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Contact CEH NORA team at
noraceh@ceh.ac.uk

1 **Size matters: body size determines functional responses of ground**
2 **beetle interactions**

3

4 Ball, S.L.^{a,b*}, Woodcock, B.A.^a, Potts, S.G.^b & Heard, M.S.^a

5

6 ^aNERC Centre for Ecology and Hydrology, Maclean Building, Wallingford, Oxfordshire OX10
7 8BB, UK.

8

9 ^bCentre for Agri-Environmental Research, School of Agriculture, Policy and Development,
10 University of Reading, Reading RG6 6AR, UK.

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22 Abstract

23 Understanding patterns in predator:prey systems and the mechanisms that underlie trophic
24 interactions provides a basis for predicting community structure and the delivery of natural pest
25 control services. The functional response of predators to prey density is a fundamental measure of
26 interaction strength and its characterisation is essential to understanding these processes. We used
27 mesocosm experiments to quantify the functional responses of five ground beetle species that
28 represent common generalist predators of north-west European arable agriculture. We investigated
29 two mechanisms predicted to be key drivers of trophic interactions in natural communities:
30 predator:prey body size ratio and multiple predator effects. Our results show regularities in foraging
31 patterns characteristic of similarly sized predators. Ground beetle attack rates increased and
32 handling times decreased as the predator:prey body-mass ratio rose. Multiple predator effects on
33 total prey consumption rates were sensitive to the identity of the interacting species but not prey
34 density. The extent of interspecific interactions may be a result of differences in body mass between
35 competing beetle species. Overall these results add to the growing evidence for the importance of
36 size in determining trophic interactions and suggest that body mass could offer a focus on which to
37 base the management of natural enemy assemblages.

38

39 Zusammenfassung

40 Das Verständnis der Muster von Räuber-Beute-Systemen und der Mechanismen, die trophischen
41 Interaktionen zugrunde liegen, bildet die Basis für Vorhersagen der Gemeinschaftsstruktur und das
42 Erbringen von natürlichen Dienstleistungen zur Schädlingskontrolle. Die funktionelle Reaktion von
43 Räubern auf die Beutedichte ist ein grundlegendes Maß der Interaktionsstärke und ihre
44 Beschreibung ist unabdingbar für das Verstehen dieser Prozesse. Wir nutzten Mesokosmos-
45 Experimente, um die funktionellen Reaktionen von fünf Laufkäferarten, die häufige generalistische
46 Räuber in nordwesteuropäischen Ackersystemen sind, zu quantifizieren. Wir untersuchten zwei
47 Mechanismen, von denen angenommen wird, dass sie Schlüsselfaktoren für trophische

48 Interaktionen in natürlichen Gemeinschaften sind: das Verhältnis der Körpergröße von Räuber und
49 Beute und die Effekte von mehreren Räubern. Unsere Ergebnisse zeigen Regelmäßigkeiten bei den
50 Beutesuchmustern, die charakteristisch für Räuber ähnlicher Größe sind. Die Angriffshäufigkeit
51 nahm bei größeren Carabiden zu und die ‚handling time‘ nahm ab. Die Effekte mehrerer Räuber auf
52 die Gesamt-Konsumptionsrate hingen von der Identität der interagierenden Arten ab, nicht aber von
53 der Beutedichte. Das Ausmaß der interspezifischen Interaktionen könnte sich aus den
54 unterschiedlichen Körpergrößen der konkurrierenden Käferarten ergeben. Insgesamt sind diese
55 Ergebnisse weitere Belege für die Bedeutung der Körpergröße für das Ergebnis trophischer
56 Interaktionen, und sie legen nahe, dass die Körpermasse ein wichtiger Aspekt für das Management
57 der Gemeinschaften von natürlichen Feinden sein könnte.

58

59 **keywords**

60 Predator:prey, functional response, attack rate, handling time, multiple predator effects, body mass
61 ratio, natural pest control, Carabidae.

