

Multiple factors, including arena size, shape the functional responses of ladybird beetles

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Abstract

1. Functional response studies are often used to determine the suitability of predators as biocontrol agents. Ladybird beetles (Coleoptera: Coccinellidae) are often used for the control of crop pests such as aphids. However, most functional response studies on coccinellids compare a limited number of species at different life stages, temperatures or sexes. A large-scale comparison of ladybird beetle functional responses is needed to evaluate the utility of these species as potential biocontrol predators and to understand the traits that influence the interaction strength between ladybird beetles and their prey.
2. We compiled 158 ladybird beetle functional responses from 30 studies and tested for effects of taxa, traits, temperature and arena size on functional response parameters using linear mixed-effects models.
3. Our results show that functional response parameters (handling time and space clearance rate) are affected by predator stage, predator mass, prey type, temperature and arena size. Although complicated by interaction terms, space clearance rate generally increased with predator size, temperature and predator stage, while handling time decreased with predator size, temperature and predator stage. Coleopteran prey induced the highest handling times.
4. Our results also show that experimental arena size has a large, consistent effect on space clearance rate. Arena size is more important in determining foraging rates at low prey densities than any other factor considered here, including predator mass and temperature. Efforts to use laboratory-based functional response experiments to evaluate the efficacy of biocontrol predators are therefore confounded by the choice of arena size.
5. *Synthesis and applications.* In addition to confirming known body mass and temperature effects, our study reveals previously unclear age-related effects and the importance of prey types, which can be used to optimize biocontrol programmes. The arena size effect is unexpected and problematic because failure to account for arena size precludes accurate comparison of biocontrol predator effectiveness. We suggest managers and biocontrol practitioners re-evaluate the efficacy of candidate biocontrol predators, perhaps by statistically controlling for arena size to minimize the influence of this widely unconsidered factor on functional response estimates.

KEYWORDS

arena size, biocontrol, Coccinellidae, functional response, ladybird beetle, larva, predator-prey interaction, space clearance rate

1 | INTRODUCTION

Ladybird beetles (Coleoptera: Coccinellidae) are commonly used as biocontrol agents to regulate herbivorous insect populations on economically important plants, including crops and ornamentals (Dixon, 2000; Evans, 2004; Koch, 2003; Obrycki & Kring, 1998). Ladybird beetles consume a variety of prey including aphids, mites, beetles and butterfly eggs (Gotoh, Nozawa, & Yamaguchi, 2004; Hodek & Honěk, 2009; Koch, Hutchison, Venette, & Heimpel, 2003; Kwang-Shing, Naotake, & Fusao, 1993). Crucial to the successful use of coccinellids—or any type of biocontrol predator—for pest control is an understanding of how effectively they suppress pest populations under various conditions. One way in which ladybird beetles and other predators are evaluated for biocontrol potential is through their functional response (Agarwala, Bardhanroy, Yasuda, & Takizawa, 2001; Gupta, Pervez, Guroo, & Srivastava, 2012; Madadi, Parizi, Allahyari, & Enkegaard, 2011).

Functional responses, which describe how predation rate changes with prey density, are one way to measure the interaction strength between a predator and its prey (Holling, 1959; Novak & Wootton, 2010). Most predators exhibit a saturating functional response (Jeschke, Kopp, & Tollrian, 2004), often described by the Holling disc equation:

$$f(N) = \frac{aN}{1+ahN} \quad (1)$$

where $f(N)$ is the predator foraging rate, a is the space clearance rate (also known as attack rate), N is prey density and h is handling time. Space clearance rate describes how quickly a predator clears a given space of prey, and handling time refers to the predator's time investment per prey consumed. The inverse of handling time is equal to the predator's maximum consumption rate, which defines the asymptote of the functional response, and space clearance rate is the slope of the functional response as it approaches the origin. Relatively high space clearance rates and low handling times indicate that a predator can consume more prey across all prey densities, which could allow a species to function as an effective biocontrol agent.

Systematic across-species variation in functional responses may arise due to the effects of body size and temperature (DeLong & Vasseur, 2012; Kalinoski & DeLong, 2016; Rall et al., 2012). Predator body size influences movement behaviours, ability to detect and subdue prey, and the relative energetic value of prey (Aljetlawi, Sparrevik, & Leonardsson, 2004; McGill & Mittelbach, 2006; Pawar, Dell, & Savage, 2012). Therefore, scaling theory predicts that space clearance rate should increase, and handling time decrease, with predator body size. Likewise, because increasing temperature increases biochemical reaction rates and movements in ectotherms, up to a point, space clearance rates should increase and handling times

should decrease with temperature (Burnside, Erhardt, Hammond, & Brown, 2014; Dell, Pawar, & Savage, 2011; Kalinoski & DeLong, 2016; Rall et al., 2012). Although temperature effects on ladybird beetle predation have been studied at the species level, no work has been done on temperature effects across coccinellid species.

An understanding of how conclusions from laboratory-based experiments can be extrapolated to ladybird beetles foraging in greenhouses, agricultural crops, or natural habitats is vital to decisions about how to effectively use ladybird beetles, or any other predator, as biocontrol agents, and for inferring the role of ladybird beetles in food webs more generally. One key aspect of this extrapolation is the nature of experimental arenas. Although some laboratory-based experiments use empty arenas and others include vegetative structure, most experiments also vary in the size of the foraging arenas used. The effect of variation in arena size on functional response parameters has previously received minimal attention, with some research suggesting that arena size may play a role in determining space clearance rate (Uiterwaal, Mares, & DeLong, 2017; Yaşar & Özger, 2005a), and others indicating that it is unimportant (van Rijn, Bakker, van der Hoeven, & Sabelis, 2005).

