

Comparative functional responses of introduced and native ladybird beetles track ecological impact through predation and competition

Steven Crookes · Emma M. DeRoy · Jaimie T. A. Dick · Hugh J. MacIsaac 

Received: 10 May 2018 / Accepted: 3 September 2018 / Published online: 10 September 2018
© Springer Nature Switzerland AG 2018

Abstract Recent advances in invasion research has highlighted that differences in the feeding ecology of native and non-native species manifest through differences in their functional responses (FRs) and that FRs track ecological impact. Further, as with plant competition studies, differential resource use patterns may illuminate competition mechanisms among animal taxa. Ladybirds are a diverse family of beetles that possess substantial variation in body mass across taxa. Further, some ladybird species have been widely introduced into novel habitats, where they may pose significant risks of ecological and economic harm. By controlling for allometric scaling, we tested the hypothesis that introduced Asian multicoloured ladybirds (*Harmonia axyridis*) are more efficient predators on aphids than trophically-analogous, native convergent ladybirds (*Hippodamia convergens*). We utilized a prey-replacement FR design, and assessed rates of

pea aphid consumption as a function of initial prey density. *H. axyridis* possessed significantly higher absolute and mass-adjusted FRs (Type II) than the native species, consistent with expectations. The higher FR was mediated by reduced handling time, suggesting that the ability of *H. axyridis* to manipulate and digest prey exceeds that of *H. convergens*. Our feeding results may explain, in part, the increasing occurrence and abundance of the introduced species, and documented declines of native species of prey and competitor in invaded habitats.

Keywords Functional response · Invasion · Non-indigenous species · Limiting similarity · Niche · Sympatry

Introduction

Biological invasions have been used to test many ecological and evolutionary theories. For example, the hypothesis of limiting similarity predicts that successful introduced species should differ functionally from native ones if they exploit common resources (Emery 2007). This hypothesis draws on Elton's (1958) assertion that successful invasive species ought to be more efficient competitors for shared resources. The probability of establishment of a large-bodied, introduced species should also depend on the size of native

S. Crookes (✉) · E. M. DeRoy · H. J. MacIsaac
Great Lakes Institute for Environmental Research,
University of Windsor, Windsor, ON N9B 3P4, Canada
e-mail: scrookes@uoguelph.ca

J. T. A. Dick
Institute for Global Food Security, School of Biological
Sciences, Queen's University Belfast, MBC,
Belfast BT9 7BL, Northern Ireland, UK

Present Address:

S. Crookes
Biodiversity Institute of Ontario, University of Guelph,
Guelph, ON N1G 2W1, Canada

competitors and the availability of resources. If, however, the ratio of metabolic activity to mass follows Kleiber's Law (1932)—which states that metabolism scales at $\frac{3}{4}$ power to that of mass—then absolutely larger species may not be superior to native species owing to their differing energetic demands. Moreover, few traits evolve in isolation, particularly those associated with life-history and body mass attributes (Snell-Rood et al. 2015). By comparing functional analogs that vie for a common resource, it is possible to test whether resource use is allometrically-based or whether the functionality of the introduced species is due to other qualities that covary with, but are separate from, allometric scaling.

Coccinellid beetles (ladybirds) exhibit substantial morphological variation. Dixon and Hemptinne (2001) found that coccinellid body size was displaced in line with species-specific prey size preference and not by physiological constraints. Though ladybirds have been introduced globally for biocontrol purposes to consume agricultural and horticultural pests, one species—the Asian multicoloured, or harlequin, ladybird *Harmonia axyridis*—has itself become a global pest. Indeed, there is gathering evidence for the displacement of North American coccinellids by Old World species, including *H. axyridis*. In North America, a clear correspondence exists between introduction of non-native species and a decrease in abundances of native species (Wheeler and Hoebeke 1995). Understanding the role—if any—of resource competition in this apparent relationship is essential for ladybird conservation.

Competition for resources may drive native ladybird decline in common habitats if they are less able to acquire and/or consume prey than introduced species (Smith and Gardiner 2013). It is possible that successful invaders possess an array of traits that collectively favour establishment and spread in novel territories (Matzek 2012). For example, *H. axyridis* successfully preys on other coccinellids (Snyder et al. 2004), and withstands parasitism better than other ladybirds (Vilcinskis et al. 2013). However, the competitive ability of *H. axyridis* versus other guild members has been limited to studies of biological control of phytophagous pests rather than invasiveness per se (Roy et al. 2016).

