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Dangerous prey is associated with a type 4 functional response in spiders

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Prey can defend themselves against predators in many different ways. Social insects, such as ants, possess particularly effective defensive systems. Some predators are better adapted to prey defence than others. We compared the capture and defence efficiency in three spider species that differ in their level of myrmecophagy. We used three ant species differing in body size and aggression in a functional response experimental set-up that measured capture frequency at different prey densities. We found a type 4, dome-shaped functional response, and we propose a new mechanistic model to describe this type. Estimated parameters (searching efficiency, handling time, inhibition by prey) were then compared among spider and ant species to quantify density-dependent defensive effects on the predator's capture efficiency. We also compared survival of spiders during experiments. We found that myrmecophagous *Zodarion* spiders hunted ants with the highest capture efficiency and had the highest survival, suggesting that these spiders are adapted to living with high densities of ants. Polyphagous *Xysticus* spiders captured ants with lower efficiency and had the lowest survival, indicating that these spiders are adapted to the capture of solitary ant workers. Polyphagous nonanteating *Pardosa* spiders did not capture ants but had high survival, and are apparently adapted to living with high densities of ants. The new proposed model of the type 4 functional response can be applied to other predator–prey systems in which the prey is dangerous and a decrease in predator hunting has a similar dependence on prey density.

Individual prey are capable of inflicting costs on foraging predators in many ways. Prey can simply make handling by the predator more difficult, specifically, inducible prey defence can lead to a lower predation rate by increasing the predator's handling time, decreasing the attack efficiency or both (Havel & Dodson 1984; Jeschke & Tollrian 2000). Some prey can even be dangerous to predators. Such prey possess morphological structures or behavioural adaptations, or contain chemical substances, that may cause injury or lead to the death of the predator (e.g. Edmunds 1974; Caro 2005). Numerous examples are available: the locking spines of ictalurid catfish can choke gape-limited predators, such as herons and grebes, during swallowing (Forbes 1989); zebras can defend themselves by kicking and biting when attacked by predators (Goodall & van Lawick 1970); and consumption of the toxic collembolan *Folsomia candida* by spiders *Pardosa prativaga* reduces survival, development and growth rate (Fisker & Toft 2004).

Colonial or social prey can use group defence (Tener 1965; Holmes & Bethel 1972; May & Robinson 1985) and the efficiency of such defence increases with the number of prey individuals, giving rise to density dependence (Jeschke 2006). Predators then try to avoid patches of high prey densities (Schaller 1972). Since prey density in natural environments will rarely be constant (Baldwin 1996), information about density dependence is essential for understanding evolutionary arms races and for predicting the predator–prey dynamics.

To quantify density-dependent defensive effects on a predator's capture efficiency the functional response can be used. It is an important component of predation (Solomon 1949) and describes the relationships between an individual predator and its prey in terms of capture frequency. Holling (1961) distinguished four types of functional response (see Table A1 and Fig. A1 in Appendix 1 for the summary of functional response types, their descriptions and examples). Of these, types 1 to 3 do not take into account prey defence and are thus useful for modelling the functional response of a predator capturing innocuous prey. Type 4 includes an additional component that can be related to prey defence. The existence of type 4 was first derived only theoretically and was expected to occur only in vertebrates (Holling 1961). In types 1 to 3 the capture frequency reaches a maximum at a certain prey density and then remains constant. Type 4 is the only type for which the capture frequency decreases at high density below the maximum achieved. Holling (1965) ascribed the decline to situations in which the predator develops a 'nonsearching' image of the prey and gives up hunting it. Studies have investigated a range of potential causes for

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the decrease in hunting frequency at higher prey densities: for instance, the predator may become confused when hunting prey in swarms or aggregations (Welty 1934; Jeschke & Tollrian 2007); prey may disturb predators (Mori & Chant 1966); predators avoid prey treated with a neurotoxic insecticide (Toft & Jensen 1998; Claver et al. 2003); heterogeneous surroundings provide refuges for prey (Vucic-Pestic et al. 2010); the nutrient content of prey is imbalanced (Bressendorff & Toft 2011); and predators' mobility is limited in tall and dense grass swards (Heuermann et al. 2011).

Our aim in this study was to investigate the functional response of true predators (capturing many prey items and killing them immediately after attack) hunting dangerous social prey. Spiders are ideal for such a study because they feed on a variety of prey and have a variety of capture adaptations (Pekár et al. 2012). Most spider species hunt innocuous prey (Pekár et al. 2012), but some catch dangerous prey, such as other spiders (e.g. Whitehouse 1987), ants (e.g. Pekár 2004) or termites (e.g. Eberhard 1991). The latter two prey types are social, possessing a unique set of defences. In our study we focused on ant-eating predators. Ants are very dangerous prey because they are also predators, possess strong mandibles, can sting, and have effective group defence (Hölldobler & Wilson 1990). Most polyphagous spiders are not able to hunt ants without risk of harming themselves, so they avoid them (e.g. Huseynov et al. 2008). With respect to predatory strategy, predators, such as spiders, can be divided into five categories: (1) species that do not hunt ants at all, (2) species that are able to catch ants but prefer other prey types, (3) species that hunt ants as frequently as other prey types, (4) species that prefer ants over other prey but still accept other prey and (5) species that exclusively hunt ants (Huseynov et al. 2008).