The widespread use of ladybird beetles for biocontrol has spurred researchers to make multiple estimates of their functional responses (Table 1). However, most of these studies investigate specific predator-pest pairs or compare a handful of conspecific ladybird beetles at different life stages, across temperatures or between sexes. Identification of broad functional response patterns is critical to an understanding of ladybird beetles as biocontrol agents, their role as integral parts of many ecosystems and the successful invasion of exotic species. Yet a large-scale comparison of ladybird beetle functional responses is not available. We compiled a database of published ladybird beetle functional responses and tested for the effects of predator body size, predator stage class (instar), temperature, prey taxonomic group and arena size on space clearance rate and handling time. Our results reaffirm the expected effects of body size and temperature, but surprisingly, our results reveal a very large effect of arena size. Furthermore, our results suggest controlling for arena size is crucial for understanding patterns and differences among species that are candidates for biocontrol introduction, calling into question the naïve translation of laboratory-based results to field settings.

2 | MATERIALS AND METHODS

We searched the literature with terms such as "ladybug," "ladybird," "coccinellid," "functional response" and "biocontrol" to find papers reporting ladybird beetle functional responses. We found a small

TABLE 1 Ladybird beetle species included in our analysis, with number of functional responses reported per species and the sources of those datasets. Additional information and data are available from the *Dryad Digital Repository* (Uiterwaal & DeLong, 2018)

Predator	Prey order	Number of functional responses	Sources
<i>Adalia bipunctata</i>	Hemiptera	7	Jalali et al. (2010) Timms, Oliver, Straw, and Leather (2008)
<i>Adalia fasciatopunctata</i>	Hemiptera	8	Atlihan, Kaydan, Yarımbatman, and Okut (2010) Yaşar and Özger (2005b)
<i>Aiolocaria hexaspilota</i>	Coleoptera	7	Kwang-Shing et al. (1993)
<i>Aphidecta oblitterata</i>	Hemiptera	4	Timms et al. (2008)
<i>Cheilomenes lunata</i>	Hemiptera	1	Ofuya and Akingbohunge (1988)
<i>Cheilomenes sexmaculata</i>	Hemiptera	1	Agarwala et al. (2001)
<i>Coccinella septempunctata</i>	Hemiptera	20	Gupta et al. (2012) Hassell, Lawton, and Beddington (1977) Shukla, Singh, and Tripathi (1990)
<i>Coccinella undecimpunctata</i>	Hemiptera	3	Cabral, Soares, and Garcia (2009)
<i>Coelophora inaequalis</i>	Hemiptera	2	Wang and Tsai (2001)
<i>Coleomegilla maculata</i>	Coleoptera	1	Munyaneza and Obrycki (1997)
<i>Cryptolaemus montrouzieri</i>	Hemiptera	3	Saljoqi et al. (2015)
<i>Cycloneda sanguinea</i>	Hemiptera	3	Işikber (2005)
<i>Eriopis connexa</i>	Hemiptera	2	Sarmento et al. (2007)
<i>Harmonia axyridis</i>	Hemiptera	51	Aqueel and Leather (2012) Lee and Kang (2004) Seko and Kazuki (2008)
	Lepidoptera	3	Koch et al. (2003)
<i>Harmonia confirmis</i>	Hemiptera	2	Asante (1995)
<i>Hippodamia convergens</i>	Hemiptera	2	Wells and McPherson (1999)
	Lepidoptera	2	Parajulee, Shrestha, Leser, Wester, and Blanco (2006)
<i>Hippodamia variegata</i>	Hemiptera	16	Farhadi, Allahyari, and Juliano (2010) Saleh, Ghaveish, Al-Zyoud, Ateyyat, and Swais (2010) Madadi et al. (2011)
<i>Nephus arcuatus</i>	Hemiptera	3	Zarghami et al. (2016)
<i>Oenopia conglobata</i>	Hemiptera	5	Yaşar and Özger (2005a)
<i>Paraprius australasiae</i>	Hemiptera	2	Asante (1995)
<i>Scymnus levillanti</i>	Hemiptera	3	Işikber (2005)
<i>Serangium japonicum</i>	Hemiptera	4	He, Zhao, Zheng, Desneux, and Wu (2012)
<i>Tenuisvalvae notata</i>	Hemiptera	3	Barbosa, Oliveira, Giorgi, Silva-Torres, and Torres (2014)

number of studies conducted in arenas consisting of plants (or stems/leaves) in a box or cylinder (Sentis, Hemptinne, & Brodeur, 2012; Xue et al., 2009). We excluded these studies because we could not accurately determine arena size (two-dimensional space available to predators/prey) and therefore prey density. Our search yielded 158 functional responses from 30 studies (Table 1). In addition to prey densities and predator foraging rates, for each

functional response we recorded the taxonomic identity of prey, predator age (by instar), predator mass, temperature and the size of the arena used for foraging trials. Prey consisted of hemipterans (20 species), coleopterans (two species) and lepidopterans (two species).

We did not use the parameters reported in the papers due to the high number of discrepancies in terms of equations and techniques

used to estimate parameters. Instead, we recalculated parameter values for each functional response using data provided in the publications or that we digitized from figures. We used raw data when available, but when not available, we used the means and reported SEs or deviations to generate simulated datasets (see below). In some cases, only mean foraging rates were presented at each prey density. For raw data reported in figures, it was sometimes unclear how many observations were represented by a single point; in such cases, we took a conservative approach and used the minimum possible number of observations based on the reported sample size. We standardized all data so that prey density was in units of prey per cm² and foraging rate in units of prey consumed per predator per day.

For studies that replaced prey in foraging arenas upon capture, we fit datasets to Equation 1. When prey were not replaced as they were consumed, we used the Roger's random predator equation to account for prey depletion:

$$N_e = N_0 - \frac{W(ahN_0e^{-a(t-hN_0)})}{ah}, \quad (2)$$

where N_e is the number of prey eaten, N_0 is the initial number of prey provided, W is the Lambert W function, t is the time of the foraging trial, and a and h are the functional response parameters as above (Bolker, 2011; Rogers, 1972). To be consistent with fits to Equation 1, we performed fits to Equation 2 with prey density (prey number per area) as well. We fit data to Equations 1 or 2 as appropriate using ordinary least squares fitting in Matlab to obtain parameters for each functional response. For data presented as means and SEs, we generated 500 bootstrapped datasets per functional response, fit the appropriate equation, and used the median values and 95% quantiles of the resulting parameter distributions as the estimate and confidence intervals, respectively. When mean foraging rates were provided without errors, we treated each data point as a single observation (i.e. one replicate per density) with zero error. These fits produced artificially large coefficients of determination (R^2) as a result of the close match of the mean data to the fitted model, and also had artificially wide confidence intervals due to the low apparent sample size. Where arena size was not reported in the paper (two studies), we only included in our analysis the results for handling time, as the units for handling time are independent of the area units of the foraging trial, whereas space clearance rates can only be compared when the arena area is known.