Differential resource utilisation between native and introduced ladybirds can be addressed by examination of their functional responses (FRs) on common prey.

The functional response describes the causal relationship between resource consumption and resource density. FR analyses have been used mainly to determine the comparative impact of introduced and non-native predators (see Dick et al. 2014, 2017; Alexander et al. 2014), though they may also be used to assess the relative abilities of co-occurring predators to consume resources. Different FRs of non-native and native coccinellids may help explain changes in their abundances. Indeed, the use of comparative FRs in assessing inter-specific competition among animal taxa has been slow in its adoption, yet very similar concepts and methodologies were developed long ago by Tilman (1977) to address plant competition. While larger coccinellid beetles produce larger eggs and larvae than smaller species, these phenotypic traits are likely governed by ecological factors rather than physiological constraints (Dixon and Hemptinne 2001). If true, this suggests that metabolic scaling need not have a limiting influence over resource consumption. Here, we adopt Dick et al.'s (2014) functional response framework to test whether FRs differ between native and introduced coccinellids after correction for metabolic scaling.

We use large, non-native *H. axyridis* and smaller, North American-native *H. convergens* ladybirds as subjects to test whether the former possesses an elevated ability to consume resources when both species are exposed to identical densities of a single prey type. We assess the relative importance of each of the parameter terms that comprise the FR, notably handling time (h), attack rate (a) and maximum feeding rate (m). We predict that although both species will exhibit a Type II response (Holling 1959; Wells and McPherson 1999; Lee and Kang 2004), *H. axyridis* will possess a lower h but higher a and m than *H. convergens*.

Materials and methods

Harmonia axyridis is native to temperate central and East Asia, and was first released in 1916 in the southern USA as a biological control agent (Gordon 1985). It was first recorded in southern Ontario in 1994 (Coderre et al. 1995), following which it was observed elsewhere in Canada (Hoebeke and Wheeler 1996).

The North American *Hippodamia convergens* has a native pan-American distribution, but suffers from

significant declines in abundance when found in sympatry with non-native coccinellids (Smith and Gardiner 2013). Although smaller in size, it is also a valued biocontrol agent due to its ability to consume aphids (Dreistadt and Flint 1996).

All *H. axyridis* individuals were collected by hand around Windsor, Ontario, primarily from Ojibway Municipal Park (latitude: 42.266607; longitude: -83.073869) during June–August 2014, and in September–October from an urban plot (latitude: 42.30521; longitude: -83.049631) where masses accumulated on wild parsnip *Pastinaca sativa*. *H. convergens* was purchased from eNASCO, USA (product number: LM00533M). Each species was kept in its own 16-L plastic container covered by 10- μ m mesh netting that allowed aeration. Moistened paper towels were used to hydrate the beetles and to allow oviposition (Hesler et al. 2012). Pea aphids *Acyrtosiphon pisum* were acquired from eNASCO and from the Manitoba Department for Agriculture, Food and Rural Development (MAFRD) to transfect broad bean *Vicia faba* and sweet pea *Lathyrus odoratus* to develop self-sustaining aphid colonies, in addition to providing sustenance for captive beetles. Containers were regularly cleaned with deionised water to minimise risk of fungal infections. Both aphids and beetles were maintained under identical conditions in environmental chambers (CMP4030, Conviron). Ambient temperature was constant 20 °C, close to the mean average maximum temperature for Windsor and also within the preferred range of both species (Lamana and Miller 1998). All organisms were kept in a photoperiod of 16L:8D at 50% relative humidity.

We used European pea aphid as prey owing to its ease of culture, naturalised status in North America, and its wide distribution. The species is consumed in both field and laboratory by *H. convergens* (e.g., Hinkleman and Tenhumberg 2013) and *H. axyridis* (e.g., Ingels et al. 2015). To standardise hunger levels, all beetles were denied food for 24 h before experimentation. They were also isolated from the general population and acclimated individually in petri dishes (100 mm diameter, 15 mm in height) furnished with moistened paper towel. Prior to the addition of beetles, experimental petri dishes were prepared with one of eight densities of pea aphid: 1, 2, 4, 8, 16, 32, 64 or 100. If any aphid died other than by predation during the counting of prey densities or during the

experimental period, they were replaced with other live individuals. All prey densities consisted of individuals belonging to the latter two ontogenetic stages (last nymph and adults), including alate (winged) individuals that were unable to evade capture if located within grasping distance of the beetles due to the physical dimensions of the dishes.