62

63 **Introduction**

64 The strength and distribution of trophic interactions between predators and their prey are
65 important in determining community stability and biodiversity, and underpin ecosystem processes
66 like natural pest control (Montoya, Pimm, & Sole, 2006). Functional responses describe the *per*
67 *capita* consumption rate of a predator as a function of prey density and are a fundamental measure
68 of interaction strengths between species (Berlow et al., 2004). They can be linear (Type I) or
69 nonlinear (e.g. hyperbolic (Type II) or sigmoid (Type III)) (Holling, 1959). While linear functional
70 responses rarely occur (Jeschke, Kopp, & Tollrian, 2004), nonlinear functional responses play key
71 roles in maintaining population and food web stability and are commonly encountered in natural
72 systems (Williams & Martinez, 2004). Their calculation requires the estimation of two key
73 parameters; attack rate (capture success influenced by processes such as searching, detection and

74 encounter, in Type III functional responses attack rate is a function of prey density) and handling
75 time (time spent to fight, subdue, ingest and digest prey) (Holling, 1959). Functional responses of
76 relatively few predator:prey systems have been characterised empirically, impeding a mechanistic
77 understanding of the key drivers of trophic interactions in natural communities (Kalinkat, Rall, Vucic-
78 Pestic, & Brose, 2011).

79 Body mass is an important factor determining predator:prey trophic interactions and
80 functional response parameters are expected to scale with the ratio between predator and prey
81 body mass (Brose, 2010). A recent meta-analysis of functional response studies within similar
82 ecosystems and metabolic types showed hump-shaped relationships between attack rates and
83 predator:prey body mass ratios (Rall et al., 2012), in line with theoretical models (Brose, 2010). This
84 is likely to be the result of alterations in relative movement speed, visual search area and visibility
85 with changing predator:prey body mass ratios. For example, reduced attack rates can occur with
86 small prey because of the short maximum distance over which a predator is able to locate them, and
87 also with large prey because predator movement speed is comparatively low (Aljetlawi, Sparrevik, &
88 Leonardsson, 2004), resulting in a hump-shaped relationship (Brose, 2010). Functional response
89 studies and theoretical models often show that handling times linearly increase with decreasing
90 predator:prey body mass ratios because predators typically take longer to subdue, ingest and digest
91 larger prey (Brose, 2010; Petchey, Beckerman, Riede, & Warren, 2008). However, Rall *et al* (2012)
92 showed that a negative hump-shaped relationship may occur if, for example, very small prey are
93 consumed whole resulting in longer handling and digestion times than larger prey which are broken
94 down into pieces.

95 Another key determinant of the strength and distribution of trophic interactions is inter- and
96 intra-specific interactions among predators (Symondson, Sunderland, & Greenstone, 2002).
97 Interactions within and between predator species can have analogous effects on trophic
98 interactions, for example, inter- and intra-specific interference commonly reduces per capita
99 consumption rates in a similar way (Hassell, 1978; Sih, Englund, & Wooster, 1998; Skalski & Gilliam,

2001). However, 'multiple predator effects' (MPE) are also possible, whereby the effects on prey consumption depend on whether predator interactions are inter- or intra-specific (Sih et al., 1998). MPE can arise from predators acting either synergistically to increase overall consumption rates (prey risk-enhancing effects) (Losey & Denno, 1998), or antagonistically to lower overall consumption rates (prey risk-reducing effects) (Rosenheim, Wilhoit, & Armer, 1993). A key aim for the development of effective natural pest control programmes is to understand the drivers of MPE among natural enemy species, in order to minimise prey risk-reducing effects and / or promote prey risk-enhancing effects (Snyder & Tylianakis, 2012). The emergence or strength of MPE may be affected by prey density (Tylianakis & Romo, 2010), prey defences (Losey & Denno, 1998), predator traits (Casula, Wilby, & Thomas, 2006; Schmitz, 2007) and relative body mass of species (Brose, 2010), but evidence for these is limited and requires further work.

While several studies have reported the emergence of MPE on prey consumption (Schmitz, 2007; Sih et al., 1998), recent evidence shows their importance may have been incorrectly estimated (McCoy, Stier, & Osenberg, 2012). This appears to be because researchers failed to account for changing prey density during experiments (due to depletion by predators), and therefore use of the 'Multiplicative Risk Model' previously used to understand predator:prey interactions is often inappropriate since it typically assumes a constant per capita consumption rate (linear Type I functional response). McCoy et al. (2012) showed that prey depletion in combination with the ubiquity of nonlinear functional responses often leads to conclusions of prey risk-enhancement or risk-reduction, when predators actually have independent effects (McCoy et al., 2012). Proper evaluation of MPE therefore requires quantification of functional responses along with statistical models accounting for prey depletion (McCoy et al., 2012).