We hypothesized that the capture of ants would give rise to the type 4 functional response, as supported by a previous study (Pekár 2005), owing to the ants' defensive ability increasing with group size. Fitting an appropriate model allowed us to estimate the capture efficiency of different spider species, which is influenced by capture tactics that increase capture rate and reduce counterattack. We used three spider species differing in the level of myrmecophagy (category 1, 3 and 5) and three ant species (see below). Parameters estimated from the functional response model (handling time, searching efficiency, prey inhibition) were then used as a quantitative measure of level of defensive abilities in the ant species and the spiders' adaptations for the capture of ants. Observed survival was used to assess defensive adaptations of spiders to hunting dangerous prey. Although spiders from category 1 do not consume ants, they frequently encounter ants of different densities in their microhabitat and thus must have evolved a strategy to survive encounters. Measurement of capture rate is irrelevant in such a case and only defence efficiency of these spiders was studied.

METHODS

The Model

Three models have been proposed for the type 4 functional response (Tostowaryk 1972; Hassell 1977; Fujii et al. 1986). We fitted all three models to our data and found their fits unsatisfactory (see Appendix 2); therefore, we proposed a new mechanistic model.

We followed Holling (1965) who based his equation on particular components of predation. The total time (T) of one capture cycle (1) is the sum of the time spent in a digestive pause (T_D), searching for prey (T_S), handling prey (T_P) and consuming prey (T_E): $T_{(1)} = T_{D(1)} + T_{S(1)} + T_{P(1)} + T_{E(1)}$ (Holling 1965). We ignored the time spent in digestive pause (T_D) as we examined the functional response over a short time period. We also ignored the time spent on consumption (T_E) because the predators mostly consumed the killed prey for only a short time owing to interruptions by other prey individuals. A new component (T_O) was added, which includes the time that the predator had to spend defending itself against dangerous prey. One capture cycle (the time it takes to catch one prey item) then included the following components: $T_{(1)} = T_{S(1)} + T_{P(1)} + T_{O(1)}$. Total searching time ($T_S$) increases with the number of prey caught (A) and decreases with prey density (N) and the predator's searching efficiency (a). The total time spent hunting prey (T_P) increases with the number of prey caught (A) and prey handling time (t_h) (Holling 1965). Furthermore, we hypothesized that the total time of predator defence (T_O) increases with the number of prey caught (A) and with prey density (N) owing to cooperative defence at some rate (c). We called this rate 'inhibition by prey' after Tostowaryk (1972). It was assumed to be positively related to ant 'aggression', in terms of attacks on spiders. Unlike Tostowaryk (1972) who assumed a quadratic relationship between prey inhibition and prey density, we observed a linear relationship between spider mortality and ant density. Therefore, the assumption of linearity was satisfied for our data (see Appendix 2).

Total hunting time (T) with a known number of cycles (a known number of prey caught) is then given by:

$$T = \frac{A}{aN} + At_h + cAN.$$

Thus, the number of prey caught (A) during a given time period T is:

$$A = \frac{aTN}{1 + at_hN + acN^2}.$$

Experiments

We used three spider species from different families and with different hunting strategies. Wolf spiders (Lycosidae) of the genus *Pardosa* (*Pardosa agrestis*) are actively hunting spiders that do not hunt ants (category 1) but live around their nests and must deal with the danger of being attacked by ants (Nentwig 1986). Crab spiders (Thomisidae) of the genus *Xysticus* (*Xysticus cristatus*) use a sit-and-wait strategy to capture ants (category 3) as well as other prey (Nyffeler & Breene 1990). Ant-eating spiders (Zodariidae) of the genus *Zodarion* (*Zodarion rubidum*) hunt only ants (category 5; Pekár 2004).

Pardosa spiders were reared in the laboratory from eggsacs, which had been collected together with females from grassland in Brno (49°15′13.48″N, 16°34′16.79″E, Czech Republic). After hatching and leaving the females, the spiderlings were fed with a mixture of small insects (springtails, flies, termites). The spiderlings were used in experiments when they had achieved a body size of about 3–3.5 mm, which corresponded to the second instar. In total, 58 *Pardosa* spider individuals were used. *Xysticus* spiders were also collected from grassland in Brno (49°15′5.52″N, 16°34′15.94″E). Juvenile and subadult individuals with an average body size of 3.5 mm were used. In total, 106 *Xysticus* spider individuals were used. Specimens of *Zodarion* spiders were collected in the vicinity of the railway station in Brno (49°15′1.48″N, 16°35′24.77″E). Individuals of *Zodarion* used in experiments were juveniles or subadults of both sexes and adult females. The average body size of spiders was 3 mm. In total, 226 *Zodarion* spider individuals were used.

All spider individuals were kept separately in test tubes with plaster of Paris at the bottom. Humidity was maintained by adding a few drops of water to the plaster each week. They were kept at room temperature (ca. 23 °C) and a natural light:dark cycle (approximately 14:10 h). Prey were offered to spiders ad libitum 5 days before running the experiments to standardize their level of hunger. *Zodarion* spiders were fed with *Tetramorium* ants; *Xysticus* and *Pardosa* spiders were fed with vestigial *Drosophila* flies.

One day before the experiments, the spiders were moved separately to 7 cm high plastic containers with circular bases 4.5 cm in