Although some sources provided predator size, many did not. In these cases, we used body sizes reported in other sources, based on the species, age and sex of the predator. If sex was not reported in the publication, we used an average of male and female body sizes. For our analyses, we used wet mass as the representative measure of body size. If this was not available, we converted length to dry mass following Sabo, Bastow, and Power (2002):

$$\text{mass (mg)} = 0.343 \times \text{length (mm)}^{1.5} \quad (3)$$

Assuming a water content to wet mass ratio of 0.7 (Sabo et al., 2002), dry mass was then converted to wet mass by dividing by 0.3. When mass was available for adults but not instars, we calculated

instar mass by multiplying adult mass by the average per cent of adult mass for the second, third or fourth instars of *Cycloneda sanguinea*, *Harmonia axyridis* and *Hippodamia convergens* as given in Dos Santos, dos Santos-Cividanes, Cividanes, and de Matos (2013).

We analysed estimated parameters using linear mixed-effects models with the natural logs of space clearance rate and handling time as dependent variables. We used temperature, predator instar, prey type, predator mass and arena size as predictor variables. Predator mass and arena size were log transformed to account for the typically power-law like relationship between functional response parameters and body size and to normalize model residuals. The variance inflation factor for all combinations of continuous predictor variables was approximately 1, indicating that multicollinearity between predictors was insignificant. We used study as a random effect to account for across-source variation. We started with an inclusive model that included all predictor variables and two-way interactions. Our dataset did not support analysis of all three-way interactions at one time. We therefore tested these sequentially. We progressively dropped terms until only significant terms remained. We selected the best-performing model for each parameter based on lowest AIC value (Tables S1, S2). Residuals in our analysis were randomly distributed.

3 | RESULTS

Our results indicated that all predictor variables (predator mass, prey type, temperature, predator instar and arena size) affected either space clearance rate or handling time, with some variables influencing both parameters (Tables 2 and 3, Figures 1 and 2). Models for space clearance rate and handling time were improved (lower AIC_c) by including source as a random effect.

Increasing temperature had the predicted positive effect on space clearance rate (Table 2, Figure 1). The best-performing model for space clearance rate indicated that this effect was increased for lepidopteran prey and decreased for third instar and older predators. Interestingly, although mass on its own did not have an effect, mass increased space clearance rate for younger predators and decreased space clearance rate for predators in larger arenas. Third instar and older predator stages had higher space clearance rates, and space clearance rates for lepidopteran prey were lower than for other prey. Arena size had a highly significant positive effect on space clearance rate, and it was a bigger determinant of space clearance rate than any other variable (Figure 2).

Increasing body mass had the predicted negative effect on handling time (Table 3, Figure 1). The best-performing model for handling time indicated that this effect was greater for coleopteran prey and third instar and older ladybird beetles. Temperature alone did not have an effect, but larger predators had decreased handling times at higher temperatures. Arena size did not have an overall effect on handling time, but arena size decreased handling times for third instar and older predators and increased it for larger predators. Handling times did not differ across prey types but did, unexpectedly, increase as predators got older.

TABLE 2 Results for the best linear model for space clearance rate. Significant terms are bolded

Term	Estimate	SE	t	p value
Intercept	-16.47	1.49	-11.05	<.001
Prey type (Lepidoptera)	-4.56	1.43	-3.18	.002
Prey type (Coleoptera)	-14.09	70.69	-0.20	.843
Predator stage (second instar)	1.81	1.61	1.12	.266
Predator stage (third instar)	3.25	1.27	2.56	.013
Predator stage (fourth instar)	3.34	1.21	2.77	.007
Predator stage (Adult)	3.16	1.21	2.60	.012
Predator mass	1.41	0.75	1.89	.064
Temperature	0.12	0.05	2.55	.013
ln(Arena size)	1.95	0.35	5.59	<.001
Prey type (Lepidoptera): Predator mass	0.63	0.25	2.49	.015
Prey type (Coleoptera): Predator mass	0.20	0.53	0.37	.710
Predator stage (second instar): Predator mass	0.36	0.14	2.50	.015
Predator stage (third instar): Predator mass	0.29	0.31	0.95	.344
Predator stage (fourth instar): Predator mass	0.21	0.39	0.55	.587
Predator stage (Adult): Predator mass	-0.04	0.31	-0.14	.892
Prey type (Lepidoptera): Temperature	0.12	0.05	2.66	.010
Prey type (Coleoptera): Temperature	0.59	2.79	0.21	.834
Predator stage (second instar): Temperature	-0.07	0.06	-1.04	.304
Predator stage (third instar): Temperature	-0.12	0.05	-2.26	.027
Predator stage (fourth instar): Temperature	-0.15	0.05	-2.67	.010
Predator stage (Adult): Temperature	-0.11	0.05	-2.09	.040
Predator mass: ln(Arena size)	-0.34	0.14	-2.49	.015

4 | DISCUSSION

Ladybird beetles are important insect predators in terrestrial ecosystems world-wide, and their ability to forage on a variety of pests has made them economically important as biocontrol agents (Dixon, 2000; Obrycki & Kring, 1998). A nuanced understanding of what factors affect interaction strengths between ladybird beetles and their prey and how to properly interpret experimental results is

TABLE 3 Results for the best linear model for handling time. Significant terms are bolded