Trials began with the introduction of a beetle with a dissecting pin into an aphid-containing petri dish. Experiments lasted 3 h and were conducted under the same conditions as per acclimation. The numbers of aphids eaten was recorded in addition to the timing of each event (from the moment the aphid was grasped by a beetle). If an attack on an aphid was not fatal, i.e., the aphid continued to move fluidly and remain viable, the attack was not recorded. However, if the attack was fatal and resulted in whole or partial consumption of the aphid's body, the attack was counted as successful and the remains removed to be replaced by a live, similar-sized aphid to maintain a constant density of prey items. Most successful attacks resulted in complete consumption of the aphid, leaving only the limbs and antennae, which were left in the arena as they did not interest beetles. During pilot trials this method of introduction had no impact upon predation, nor did it elicit detectable defensive or evasive behaviour. Our 'prey replacement' design provides the most accurate estimates of functional response parameters (Dick et al. 2014). At the end of the trial, each beetle was weighed using a Mettler Toledo balance (model: MS104S). All prey treatments were replicated five times per species in the first instance.

Standard descriptive statistics (mean and standard errors, SE) were calculated for beetle body mass (mg), total numbers of aphids consumed after 3 h, and mass-specific predation rate (total number of aphids eaten per mg of beetle mass). To determine whether mass was differentially distributed between the two species and among aphid density classes—and whether this had an impact on the numbers of aphids consumed—multiple ANOVAS (MANOVA) were performed, after confirming normality of data (Shapiro–Wilk test, $p > 0.05$), denoting 'species' and 'aphid density' as factorial predictor variables and 'mass' and the 'number of aphids eaten' as response variables. We analyzed whether beetle body mass was randomly allotted among aphid densities, with aphid density as a predictive factor. A non-random assortment of body mass across aphid densities would have introduced a

significant source of bias into subsequent analyses. We then applied linear regression to aphid consumption data and to beetle body mass to determine if body mass and the numbers of aphids eaten were related.

We used non-linear, curve-fitting analysis (Juliano 2001) on raw consumption data using the R statistical package ‘frair’ to formulate a functional response model for each species (Pritchard 2014). Data for predatory foragers tend to conform to either a Type II or a Type III model (Holling 1959). We expected both *H. axyridis* and *H. convergens* to conform to a Type II curve (Wells and McPherson 1999; Lee and Kang 2004). The latter model predicts that relative resource consumption decreases exponentially with increasing resource density. The Type III model is similar except that at low resource density rates of consumption are also low, until a density threshold is met after which a decreasingly exponential relationship is attained. Initially, we explored which of these two models best fit the data (sensu Juliano 2001). This test focuses on the logistic regression between these variables at low densities and the expected difference in shape and magnitude of the relationship between prey density and consumption rate. This module was implemented in frair by choosing the ‘frair test’ option. The ‘preferred’ model was then more robustly tested by using a strict application of the model under question to the consumption data and compared to other models using the Akaike Information Criterion (AIC). For replacement data, the most appropriate Type II model is Holling’s original ‘disc equation’ (1959):

$$N_e = \frac{aN_0T}{1 + aN_0h}$$

where N_e is the number of prey eaten, a is the attack rate, N_0 is the number of aphid prey (density) at time = 0, T is the total time spent feeding, and h = the handling time. The maximum feeding rate (m) is defined as $1/h$. According to Hassell et al. (1977), with a Type III model the attack rate a becomes a function of prey density, expressed algebraically as: $(b \cdot N_0) / (1 + c \cdot N_0)$, where b and c are coefficients to be estimated (Pritchard 2014). For both models, data were fitted using a maximum likelihood function in the R module mle2 embedded within the package bbmle. For the model fit, we derived standard errors and 95% confidence intervals from bootstrapping, utilising the boot function in R. Initially, model-fitting and the derivation of parameters was performed using the

standard models. Further analysis utilised allometric scaling factors to account for the size difference among beetles, initially using Kleiber’s Law (1932) that states that metabolism scales at $\frac{3}{4}$ power to that of mass, assuming that parameters in the FR models scale in a similar fashion (Kalinkat et al. 2013). For Holling’s Type II equation, the parameters to be estimated are a_0 and h_0 , which are constants scaled by the masses of both prey and predator. Following Yodzis and Innes (1992):