In this study we quantified the functional response of ground beetles species (Coleoptera: Carabidae), to determine whether natural enemies foraging on shared prey exhibit MPE. These beetles are commonly found in north-west European arable farming systems and although morphologically similar, exhibit large inter-specific differences in body mass (Luff, 2002). Whilst

126 competition for resources has been documented for ground beetles (Lang, Rall, & Brose, 2012), we
127 are unaware of any studies using a functional response approach to compare intra- versus inter-
128 specific effects on prey consumption. We tested whether the emergence of MPE was influenced by
129 prey density and predator identity, and examined the relationship between functional response
130 parameters and predator:prey body mass ratios.

131

132 **Materials and methods**

133 *Study organisms*

134 Five generalist predatory ground beetles species, covering a range of body sizes, were
135 selected: *Anchomenus dorsalis* (18.7 ± 5.50 mg); *Calathus fuscipes* (110.9 ± 28.98 mg); *Pterostichus*
136 *madidus* (143.6 ± 3.99 mg); *P. melanarius* (159.3 ± 5.04 mg); *P. niger* (249.5 ± 8.00 mg). All beetles
137 were collected using pitfall trapping at Hillesden farm, Buckinghamshire, England (Long. $1^{\circ}00'W$; Lat.
138 $51^{\circ}57'N$) between 21/05/2012 and 08/06/2012. After collection individuals were stored in species
139 monocultures in plastic tanks (600 x 400 x 200 mm) lined with moist vermiculite (Sinclair, Lincoln UK)
140 under controlled conditions ($16^{\circ}C$; 18:6 h light: dark cycle; 40% humidity). Beetles were provided
141 with drinking water and fed *ad libitum* with the prey species used in subsequent experiments (see
142 below). This was supplemented with dog food which is a rich source of protein, fat and vitamins and
143 minerals (Toft & Bilde, 2002). Prior to experiments the beetles were starved for 48 h during which
144 time they were kept individually in plastic jars containing moist vermiculite.

145 Dead cabbage moth caterpillars (*Mamestra brassicae* L. (Noctuidae)) reared from laboratory
146 cultures were used as the prey item in all experiments. Lepidopteran larvae form part of the natural
147 diet of ground beetles (Toft & Bilde, 2002). In this case dead prey represent sedentary or low-
148 mobility pest species, such as invertebrate eggs (Prasad & Snyder, 2004) and slugs (Symondson,
149 1993) which are frequently consumed by ground beetles under field conditions. To ensure
150 consistency in prey state and size across the experiments, cabbage moth caterpillars were harvested

151 in their late 3rd instars c. 8 days after hatching (mean weight 5.9 mg), freeze-killed and stored frozen.
152 For the experiments, thawed prey was placed evenly on a petri dish (diameter 80 mm) at different
153 densities. This was then placed in the arenas used to assess functional responses. Predator:prey
154 body mass ratios ranged from approximately 3.17 to 42.29.

155

156 *Experimental design*

157 Quantification of ground beetle functional responses and multiple predator effects were
158 undertaken in plastic mesocosm arenas (175 x 115 x 60 mm) into which 150 ml of vermiculite mixed
159 with 50 ml water was added. Individual beetles were used only once and assignment of individuals
160 to treatments was randomised. To measure the functional response of each single species, one
161 individual was introduced into an arena with one of five prey densities (5, 10, 25, 50, 100 larvae).
162 This was replicated five or six times (depending on the availability of ground beetles) for each prey
163 density. During the experiments arenas were positioned randomly inside a controlled temperature
164 chamber. After 24 hours the number of larvae consumed in an arena was recorded, partial
165 consumption was not observed. Prey items were not replaced once eaten.

166 Multiple predator experiments were investigated at three prey densities (25, 50, 100 larvae),
167 each replicated six times. The multiple predator treatments used a substitutive experimental design,
168 whereby overall predator density was held constant while predator species combinations were
169 manipulated. This approach meant that effects of intraspecific versus interspecific interactions on
170 prey consumption were not confounded by increasing predator density (Griffen, 2006). Arenas
171 contained two individuals representing one of five combinations (three intraspecific and two
172 interspecific) of three ground beetle species: (i) *P. melanarius*:*P. melanarius* (ii) *C. fuscipes*:*C. fuscipes*
173 (iii) *P. madidus*:*P. madidus* (iv) *P. melanarius*:*C. fuscipes* (v) *P. melanarius*:*P. madidus*. The selection
174 of beetle species used for multiple predator experiments was restricted to those where an adequate
175 number of individuals were available. The experimental design allowed us to compare the effects of
176 predator interactions on prey consumption when predators competed with an individual of the

177 same species versus a second species. In addition, because we tested *P. melanarius* competing with
 178 a species of similar (*P. madidus* at 143 mg) and smaller (*C. fuscipes* at 110 mg) body size, this design
 179 was also used to look at the impact of differences in relative predator body size on the emergence of
 180 MPE.