Term	Estimate	SE	t	p value
Intercept	-7.62	4.56	-1.67	.097
Prey type (Lepidoptera)	-2.16	1.65	-1.31	.195
Prey type (Coleoptera)	0.96	1.09	0.89	.378
Predator stage (second instar)	2.99	3.68	0.81	.419
Predator stage (third instar)	19.03	5.74	3.32	.001
Predator stage (fourth instar)	31.13	8.36	3.73	<.001
Predator stage (Adult)	36.51	8.15	4.48	<.001
Predator mass	-9.56	3.38	-2.83	.006
Temperature	-0.06	0.05	-1.31	.193
ln(Arena size)	1.88	1.18	1.59	.115
Prey type (Lepidoptera): Predator mass	0.84	0.48	1.74	.085
Prey type (Coleoptera): Predator mass	-0.79	0.36	-2.16	.033
Predator stage (second instar): Predator mass	-0.16	0.27	-0.60	.548
Predator stage (third instar): Predator mass	-0.92	0.36	-2.58	.011
Predator stage (fourth instar): Predator mass	-0.91	0.37	-2.46	.016
Predator stage (Adult): Predator mass	-1.66	0.46	-3.61	.001
Predator mass: Temperature	-0.04	0.02	-2.11	.037
Predator stage (second instar): ln(Arena size)	-1.09	0.99	-1.09	.277
Predator stage (third instar): ln(Arena size)	-5.07	1.46	-3.47	.001
Predator stage (fourth instar): ln(Arena size)	-8.19	2.03	-4.03	<.001
Predator stage (Adult): ln(Arena size)	-9.07	2.00	-4.53	<.001
Predator mass: ln(Arena size)	2.68	0.81	3.32	.001

paramount to our understanding of how ladybird beetles function as biocontrol predators.

Our results indicate that space clearance rate estimates are dependent on the size of arenas used in foraging trials. Interestingly, van Rijn et al. (2005) found no effect of a twofold difference in arena size on foraging rates at a single prey density. However, our study is the first to compare entire functional responses across a wide range (approximately 50-fold) of arena sizes. Our results suggest that the spatial constraints imposed by arenas affect the behaviour of predators, prey or both, resulting in more efficient predation in larger arenas. These findings indicate that there is a serious issue with the current methodology for measuring functional responses in the laboratory.

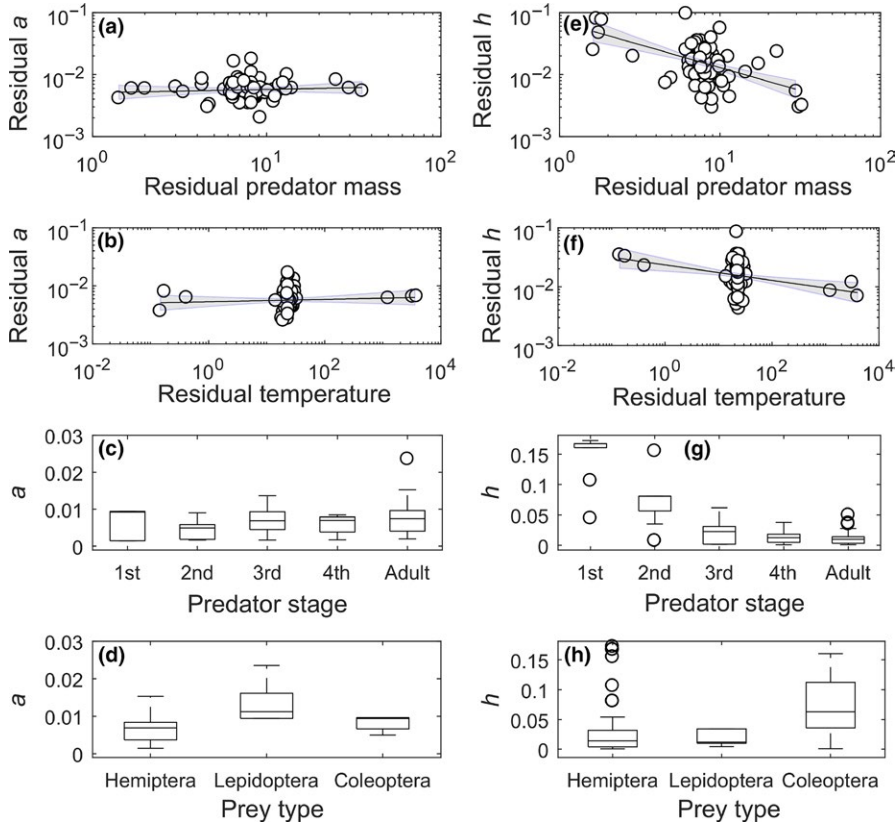


FIGURE 1 Effects of predator mass (mg) (a and e), temperature (°C) (b and f), predator stage (c and g) and prey type (d and h) on functional response parameters space clearance rate (cm² per predator per day) (left column) and handling time (days) (right column). Partial regression results are shown from the optimal model for predator mass and temperature. Model fitted effects are shown for predator stage and prey type. In (c) and (d), the y-axis is limited to 0.03 cm² per predator per day for clarity and one outlier is not shown

Our analysis shows that it is difficult to determine whether any particular ladybird beetle is more effective at controlling pests than another, since arena size has a larger effect on space clearance rate than even body size or temperature. In other words, a given ladybird beetle might be deemed a good biocontrol agent when tested in a large arena and an inefficient control agent when tested in a small arena. Thus, we recommend controlling for arena size statistically, using for example the relationship shown in Figure 2, to standardize estimates of space clearance rate across studies. For taxa where such a relationship has not been established, controlling for arena size—statistically or with similar-sized arenas—is critical to accurately assessing relative foraging ability of candidate biocontrol predators through differences in their space clearance rate.

Predator age is an important predictor of both space clearance rate and handling time. Our models show that predators in older stages of development have both higher space clearance rates and handling times. However, the age effect on handling time is reduced for larger predators. Intuitively, it makes sense that older predators have increased space clearance rates, as older predators likely move faster, are more experienced and can see prey from farther distances because of their typically larger size. The increased handling time for older ladybirds, however, could result from additional time spent digesting (e.g. more complete digestion) or time spent on non-foraging activities (e.g. searching for mates; Li, Rall, & Kalinkat, 2017). Overall, the effects of age on functional response parameters suggest that biocontrol could be optimized at low pest densities when older ladybirds are foraging and at high pest densities when younger ladybirds are foraging.

