. Indirect signs of the presence of a predator can have a
372 strong effect on community structure (Lima & Valone 1991; Brown & Kotler 2004).
373 Scent marks are used by the majority of mammal species for intra and interspecific
374 communication (Eisenberg & Kleiman 1972), and in marsupials and rodents it is
375 confirmed by the large size of brain structures related to the olfactory system (Meyer
376 1981; Pirlot 1981). Species of *Didelphis* are nocturnal (Kimble 1997; Bittencourt et al.
377 1999; Cáceres & Monteiro-Filho 2001), and use space in a flexible system of
378 overlapping home ranges (Holmes 1992; Cáceres & Monteiro-Filho 2001). Scent marks
379 are especially appropriate in such conditions, and species of *Didelphis* possess anal
380 glands that produce a secretion liberated with the feces (Grassé 1973). The primary use
381 of this secretion must be intraspecific communication (Holmes 1992), but secondarily it
382 also must reveal the presence of species of *Didelphis* to other small mammals.

383 The static method assumes that microhabitat variables associated with each
384 species are incorporated into the regression analyses. Accordingly, the significant
385 microhabitat associations found were incorporated, but some species were not
386 associated with any of the measured variables or their principal components. For these,
387 it can be argued that the appropriate variables were not identified, a recurrent issue in
388 studies of microhabitat selection (Jorgensen 2004). Negative spatial associations with

389 other species could result from distinct microhabitat preferences that went undetected
390 rather than interference competition. Two pieces of evidence suggest that this is not the
391 case. First, convincing habitat selection patterns were detected in Garrafão using the
392 same microhabitat variables, but working at a larger spatial scale, measuring selection in
393 areas of 188 m² (Moura et al. 2005). At a lower spatial scale, measuring selection at trap
394 stations, species were less selective relative to the same habitat variables (Freitas *et al.*
395 1997). At an even lower scale, comparing sections within a 3-m radius circle, the same
396 species become completely unselective (Moura et al. 2005). Thus, the habitat variables
397 used are able to detect habitat selection. Failure to detect it should be interpreted as true
398 lack of selection at the spatial scale of analysis (Morris 1987; Jorgensen 2004). Second,
399 if individuals of a species were associated with unmeasured habitat features, they would
400 be more abundant in certain regions or trap stations with those features. However,
401 captures of different individuals occurred throughout the area of the grids in the two
402 study areas. Therefore, there is no evidence that spatial segregation resulted from
403 unmeasured habitat characteristics.

404 The negative intraspecific term in most regressions of the dynamic method
405 suggests the occurrence of negative feedbacks within the populations in both study
406 areas. This study was not designed to detect density dependence from time series data,
407 which would require more appropriate analyses and probably longer time series (Dennis
408 & Taper 1994). Nevertheless, the negative feedbacks detected point to density
409 dependence processes, which has already been suggested for populations of *Didelphis*
410 (Rademaker & Cerqueira 2006). Also, from 1998 to 2002 when the abundance of *D.*
411 *aurita* increased in Garrafão, the average mass of adults decreased, suggesting
412 regulation by resource availability (Mendel *et al.* 2008).

413 The combination of the dynamic and static regression methods allowed the
414 inference of the relative roles of exploitation competition and direct spatial interactions
415 of *D. aurita* with other small mammals. Direct spatial interaction was the strong
416 mechanism, not exploitation competition, possibly leading to reduction in species
417 richness and diversity of small mammals as suggested by Fonseca & Robinson (1990).
418 Spatial segregation would be a result of the presence of *D. aurita* or its signs, and its
419 potential as both predator and competitor. Future studies of small mammal assemblages
420 in the Neotropical region should pay special attention to species of *Didelphis*,
421 particularly in habitats disturbed and fragmented by human activities.

422

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Table 1. Microhabitat variables measured at each trap station of the grids in Garrafão.

Variables	Description
PLANT	Plant cover (%)
LITTER	Litter cover (%)
ROCK	Rock cover (%)
CANOPY	Canopy cover (%)
OBSTR1	Obstruction at 0 - 0.5 m high
OBSTR2	Obstruction at 0.5 - 1.0 m high
OBSTR3	Obstruction at 1.0 - 1.5 m high
LOGS	Number of logs

Table 2. Microhabitat variables measured at trap stations of the grids in Barra de Maricá.

VARIABLES	DESCRIPTION
CH	Canopy height
WD	Wood species density
HD	Herbaceous density
OBSTR1	Obstruction at 0 - 0.5 m high
OBSTR2	Obstruction at 0.5 - 1.0 m high
OBSTR3	Obstruction at 1.0 - 1.5 m high
LD	Litter Density
LOGS	Number of logs

Table 3. Regression coefficients of the dynamic method in Garrafão. The dependent variable was the observed growth rate of a species between trapping sessions, $N(t+1)/N(t)$. Independent variables were the abundances at $t = 1$ of *D. aurita* [$N_{\text{did}}(t)$] and the of the species itself [$N_{\text{intra}}(t)$]. For all species, $N = 36$. Boldface indicates significant values.