181

182 *Statistical analysis*

183 An effective way to distinguish Type I, II and III functional responses involves logistic
 184 regression of the proportion of prey consumed versus initial prey density (Juliano, 2001), which was
 185 modelled for each species using generalised linear models. Since all beetle species showed a Type II
 186 functional response (see results) the model used for estimating functional response parameters a
 187 and T_h is:

188

$$189 \quad N_e = N_0 \{1 - \exp[a (T_h N_e - T)]\}$$

190

191 Where N_e = number eaten, a = attack rate, N_0 = initial prey density, T = total time available and T_h
 192 = handling time. To account for prey depletion in the estimation of functional responses this
 193 incorporates Rogers' random predator equation (Juliano, 2001; Rogers, 1972). Following McCoy *et*
 194 *al.* (2012) this non-linear model was fitted to functional response data for each species using
 195 maximum likelihood estimation under the *mle2* function within the R package 'bbmle' (Bolker & R
 196 Development Core Team, 2012). The relationship between functional response parameters (a and
 197 T_h) and predator:prey body mass ratio was investigated using general linear models. For simplicity,
 198 predator body mass was used as the independent variable since variance in body mass ratios arose
 199 from changes in predator body mass only.

200 Using estimates of a and T_h , MPE were assessed by applying the McCoy *et al.* (2012)
 201 numerical integration to calculate predicted prey survival when two predator individuals foraged
 202 independently. The response variable for detecting MPE was calculated by subtracting experimental

203 observed values (O) from the predicted expected prey consumption rates (E). A general linear model
 204 was used to determine whether there were significant differences in O-E values between the multi-
 205 predator treatment combinations. The role of resource density in the emergence of MPE was
 206 explored via investigation of the dependency of these differences on prey density. A maximal model
 207 with a two-way interaction between multi-predator treatment combination and prey density was
 208 fitted and then simplified using the likelihood ratio test until the most parsimonious model was
 209 identified. Where a significant overall effect of multiple predator treatment was detected,
 210 orthogonal post-hoc contrasts were performed to identify whether there were significant
 211 differences between the levels of the predator combination treatments. This was done with user-
 212 specified comparisons of groups (Crawley, 2009); we identified whether O-E values for (a) *P.*
 213 *melanarius*:*P. madidus* were significantly different to those for *P. melanarius*:*P. melanarius* or *P.*
 214 *madidus*:*P. madidus*, or (b) *P. melanarius*:*C. fuscipes* were significantly different to those for *P.*
 215 *melanarius*: *P. melanarius* or *C. fuscipes*:*C. fuscipes*. All analyses were performed in R (R
 216 Development Core Team, 2009) and where appropriate models were validated graphically using
 217 residual plots to check for normality and homogeneity of variance.

218

219 **Results and Discussion**

220 *Functional response parameters and predator:prey body mass ratio*

221 Logistic regression showed the proportion of prey consumed decreased with increasing
 222 initial prey density for all five beetle species, demonstrating a Type II form (Juliano, 2001). This
 223 negative relationship was significant for all five species: *A. dorsalis* ($t_{1,23} = 2.79$, $P = 0.01$, slope = -
 224 0.022); *C. fuscipes* ($t_{1,28} = 5.38$, $P = <0.0001$, slope = -0.029); *P. madidus* ($t_{1,28} = 5.54$, $P = <0.0001$,
 225 slope = -0.032); *P. melanarius* ($t_{1,28} = 7.05$, $P = <0.0001$, slope = -0.030); *P. niger* ($t_{1,25} = 5.88$, $P =$
 226 <0.0001 , slope = -0.029). After determining attack rates (a) and handling time (T_h) for each species
 227 using Type II functional responses (Fig. 1), the relationship between these parameters and predator

228 body mass were determined. Attack rates were positively ($t_{1,3} = 4.05$, $P = 0.027$, slope = 0.01) and
229 handling times were negatively ($t_{1,3} = 4.72$, $P = 0.018$, slope = -0.18) correlated with increasing
230 predator body mass (Fig. 2). This indicated that when ground beetle species were larger relative to
231 their prey they encountered and captured resources at a higher rate and required less time for
232 digestion.