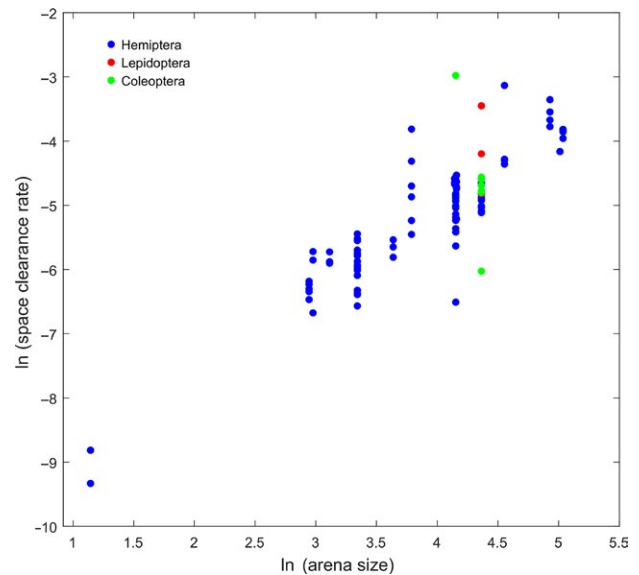


FIGURE 2 Log-log relationship between the size of the foraging arenas (cm²) used in functional response experiments and the estimated functional response parameter space clearance rate (cm² per predator per day) [Colour figure can be viewed at wileyonlinelibrary.com]

Interestingly, there is also an interaction between predator age and arena size for handling time, and these effects become more dramatic with age. This suggests that older ladybird beetles are more sensitive to the amount of space available to them.

Predator mass is known to increase space clearance rate and decrease handling time for many taxa (DeLong & Vasseur, 2012; DeLong et al., 2015; Rall et al., 2012). Larger predators can move faster, detect prey from longer distances and more easily subdue prey. Our results confirm this for ladybird beetles, suggesting that larger predators are more efficient at consuming prey and acting as biocontrol agents. Our best-performing models also showed negative interactions between mass and older predator stages for handling time and positive interactions between mass and younger predator stages for space clearance rate. The effect of increasing body mass augments the effect of older stages reducing handling times, yet increasing body size diminishes the effect of older stages increasing space clearance rate. This suggests that increasing size benefits ladybird beetle foraging at higher prey densities (by raising the maximum foraging rate) but works against foraging when prey are scarce. Since ladybird beetles can disperse to patches of high aphid density, however, the cost of this negative effect may be minimal.

Ladybird beetles foraging on lepidopteran prey showed higher space clearance rates than when foraging on the other prey. This may arise as a result of a higher attack success rate (Aljetlawi et al., 2004; Pawar et al., 2012; Uiterwaal et al., 2017), since all lepidopteran prey were either in the egg or first instar stage and therefore would be relatively easy to subdue. The space clearance rate model further supported an interaction between lepidopteran prey and mass, indicating that larger predators are more efficient at foraging on lepidopterans. Although there were no significant differences in handling times for different prey types, the handling time model supports an interaction between predator mass and coleopteran prey. This interaction was negative, indicating that beetles can be handled faster by larger predators.

Temperature plays a key role in determining predator-prey interaction strengths for many ectotherms (Burnside et al., 2014; Dell, Pawar, & Savage, 2014; Englund, Öhlund, Hein, & Diehl, 2011). This is consistent with our findings that higher temperatures increase space clearance rate. Our results also suggest that this effect is somewhat reduced for older predators, indicating that younger predators benefit more from higher temperatures. This suggests that, at low prey populations and warmer conditions, younger predators may be more effective biocontrol agents. The space clearance rate model also supports a positive interaction between temperature and lepidopteran prey, indicating that the importance of temperature varies with prey type. Although warmer temperatures have been shown to increase space clearance rate in other taxa (Englund et al., 2011; Kalinoski & DeLong, 2016; Rall et al., 2012), temperature only affected the space clearance rate for lepidopteran prey, possibly because this taxonomic groups differs in movement patterns from the other prey types (Dell et al., 2014). Thus, the choice of predators to use in biocontrol programmes may vary with temperature and prey type. Both factors should be considered when developing biocontrol programmes.

Although our results suggest that ladybird beetles have higher space clearance rates at higher temperatures, indicating that they

can most successfully reduce low density prey populations in warmer environments, many organisms have peak foraging rates at intermediate temperatures (Englund et al., 2011). Thus, the underlying relationship between space clearance rate and temperature in ladybird beetles may be unimodal rather than monotonically increasing. Englund et al.'s (2011) compilation suggests a peak in space clearance rate for some species in the high 20s, and other parameters such as intrinsic rate of population increase also peak around 30°C for ladybird beetles (Hodek, Emden, & Honek, 2012). However, the maximum temperature considered here was just 30°C (Işıkber, 2005; Zarghami, Mossadegh, Kocheili, Allahyari, & Rasekh, 2016), which could have led to an apparent linear response to temperature in our dataset. A unimodal response to temperature may become apparent when data are collected at temperatures that approach the extremes experienced by wild ladybird beetles (up to 40°C or so).

Although the handling time model indicates that temperature alone does not have an effect, there is a negative interaction between mass and temperature such that larger predators benefit more from higher temperatures. This means that in warmer climates larger ladybeetles should be used to control dense prey populations, while in cooler climates predator body size is less important. Our results also suggest that temperature interacts with arena size so that predators have the highest time cost per prey when exposed to high temperatures in large arenas. Although it is unclear why this is the case, it may be due to the potential for higher activity rates in larger spaces at higher temperatures. As ectotherms, the prey of ladybird beetles depend on heat to increase metabolism and movement rates; this may be especially so the less limited they are by spatial constraints. For both space clearance rate and handling time, the effect of temperature may have been driven by just a few studies, as most studies were conducted around 22°C. Nonetheless, our results correspond with direct tests of temperature effects on ladybird beetle foraging rates (Işıkber, 2005; Jalali, Tirry, & Clercq, 2010), indicating that our findings are valid.