$$a = a_0 * ma^{-1} * mb^{0.75}$$

and

$$h = h_0 * ma * mb^{-0.75}$$

describe the attack rate and handling time, respectively, whereby ma is the mass of the aphid prey (mg) and mb is beetle mass (mg) [here mb is scaled 0.75, sensu Kleiber, but see Kalinkat et al. (2013) for details]. The allometric-scaled FR parameters were plugged into Holling’s equation, adopting the mean mass of each species of beetle for mb and the mean mass of adult pea aphids, reared at sites across North America at temperatures close to our rearing temperature (20.6 °C, Lamb et al. 1987), as ma . We adopted scaling factors estimated by Kalinkat et al. (2013) into FR analyses. These factors were derived from a variety of arthropod predators and their prey, whereby the negative power-law exponent of the relationship between handling time and predator mass was lower than previously suggested (mb scaled to -0.28 , as opposed to -0.75) and that the converse increase in handling time with prey mass was 0.56.

Modifications to code are unavailable to implement in frair, but parameter estimation was achieved through non-linear least squares regression in the *nls* module in R, through which we calculated standard errors and 95% confidence intervals from 1000 bootstrap repetitions of the data (R: *boot*). All FR analyses were conducted on consumption data from the first 15 min only, and from aphid density categories D2 to D100, because data can only be fitted to FR models if variability exists in consumption below an aphid density cap, particularly at low prey densities where the probability of an aphid being eaten approaches one with increasing time. All other data were taken from the full 3 h and all density categories.

For all analyses, FR parameters (a , h and m)—or their scaled-equivalents were quantified through re-sampling of the data by bootstrapping ($n = 100$). Although some convergence of parameter values was expected when beetle mass was taken into account, a significant difference between FR parameters was still expected, suggesting that any functional divergence is due to phenotypic characters that may covary with body mass and not solely by the energetic demands of maintaining a greater or smaller body mass. Significant differences in mean estimates of FR parameters between beetle species were assessed using one-way ANOVAs, applying Tukey’s post hoc tests.

Results

Harmonia axyridis was significantly larger in body mass than *H. convergens* (respective means = 38.93 mg, SE = 1.02 and 21.30 mg, SE = 0.66; $t = 14.8$, d.f. = 7, $p < 0.01$). A significant positive relationship was observed between body mass and resource consumption both across and within species ($p < 0.01$; Fig. 1). However, the two beetle species differed significantly in their capacity to consume aphids (Fig. 1, Table 1; $F = 216.3$, $p < 0.01$). Beetle

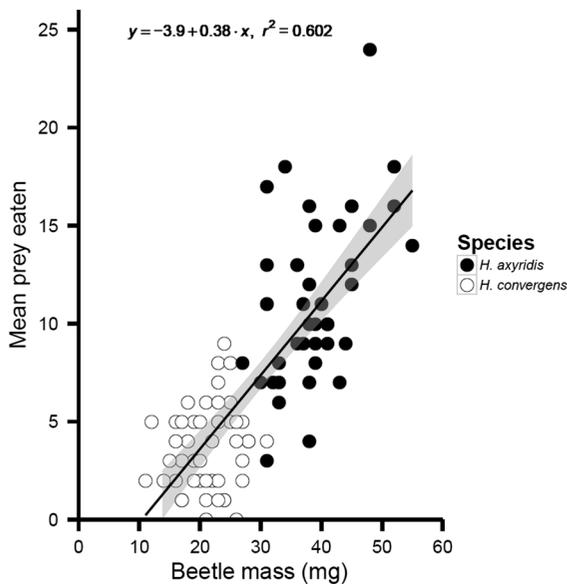


Fig. 1 The relationship between body mass and predation ability for *H. axyridis* and *H. convergens*. Shaded area represents 95% confidence interval of the line of best-fit for both species

Table 1 Multiple analyses of variance (MANOVA) assessing the impact of the predictor variables [species, aphid density and their potential interaction (indicated by the asterisk)] in directing the variance of the response variables (ladybird body mass and the total number of aphids eaten)