233 The scaling of functional response parameters with predator body mass (and therefore
234 predator:prey body mass ratios) adds to the mounting evidence for the importance of body size in
235 determining predator:prey interactions (Berlow et al., 2009; Ings et al., 2009). Linear responses
236 between predator:prey body mass ratios and both attack rates (Hassell, Lawton, & Beddington,
237 1976) and handling times (Brose, 2010) have been reported elsewhere, however, our results do not
238 confirm the findings of a recent meta-analysis which showed hump-shaped and negative hump-
239 shaped relationships for attack rates and handling times, respectively (Rall et al., 2012). One reason
240 for this could be that the range of body mass ratios considered here was too limited such that the
241 observed patterns represent only sections of the humped / negatively humped relationships (Brose,
242 2010). Attack rates may decrease with smaller prey than considered in this study (i.e. greater
243 predator:prey body mass ratios) because the reactive distance (the maximum distance at which a
244 predator can locate a prey (Holling, 1959)) is typically lower for smaller prey items (Aljetlawi et al.,
245 2004). Indeed, large ground beetle species are reported to be inefficient at locating invertebrate
246 eggs (Toft & Bilde, 2002). Likewise, at greater predator:prey body mass ratios than considered in this
247 study handling times may increase if, for example, smaller prey take longer to digest because they
248 are consumed whole, leading to lengthier digestion and overall handling time (Rall et al., 2012).

249 Another reason why hump-shaped relationships between predator:prey body mass ratios
250 and functional response parameters were not detected could be related to the immobility of the
251 prey items used. Mobile prey typically have a greater ability to outmanoeuvre relatively large
252 predators (Brose, 2008), therefore capture success and overall attack rates can be reduced at high
253 body mass ratios, resulting in the hump-shaped relationship often reported between attack rate and

254 predator:prey body mass ratio (Brose, 2010). The dead caterpillars used for this study may be
255 representative of sedentary prey, where high capture success may be expected once predators have
256 located them. *P. niger* is one of the largest ground beetle species inhabiting north-west European
257 arable fields and so may commonly have the greatest predator:prey body mass ratio. However, *P.*
258 *niger* is unlikely to consistently be the optimum size for highest consumption of very small and/or
259 mobile pest species. Indeed, Vucic-Pestic, Rall, Kalinkat and Brose (2010) found intermediate-sized
260 ground beetles to have the highest attack rates with mobile prey. This highlights the need for
261 systematic explorations of optimum body mass ratios across different prey groups (e.g. mobile
262 versus sedentary) (Brose, 2010). Another important consideration for future research is intra-specific
263 variation between sexes, since females tend to be larger and can have different dietary needs and
264 foraging behaviours (Lovei & Sunderland, 1996).

265

266 *Multiple predator effects on prey consumption rates*

267 Emergent MPE on prey consumption were identified for *P. melanarius* when this species
268 foraged with *P. madidus* (Fig. 3). This is based on an overall significant predator species combination
269 treatment effect on O-E values of prey consumption rates ($F_{4,85} = 2.50$, $P = 0.049$), and post-hoc
270 comparisons showing the mean values of *P. melanarius*:*P. melanarius* and *P. melanarius*:*P. madidus*
271 species combinations to differ significantly ($t_{1,85} = 2.28$, $P = 0.025$). The positive O-E values of the
272 single species *P. melanarius*:*P. melanarius* combination suggests that intraspecific facilitation for this
273 species resulted in higher consumption rates of prey than expected if predators foraged
274 independently. In contrast, when competing with *P. madidus* there is evidence of negative
275 interspecific interactions with *P. melanarius* reducing consumption rates below what was expected.
276 Thus, the emergence of MPE was due to a combination of prey risk-enhancing effects in the *P.*
277 *melanarius*:*P. melanarius* treatment and prey risk-reducing effects in the *P. melanarius*:*P. madidus*
278 treatment.