Although the purpose of our meta-analysis was to consider a broad range of influences on functional response parameters, including predator mass, temperature and arena size, several variables not considered here. Prey defences, predator-prey body mass ratio, predator condition and predator interference have also been shown to shape functional responses in other species (Kalinoski & DeLong, 2016; Li et al., 2017; Tschanz, Bersier, & Bacher, 2007; Uiterwaal et al., 2017). For the effective development of biocontrol programmes, such factors should be considered jointly with our findings. Additionally, although we only used data from experiments conducted in strictly two-dimensional arenas (e.g. leaf discs), arena complexity alters functional responses (Barrios-O'Neill) as well. How the size of more complex arenas (e.g. whole plants) affects foraging remains unclear.

4.1 | Management implications

Our study demonstrates that multiple factors influence the experimental functional responses of ladybird beetles, emphasizing the

challenge of fine-tuning biocontrol programmes. The optimal biocontrol ladybird beetle for any given pest may change as climates change and may vary with prey type and body size. Our study also shows that experimental arena size has an enormous impact on functional response parameters, most notably space clearance rate, which is the parameter that signifies the ability of predators to search space and find prey. In the light of the role that arena size plays in determining foraging behaviours, we suggest managers and biocontrol practitioners re-evaluate the efficacy of past and future candidate biocontrol predators for which functional response experiments were important in their choice of predator. Arena size also should be considered when attempting to extrapolate laboratory results to the field. Although much work needs to be done to determine the mechanisms of the arena size effect, acknowledging its presence is a crucial step towards accurately interpreting functional response experiments and informing biocontrol programmes.

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AUTHORS' CONTRIBUTIONS

S.F.U. compiled the data. Both authors analysed the data. S.F.U. wrote the first draft. Both authors contributed towards the final version of the manuscript and gave approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.gq224h3> (Uiterwaal & DeLong, 2018).

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REFERENCES

- Agarwala, B. K., Bardhanroy, P., Yasuda, H., & Takizawa, T. (2001). Prey consumption and oviposition of the aphidophagous predator *Menochilus sexmaculatus* (Coleoptera: Coccinellidae) in relation to prey density and adult size. *Environmental Entomology*, *30*, 1182–1187. <https://doi.org/10.1603/0046-225X-30.6.1182>
- Aljetlawi, A. A., Sparrevik, E., & Leonardsson, K. (2004). Prey-predator size-dependent functional response: Derivation and rescaling to the real world. *Journal of Animal Ecology*, *73*, 239–252. <https://doi.org/10.1111/j.0021-8790.2004.00800.x>
- Aqueel, M. A., & Leather, S. R. (2012). Nitrogen fertiliser affects the functional response and prey consumption of *Harmonia axyridis* (Coleoptera: Coccinellidae) feeding on cereal aphids. *Annals of Applied Biology*, *160*, 6–15. <https://doi.org/10.1111/j.1744-7348.2011.00514.x>
- Asante, S. K. (1995). Functional responses of the European Earwig and two species of Coccinellids to densities of *Eriosoma lanigerum* (Hausmann) (Hemiptera: Aphididae). *Journal of Entomological Society of Australia*, *34*, 105–109. <https://doi.org/10.1111/j.1440-6055.1995.tb01295.x>
- Atlihan, R., Kaydan, M. B., Yarımbatman, A., & Okut, H. (2010). Functional response of the coccinellid predator *Adalia fasciatopunctata* revealieri to walnut aphid (*Callaphis juglandis*). *Phytoparasitica*, *38*, 23–29. <https://doi.org/10.1007/s12600-009-0075-y>
- Barbosa, P. R. R., Oliveira, M. D., Giorgi, J. A., Silva-Torres, C. S. A., & Torres, J. B. (2014). Predatory behavior and life history of *Tenuisvalvae notata* (Coleoptera: Coccinellidae) under variable prey availability conditions. *Florida Entomologist*, *97*, 1026–1034. <https://doi.org/10.1653/024.097.0304>
- Bolker, B. M. (2011). *Ecological models and data in R*. Princeton, CA: Princeton University Press.
- Burnside, W. R., Erhardt, E. B., Hammond, S. T., & Brown, J. H. (2014). Rates of biotic interactions scale predictably with temperature despite variation. *Oikos*, *123*, 1449–1456. <https://doi.org/10.1111/oik.01199>
- Cabral, S., Soares, A. O., & Garcia, P. (2009). Predation by *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) on *Myzus persicae* Sulzer (Homoptera: Aphididae): Effect of prey density. *Biological Control*, *50*, 25–29. <https://doi.org/10.1016/j.biocontrol.2009.01.020>
- Dell, A. I., Pawar, S., & Savage, V. M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 10591–10596. <https://doi.org/10.1073/pnas.1015178108>
- Dell, A. I., Pawar, S., & Savage, V. M. (2014). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*, *83*, 70–84. <https://doi.org/10.1111/1365-2656.12081>
- DeLong, J. P., Gilbert, B., Shurin, J. B., Savage, V. M., Barton, B. T., Clements, C. F., ... O'Connor, M. I. (2015). The body size dependence of trophic cascades. *The American Naturalist*, *185*, 354–366. <https://doi.org/10.1086/679735>
- DeLong, J. P., & Vasseur, D. A. (2012). A dynamic explanation of size-density scaling in carnivores. *Ecology*, *93*, 470–476. <https://doi.org/10.1890/11-1138.1>
- Dixon, A. F. G. (2000). *Insect predator-prey dynamics: Ladybird beetles and biological control*. Cambridge, UK: Cambridge University Press.
- Dos Santos, L. C., dos Santos-Cividanes, T. M., Cividanes, F. J., & de Matos, S. T. S. (2013). Biological aspects of *Harmonia axyridis* in comparison with *Cycloneda sanguinea* and *Hippodamia convergens*. *Pesquisa Agropecuária Brasileira*, *48*, 1419–1425. <https://doi.org/10.1590/S0100-204X2013001100001>
- Englund, G., Öhlund, G., Hein, C. L., & Diehl, S. (2011). Temperature dependence of the functional response. *Ecology Letters*, *14*, 914–921. <https://doi.org/10.1111/j.1461-0248.2011.01661.x>
- Evans, E. W. (2004). Habitat displacement of North American ladybirds by an introduced species. *Ecology*, *85*, 637–647. <https://doi.org/10.1890/03-0230>
- Farhadi, R., Allahyari, H., & Juliano, S. A. (2010). Functional response of larval and adult stages of *Hippodamia variegata* (Coleoptera: Coccinellidae) to different densities of *Aphis fabae* (Hemiptera: Aphididae). *Environmental Entomology*, *39*, 1586–1592. <https://doi.org/10.1603/EN09285>
- Gotoh, T., Nozawa, M., & Yamaguchi, K. (2004). Prey consumption and functional response of three acarophagous species to eggs of the two-spotted spider mite in the laboratory. *Applied Entomology and Zoology*, *39*, 97–105. <https://doi.org/10.1303/aez.2004.97>
- Gupta, R. K., Pervez, A., Guroo, M. A., & Srivastava, K. (2012). Stage-specific functional response of an aphidophagous ladybird, *Coccinella septempunctata* (Coleoptera: Coccinellidae), to two aphid species. *International Journal of Tropical Insect Science*, *32*, 136–141. <https://doi.org/10.1017/S1742758412000227>