Species	Variance explained and significance of the model			Significance of individual coefficients			
	R^2	F	P	Constant	$N_{\text{intra}}(t)$	$N_{\text{did}}(t)$	
<i>Philander frenatus</i>	0.414	11.635	< 0.001	Coefficient	0.942	-2.142	0.017
				t	6.293	-4.706	1.396
				P	<0.001	<0.001	0.172
<i>Marmosops incanus</i>	0.295	6.891	0.003	Coefficient	1.179	-0.042	-0.018
				t	7.764	-3.336	-1.455
				P	<0.001	0.002	0.155
<i>Metachirus nudicaudatus</i>	0.295	6.891	0.003	Coefficient	0.837	-0.057	0.007
				t	7.824	-3.248	0.949
				P	<0.001	0.003	0.350
<i>Micoureus travassossi</i>	0.364	4.285	0.034	Coefficient	0.741	-0.180	0.019
				t	3.907	-2.706	1.355
				P	0.001	0.016	0.196

Table 4. Effect of *Didelphis aurita* on small mammal species in Garrafão estimated by the static method (α = competition coefficient, P = probability of the results under the null hypothesis, R^2 = variance explained by the model).

	<i>Marmosops</i>	<i>Metachirus</i>	<i>Philander</i>	<i>Micoureus</i>
	<i>incanus</i>	<i>nudicaudatus</i>	<i>frenatus</i>	<i>travassossi</i>
α	-0.867	-0.827	-0.758	-0.584
P	<0.001	<0.001	<0.001	<0.001
R^2	0.727	0.690	0.576	0.376
N	562	474	456	402

Table 5. Regression coefficients of the dynamic method in Barra de Maricá. The dependent variable was the observed growth rate of a species between trapping sessions, $N(t+1)/N(t)$. Independent variables were the abundances at $t = 1$ of *D. aurita* [$N_{\text{did}}(t)$] and the species [$N_{\text{intra}}(t)$]. For *M. nudicaudatus* $N = 9$, but $N = 17$ for the others. Boldface indicates significant values.

Species	Variance explained and significance of the model			Significance of individual coefficients			
	R^2	F	P	Constant	$N_{\text{intra}}(t)$	$N_{\text{did}}(t)$	
<i>Philander frenatus</i>	0.457	4.630	0.035	Coefficient	1.055	-0.004	-0.010
				t	6.793	-2.825	-0.318
				P	<0.001	0.017	0.757
<i>Metachirus nudicaudatus</i>	0.489	1.434	0.036	Coefficient	0.948	-0.149	0.061
				t	2.714	-1.619	0.563
				P	0.073	0.204	0.613
<i>Akodon cursor</i>	0.265	1.981	0.184	Coefficient	0.910	-0.022	0.034
				t	7.521	-1.978	0.865
				P	<0.001	0.074	0.406
<i>Trinomys eliasi</i>	0.368	3.206	0.080	Coefficient	1.042	-0.067	0.041
				t	8.047	2.458	1.224
				P	<0.001	0.032	0.246

Table 6. Effect of *Didelphis aurita* on small mammal species in Barra de Maricá estimated by the static method. (α = competition coefficient, P = probability of the results under the null hypothesis, R^2 = variance explained by the model).

	<i>Philander</i>	<i>Metachirus</i>	<i>Akodon</i>	<i>Trinomys</i>
	<i>frenatus</i>	<i>nudicaudatus</i>	<i>Cursor</i>	<i>eliasi</i>
α	-0.956	-0.930	-0.781	-0.918
P	<0.001	<0.001	<0.001	<0.001
R^2	0.924	0.880	0.612	0.842
N	325	89	278	152

Appendix 1

Loadings of the original variables on the first three principal components of each locality. Boldface indicates variables with loadings > 0.65, considered significantly associated with the component.

	GARRAFÃO				BARRA DE MARICÁ		
	PC1:	PC2:	PC3:	Variables	PC1:	PC2:	PC3:
	Openeness of the understory	Proportion of bare soil	Absence of rocks/Plant cover		Obstruction	Herbaceous density	Abundance of logs and litter
PLANT	-0.398	0.360	0.658	CH	-0.347	0.067	0.135
LITTER	0.326	-0.805	-0.085	WD	0.526	0.147	0.122
ROCK	-0.240	0.313	-0.765	HD	0.333	0.749	-0.032
CANOPY	0.400	-0.427	0.058	OBSTR1	0.683	0.323	0.005
OBSTR1	-0.892	-0.167	-0.090	OBSTR2	0.828	-0.254	0.086
OBSTR2	-0.926	-0.251	-0.012	OBSTR3	0.699	-0.448	0.140
OBSTR3	-0.851	-0.294	-0.019	LD	-0.142	-0.250	0.673
LOGS	-0.071	-0.273	0.278	LOGS	-0.110	0.328	0.758
Eigenvalue	2.868	1.312	1.117	Eigenvalue	2.185	1.128	1.090
Percentage of explained variance	35.8	16.4	13.9	Percentage of explained variance	27.31	14.11	13.62