279 Prey risk-enhancing effects have previously been attributed to changes in prey behaviour,
280 for example when prey increase their activity in response to a searching predator (Sih et al., 1998).
281 However, there is little evidence from previous research on inactive prey for why prey risk-
282 enhancing effects may occur when multiple *P. melanarius* forage simultaneously. It could be that
283 increased per capita consumption rate in the presence of competitors is an adaptation to perceived
284 competition for food resources. The likely mechanism for prey risk-reduction when *P. madidus* and
285 *P. melanarius* forage simultaneously is negative interspecific interactions which result in less time
286 available for foraging and a reduction in *per capita* prey consumption (Skalski & Gilliam, 2001). In all
287 other post-hoc comparisons, the means of the O-E values did not differ significantly: *P. madidus*:*P.*
288 *madidus* and *P. melanarius*:*P. madidus* ($t_{1,85} = 0.79, P > 0.05$); *P. melanarius*:*P. melanarius* and *P.*
289 *melanarius*:*C. fuscipes* ($t_{1,85} = 0.08, P > 0.05$); *C. fuscipes*:*C. fuscipes* and *P. melanarius*:*C. fuscipes* (t
290 $_{1,85} = 0.50, P > 0.05$) (Fig. 3). This indicates that intra- and inter-specific interactions had similar effects
291 on prey consumption for *P. madidus* when it foraged with *P. melanarius*, *P. melanarius* when it
292 foraged with *C. fuscipes*, and *C. fuscipes* when it foraged with *P. melanarius*.

293 The results show interspecific interactions caused emergent MPE on prey consumption
294 when *P. melanarius* foraged with *P. madidus* but not *C. fuscipes*. This demonstrates that differences
295 in the effect of within- and between-species interactions on prey consumption depend on the
296 identity of the competing species. Previous studies have also found predator identity to be
297 important in determining the effect of interference (Siddon & Witman, 2004; Vance-Chalcraft &
298 Soluk, 2005), whereas others have showed that non-independent effects were a consequence of
299 changes in predator density rather than species richness (Schmitz & Sokol-Hessner, 2002; Sokol-
300 Hessner & Schmitz, 2002; Vance-Chalcraft, Soluk, & Ozburn, 2004). However, due to the ubiquity of
301 nonlinear functional responses, many published studies violate the Type I (i.e. linear) functional
302 response assumption of the Multiplicative Risk Model used to estimate prey consumption. As a
303 result, apparent MPE may instead reflect non-linearities in predator functional responses (McCoy et
304 al., 2012). Because we estimated predator functional responses independently and used Rogers

305 random predator equation to account for prey depletion, differences in prey consumption rates are
306 more likely to reflect true MPE. That MPE were detected when *P. melanarius* foraged with *P.*
307 *madidus* (a species of equivalent body size) but not *C. fuscipes* (a species approximately two thirds of
308 the size) suggests that relative predator size may be a contributing factor for the emergence of MPE,
309 more specifically, inter-specific interference may be stronger when predator species are more
310 equally matched (Brose, 2010).

311 There was no significant effect of initial prey density on the O-E consumption rates ($F_{1,84} =$
312 $1.442, P = 0.233$), suggesting that the effect of within- and between-species interactions on prey
313 consumption were consistent over changes in prey density. Alteration to MPE with increasing prey
314 density have been attributed to increased foraging effort associated with individual functional
315 responses, resulting in more frequent interactions with other consumers (Griffen, 2006). The
316 multiple predator experiments in this study were conducted at prey densities of 25 prey 0.02 m^{-2} or
317 greater, where the Type II functional responses of predators have almost reached the asymptote
318 representing predators limited by handling time only (Holling, 1959). Thus prey density may be most
319 important in mediating trophic interactions at very low densities when interacting predator foraging
320 behaviours change with prey availability (Tylianakis & Romo, 2010). Our findings complement a
321 recent study showing synergistic interspecific interactions between predators emerged only at low
322 prey densities because antagonistic intraspecific interactions were more likely (Wilby & Orwin,
323 2013). This also suggests that changes in the effects of intra- and inter-specific interactions with prey
324 density are most likely to occur when the effects on prey risk are opposing i.e. prey risk-reduction
325 versus prey risk-enhancement.