- Hassell, M. P., Lawton, J. H., & Beddington, J. R. (1977). Sigmoid functional responses by invertebrate predators and parasitoids. *Journal of Animal Ecology*, 46, 249–262. <https://doi.org/10.2307/3959>
- He, Y., Zhao, J., Zheng, Y., Desneux, N., & Wu, K. (2012). Lethal effect of imidacloprid on the coccinellid predator *Serangium japonicum* and sublethal effects on predator voracity and on functional response to the whitefly *Bemisia tabaci*. *Ecotoxicology*, 21, 1291–1300. <https://doi.org/10.1007/s10646-012-0883-6>
- Hodek, I., Emden, H. F., & vanHonek, A. (2012). *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. Hoboken, NJ: John Wiley & Sons. <https://doi.org/10.1002/9781118223208>
- Hodek, I., & Honěk, A. (2009). Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds. *Biological Control, Trophic Ecology of the Coccinellidae*, 51, 232–243. <https://doi.org/10.1016/j.biocontrol.2009.05.018>
- Holling, C. S. (1959). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist*, 91, 293–320. <https://doi.org/10.4039/Ent91293-5>
- Işikber, A. A. (2005). Functional response of two coccinellid predators, *Scymnus levaillanti* and *Cycloneda sanguinea*, to the Cotton Aphid, *Aphis gossypii*. *Turkish Journal of Agricultural and Forestry*, 29, 347–355.
- Jalali, M. A., Tirry, L., & Clercq, P. D. (2010). Effect of temperature on the functional response of *Adalia bipunctata* to *Myzus persicae*. *BioControl*, 55, 261–269. <https://doi.org/10.1007/s10526-009-9237-6>
- Jeschke, J. M., Kopp, M., & Tollrian, R. (2004). Consumer-food systems: Why type I functional responses are exclusive to filter feeders. *Biological Reviews*, 79, 337–349. <https://doi.org/10.1017/S1464793103006286>
- Kalinowski, R. M., & DeLong, J. P. (2016). Beyond body mass: How prey traits improve predictions of functional response parameters. *Oecologia*, 180, 543–550. <https://doi.org/10.1007/s00442-015-3487-z>
- Koch, R. L. (2003). The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science*, 3, 1–16.
- Koch, R. L., Hutchison, W. D., Venette, R. C., & Heimpel, G. E. (2003). Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danaeinae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biological Control*, 28, 265–270. [https://doi.org/10.1016/S1049-9644\(03\)00102-6](https://doi.org/10.1016/S1049-9644(03)00102-6)
- Kwang-Shing, C., Naotake, M., & Fusao, N. (1993). The functional response of a coccinellid beetle, *Aiolocaria hexaspilota* to its prey, the Walnut Leaf Beetle (*Gastrolina depressa*). *Chinese Journal of Entomology*, 13, 187–193.
- Lee, J.-H., & Kang, T.-J. (2004). Functional response of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) to *Aphis gossypii* Glover (Homoptera: Aphididae) in the laboratory. *Biological Control*, 31, 306–310. <https://doi.org/10.1016/j.biocontrol.2004.04.011>
- Li, Y., Rall, B. C., & Kalinkat, G. (2017). Experimental duration and predator satiation levels systematically affect functional response parameters. *Oikos*, 127(4), 590–598. <https://doi.org/10.1111/oik.04479>
- Madadi, H., Parizi, E. M., Allahyari, H., & Enkegaard, A. (2011). Assessment of the biological control capability of *Hippodamia variegata* (Col.: Coccinellidae) using functional response experiments. *Journal of Pest Science*, 84, 447–455. <https://doi.org/10.1007/s10340-011-0387-9>
- McGill, B. J., & Mittelbach, G. C. (2006). An allometric vision and motion model to predict prey encounter rates. *Evolutionary Ecology Research*, 8, 691–701.
- Munyanza, J., & Obrycki, J. J. (1997). Functional response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Colorado potato beetle eggs (Coleoptera: Chrysomelidae). *Biological Control*, 8, 215–224. <https://doi.org/10.1006/bcon.1997.0509>
- Novak, M., & Wootton, J. T. (2010). Using experimental indices to quantify the strength of species interactions. *Oikos*, 119, 1057–1063. <https://doi.org/10.1111/j.1600-0706.2009.18147.x>
- Obrycki, J. J., & Kring, T. J. (1998). Predaceous Coccinellidae in biological control. *Annual Review of Entomology*, 43, 295–321. <https://doi.org/10.1146/annurev.ento.43.1.295>
- Ofuya, T. I., & Akingbohunge, A. E. (1988). Functional and numerical responses of *Cheilomenes lunata* (Fabricius) (Coleoptera: Coccinellidae) feeding on the Cowpea Aphid, *Aphis craccivora* Koch (Homoptera: Aphididae). *International Journal of Tropical Insect Science*, 9, 543–546. <https://doi.org/10.1017/S1742758400011127>
- Parajulee, M. N., Shrestha, R. B., Leser, J. F., Wester, D. B., & Blanco, C. A. (2006). Evaluation of the functional response of selected arthropod predators on bollworm eggs in the laboratory and effect of temperature on their predation efficiency. *Environmental Entomology*, 35, 379–386. <https://doi.org/10.1603/0046-225X-35.2.379>
- Pawar, S., Dell, A. I., & Savage, V. M. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature*, 486, 485–489. <https://doi.org/10.1038/nature11131>
- Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., & Petchey, O. L. (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 367, 2923–2934. <https://doi.org/10.1098/rstb.2012.0242>
- van Rijn, P. C. J., Bakker, F. M., van der Hoeven, W. A. D., & Sabelis, M. W. (2005). Is arthropod predation exclusively satiation-driven? *Oikos*, 109, 101–116. <https://doi.org/10.1111/j.0030-1299.2005.12987.x>
- Rogers, D. (1972). Random search and insect population models. *Journal of Animal Ecology*, 41, 369–383. <https://doi.org/10.2307/3474>
- Sabo, J. L., Bastow, J. L., & Power, M. E. (2002). Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society*, 21, 336–343. <https://doi.org/10.2307/1468420>
- Saleh, A., Ghaveish, I., Al-Zyoued, F., Ateyyat, M., & Swais, M. (2010). Functional response of the predator *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae) feeding on the aphid *Brachycaudus helichrysi* (Kaltenbach) infesting chrysanthemum in the Laboratory. *Jordan Journal of Biological Sciences*, 3, 17–20.
- Saljoqi, A.-U.-R., Nasir, M., Khan, J., Ehsan-ul-Haq, M., Salim, M., Nadeem, M., ... Rehman, S. (2015). Functional response study of *Cryptolaemus Montrouzieri* Mulsant (Coleoptera: Coccinellidae) fed on cotton mealy bug, *Phenacoccus solenopsis* Tinsley under laboratory conditions. *Journal of Entomology and Zoology Studies*, 3, 411–415.
- Sarmento, R. A., Pallini, A., Venzon, M., de Souza, O. F. F., Molina-Rugama, A. J., & de Oliveira, C. L. (2007). Functional response of the predator *Eriopsis connexa* (Coleoptera: Coccinellidae) to different prey types. *Brazilian Archives of Biology and Technology*, 50, 121–126. <https://doi.org/10.1590/S1516-89132007000100014>
- Seko, T., & Kazuki, M. (2008). Functional response of the lady beetle *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) on the aphid *Myzus persicae* (Sulzer) (Homoptera: Aphididae). *Applied Entomology and Zoology*, 43, 341–345. <https://doi.org/10.1303/aez.2008.341>
- Sentis, A., Hemptinne, J.-L., & Brodeur, J. (2012). Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency. *Oecologia*, 169, 1117–1125. <https://doi.org/10.1007/s00442-012-2255-6>
- Shukla, A. N., Singh, R., & Tripathi, C. P. M. (1990). Effect of predation period on the functional response of *Coccinella septempunctata* Linn. (Coleoptera: Coccinellidae), a predator of *Lipaphis erysimi* Kait. (Hemiptera: Aphididae). *Journal of Advanced Zoology*, 11, 27–32.
- Timms, J. E., Oliver, T. H., Straw, N. A., & Leather, S. R. (2008). The effects of host plant on the coccinellid functional response: Is the conifer specialist *Aphidecta oblitterata* (L.) (Coleoptera: Coccinellidae) better adapted to spruce than the generalist *Adalia bipunctata* (L.)