Predictor variable	Response variable			
	D.F.	SS	F	P
<i>Beetle body mass (mg)</i>				
Species	1	6607	216.31	< 0.01
Density	7	205	0.96	0.47
Species * density	7	246	1.15	0.34
<i>No. aphids eaten</i>				
Species	1	1215	151.74	< 0.01
Density	7	264	4.72	< 0.01
Species * density	7	128	2.27	0.04

mass did not bias consumption results, as it did not deviate significantly across aphid density categories (see Table 1: $F < 1.0$, $p = 0.47$). *H. axyridis* consumed significantly more aphids than *H. convergens* (means = 11.25, SE = 0.68 and 3.65, SE = 0.32; $t = 10.5$, d.f. = 7, $p < 0.01$), even after adjusting for body mass (*H. axyridis*: mean = 0.29, SE = 0.02, *H. convergens*: mean = 0.18, SE = 0.02; $t = 5.1$, d.f. = 7, $p < 0.01$). There was a positive significant species-specific effect and a positive beetle body mass effect regarding the number of aphids eaten (MANOVA analysis, $p < 0.01$ in both cases). In addition, consumption of aphids increased with aphid density ($p < 0.01$; Table 1).

Harmonia axyridis dramatically out-performed the native beetle in consuming aphids at every prey density, with an overall consumption rate ~ 316% higher (Fig. 2a). Mean mass-adjusted consumption of aphids was also significantly higher for *H. axyridis* versus *H. convergens*, averaging 161% higher across density categories (Fig. 2b). Differences in overall consumption were particularly strong at low prey densities excepting for cases where a single aphid was offered.

Consumption data for both beetles were consistent with a Type II FR (*H. axyridis*: $z = -10.1$, $p < 0.01$; *H. convergens*: $z = -7.6$, $p < 0.01$); fit of Type III models was always lower. Consumption data for both species adhered most closely to Holling’s Type II FR rather than Hassell’s prey-replacement Type III model

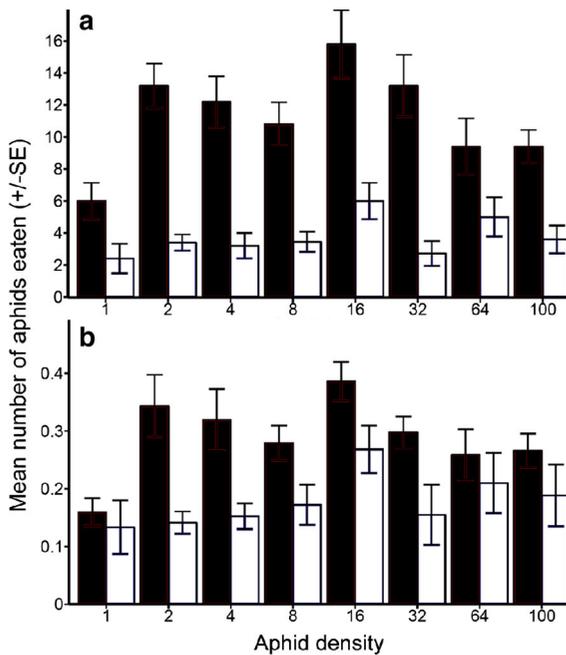


Fig. 2 Comparison of mean prey consumption between *H. axyridis* (black) and *H. convergens* (white) for each aphid density after the full duration of the experiment (**a**). The lower panel (**b**) corrects for differential body mass. Bars depict the standard error associated with each mean value

(Table 2). In addition, *H. axyridis* possessed a higher Type II FR curve than did *H. convergens* (Fig. 3). Indeed, *H. axyridis* maintained a higher consumption rate over the entire 3 h, reflecting both higher detection ability and higher maximum feeding.

Harmonia axyridis exhibited a significantly higher absolute attack and maximum feeding rate than *H. convergens*, with a concomitantly lower handling (see Table 3 and Fig. 4). However, body-mass adjusted patterns showed significant convergence of the scaled attack rate (a_0) between the two species, with a significant reversal under the scaled models (Table 3 and Fig. 4). However, the scaled-handling time (h_0)

remained significantly lower for *H. axyridis* than for *H. convergens* under both allometric models. Consequently, scaled-maximum feeding rate (m_0) was higher for *H. axyridis* than *H. convergens* for all models (Table 3 and Fig. 4).