326 In conclusion, using mesocosms and a functional response approach we have demonstrated
327 that the emergence of MPE among ground beetle natural enemy species critically depends on the
328 identity of the competing species. Our results suggest body size may be a key driver of such identity
329 effects, warranting further investigation in more realistic environments. In addition, body size was
330 significantly related to functional response parameters. Integration of body size into natural pest

331 control programmes may help us understand the circumstances under which natural enemy species
332 interact beneficially. Although ground beetle diversity can be promoted by agri-environmental
333 management (Woodcock et al., 2010), it remains unclear whether it is possible to manage for
334 particularly beneficial species or groups. Body size could be a realistic focus on which to base
335 management of natural enemy assemblages through habitat manipulation, since size can be
336 important in determining species' environmental responses (Tschardtke, Steffan-Dewenter, Kruess,
337 & Thies, 2002).

338

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345

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450

451 **Figure captions**

452

453 **Fig. 1.** Type II functional responses of the five predator beetle species modelled using Rogers'
454 random predator equation; (A) *Anchomenus dorsalis* (B) *Calathus fuscipes* (C) *Pterostichus*
455 *melanarius* (D) *P. madidus* (E) *P. niger*. Initial prey density is the number of prey per 0.02 m².

456

457 **Fig. 2.** The response of carabid species (A) attack rates and (B) handling times to predator body
458 mass. Lines depict fitted values from general linear models. Attack rate per unit area (0.02 m²) and
459 time (24 h) is given.

460

461 **Fig. 3.** Mean experimentally observed minus expected values if ground beetles forage independently
462 across multiple predator treatments. The table shows the beetle species present in each multiple
463 predator treatment combination and their mean weights (Cf = *Calathus fuscipes*, Pmad =
464 *Pterostichus madidus*, Pm = *P. melanarius*). Bars which share letters were compared in post-hoc
465 contrasts and those underlined differed significantly (p<0.05).

466

467 **Figures**

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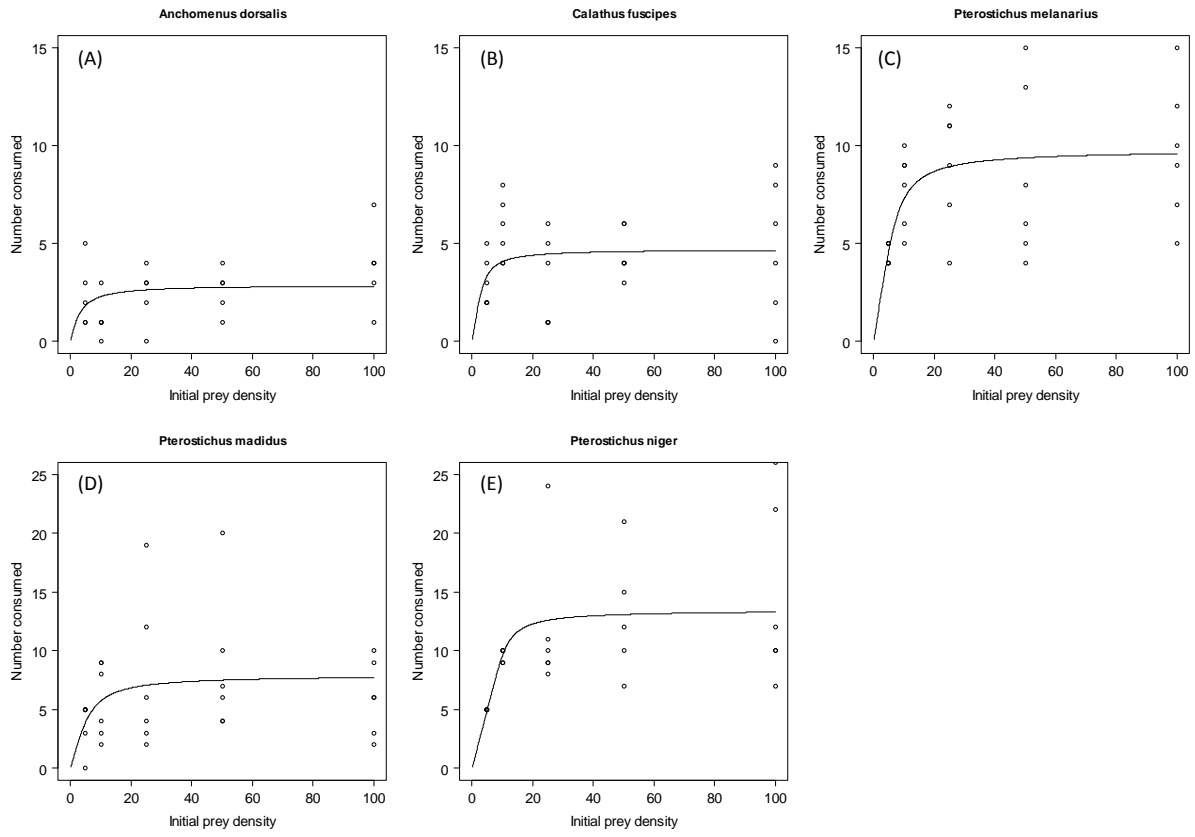
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478 **Fig. 1**

