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Size matters: Body size determines functional responses of ground beetle interactions

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Abstract

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

Zusammenfassung

Das Verständnis der Muster von Räuber-Beute-Systemen und der Mechanismen, die trophischen Interaktionen zugrunde liegen, bildet die Basis für Vorhersagen der Gemeinschaftsstruktur und das Erbringen von natürlichen Dienstleistungen zur Schädlingskontrolle. Die funktionelle Reaktion von Räubern auf die Beutedichte ist ein grundlegendes Maß der Interaktionsstärke und ihre Beschreibung ist unabdingbar für das Verstehen dieser Prozesse. Wir nutzten Mesokosmos-Experimente, um die funktionellen Reaktionen von fünf Laufkäferarten, die häufige generalistische Räuber in nordwesteuropäischen Ackersystemen sind, zu quantifizieren. Wir untersuchten zwei Mechanismen, von denen angenommen wird, dass sie Schlüsselfaktoren für trophische Interaktionen in natürlichen Gemeinschaftensind: das Verhältnis der Körpergröße von Räuber und Beute und die Effekte von mehreren Räubern. Unsere Ergebnisse zeigen Regelmäßigkeiten bei den Beutesuchmustern, die charakteristisch für Räuber ähnlicher Größe sind. Die Angriffshäufigkeit nahm bei größeren Carabiden zu und die‘ handling time’ nahm ab. Die

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Effekte mehrerer Räuber auf die Gesamt-Konsumptionsrate hingen von der Identität der interagierenden Arten ab, nicht aber von der Beutedichte. Das Ausmaß der interspezifischen Interaktionen könnte sich aus den unterschiedlichen Körpergrößen der konkurrierenden Käferarten ergeben. Insgesamt sind diese Ergebnisse weitere Belege für die Bedeutung der Körpergröße für das Ergebnis trophischer Interaktionen, und sie legen nahe, dass die Körpermasse ein wichtiger Aspekt für das Management der Gemeinschaften von natürlichen Feinden sein könnte.

Keywords: Predator:prey; Functional response; Attack rate; Handling time; Multiple predator effects; Body mass ratio; Natural pest control; Carabidae

Introduction

The strength and distribution of trophic interactions between predators and their prey are important in determining community stability and biodiversity, and underpin ecosystem processes like natural pest control (Montoya, Pimm, & Sole, 2006). Functional responses describe the per capita consumption rate of a predator as a function of prey density and are a fundamental measure of interaction strengths between species (Berlow et al., 2004). They can be linear (Type I) or nonlinear (e.g. hyperbolic (Type II) or sigmoid (Type III)) (Holling, 1959). While linear functional responses rarely occur (Jeschke, Kopp, & Tollrian, 2004), nonlinear functional responses play key roles in maintaining population and food web stability and are commonly encountered in natural systems (Williams & Martinez, 2004). Their calculation requires the estimation of two key parameters; attack rate (capture success influenced by processes such as searching, detection and encounter, in Type III functional responses attack rate is a function of prey density) and handling time (time spent to fight, subdue, ingest and digest prey) (Holling, 1959). Functional responses of relatively few predator:prey systems have been characterised empirically, impeding a mechanistic understanding of the key drivers of trophic interactions in natural communities (Kalinkat, Rall, Vucic-Pestic, & Brose, 2011).

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

Another key determinant of the strength and distribution of trophic interactions is inter- and intra-specific interactions among predators (Symondson, Sunderland, & Greenstone, 2002). Interactions within and between predator species can have analogous effects on trophic interactions, for example, inter- and intra-specific interference commonly reduces per capita 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 (Sih et al., 1998; Schmitz, 2007), 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