- (Coleoptera: Coccinellidae)? *Biological Control*, 47, 273–281. <https://doi.org/10.1016/j.biocontrol.2008.08.009>
- Tschanz, B., Bersier, L.-F., & Bacher, S. (2007). Functional responses: A question of alternative prey and predator density. *Ecology*, 88, 1300–1308. <https://doi.org/10.1890/06-1512>
- Uiterwaal, S. F., & DeLong, J. P. (2018). Data from: Multiple factors, including arena size, shape the functional responses of ladybird beetles. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.gq224h3>
- Uiterwaal, S. F., Mares, C., & DeLong, J. P. (2017). Body size, body size ratio, and prey type influence the functional response of damselfly nymphs. *Oecologia*, 185, 339–346. <https://doi.org/10.1007/s00442-017-3963-8>
- Wang, J.-J., & Tsai, J. H. (2001). Development and functional response of *Coelophora inaequalis* (Coleoptera: Coccinellidae) feeding on brown citrus aphid, *Toxoptera citricida* (Homoptera: Aphididae). *Agricultural and Forest Entomology*, 3, 65–69. <https://doi.org/10.1046/j.1461-9563.2001.00091.x>
- Wells, M. L., & McPherson, R. M. (1999). Population dynamics of three Coccinellids in Flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). *Environmental Entomology*, 28, 768–773. <https://doi.org/10.1093/ee/28.4.768>
- Xue, Y., Bahlai, C. A., Frewin, A., Sears, M. K., Schaafsma, A. W., & Hallett, R. H. (2009). Predation by *Coccinella septempunctata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Homoptera: Aphididae). *Environmental Entomology*, 38, 708–714. <https://doi.org/10.1603/022.038.0322>
- Yaşar, B., & Özger, Ş. (2005a). Functional response of *Oenopia conglobata* (L.) (Coleoptera: Coccinellidae) on *Hyalopterus pruni* (Geoffroy) (Homoptera: Aphididae) in three different size arenas. *Turkish Journal of Entomology*, 29, 91–99
- Yaşar, B., & Özger, Ş. (2005b). Development, feeding and reproduction responses of *Adalia fasciatopunctata revelierei* (Mulsant) (Coleoptera: Coccinellidae) to *Hyalopterus pruni* (Geoffroy) (Homoptera: Aphididae). *Journal of Pest Science*, 78, 199–203. <https://doi.org/10.1007/s10340-005-0089-2>
- Zarghami, S., Mossadegh, M. S., Kocheili, F., Allahyari, H., & Rasekh, A. (2016). Functional responses of *Nephus arcuatus* Kapur (Coleoptera: Coccinellidae), the most important predator of spherical Mealybug *Nipaecoccus viridis* (Newstead) [WWW document]. *Psyche: A Journal of Entomology*, 2016, 1–9. <https://doi.org/10.1155/2016/9417496>

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