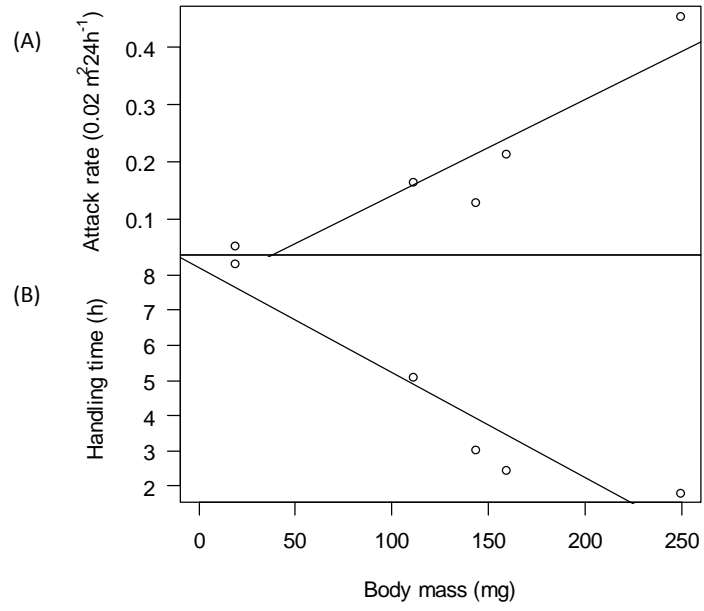
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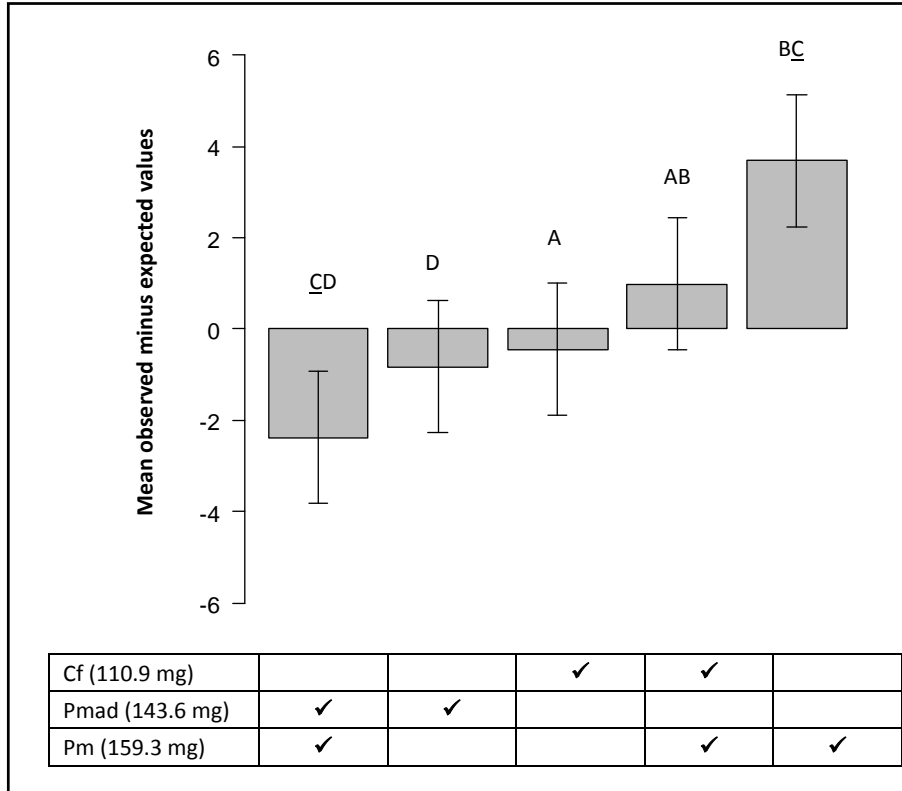
483 **Fig. 2**

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486 **Fig. 3**

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