Discussion

Introduced *H. axyridis* was a superior consumer of aphids over native *H. convergens*, whilst accounting for allometric-scaling. Its higher maximum feeding rate was mediated by its lower prey handling times, but not by the attack rate, for which there may be an allometric component. These findings are consistent with the hypothesis that there exists a significant non-allometric component to the differential functional responses exhibited by the two beetle species, and that this difference may in part explain differential resource utilisation. Our findings are also consistent with numerous studies that identified higher maximum feeding rates in ecologically damaging introduced versus native species (Dick et al. 2014, 2017; Alexander et al. 2014).

The hypothesis that introduced species are competitively dominant versus native ones is historically rooted (e.g., Elton 1958). Body mass is an important component of an organism's existence, potentially impacting all aspects of life-history. For example, body mass is a predictor of competitive dominance between species with significant dietary overlap (Poling and Hayslette 2006). However, surveys of body mass across invasive taxa are generally negatively correlated with establishment success, particularly in insects (Lawton and Brown 1986). Furthermore, larger competitors may be at a disadvantage when resource availability is insufficient to maintain somatic and reproductive tissues (e.g.,

Table 2 Model comparison of functional response curves fitted to the experimental aphid consumption data, indicating the most favourable fit (Rank = 1)

Species	Model	– Log likelihood	AIC	Rank
<i>Harmonia axyridis</i>	Holling's type II	105.08	109.08	1
	Hassell's type III	105.05	110.86	2
<i>Hippodamia convergens</i>	Holling's type II	124.57	128.58	1
	Hassell's type III	120.62	128.79	2

Fig. 3 Type II functional response curves fitted to the 15-min aphid consumption windows for *H. axyridis* (upper left) and *H. convergens* (upper right). Mean aphid consumption (with \pm SE bars) is plotted against density as a continuous predictor variable. The lower panels show the bootstrapping repetitions (thin lines) that determine the 95% confidence intervals (thick lines) for each curve

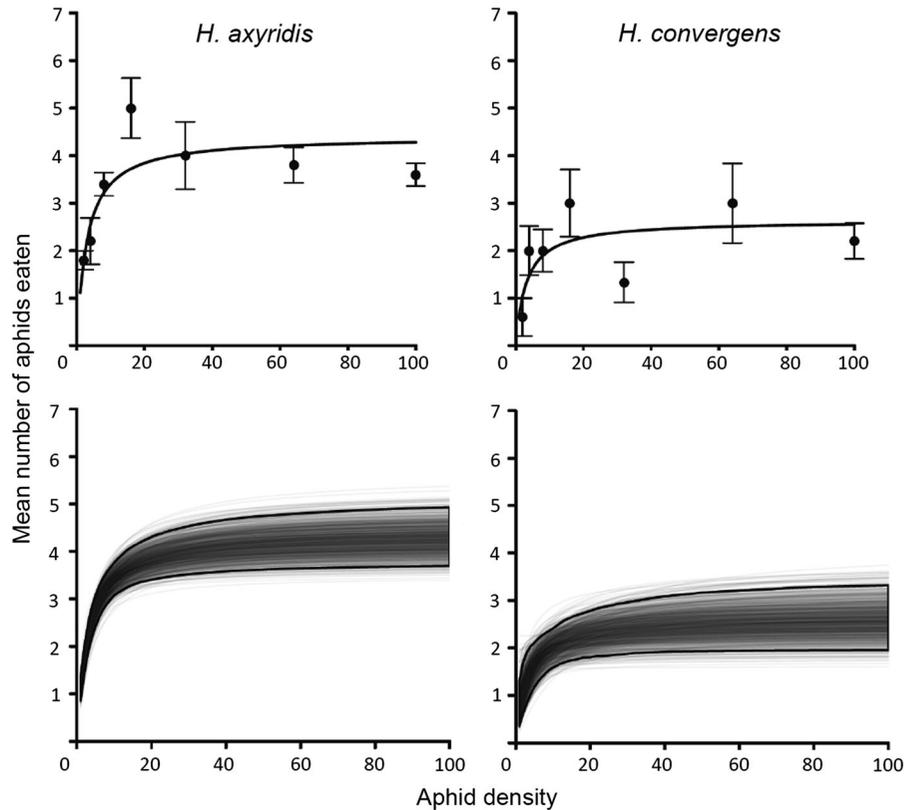


Table 3 Type II functional response parameters estimated by bootstrap resampling ($n = 100$) of non-linear least squares regression model-fitting

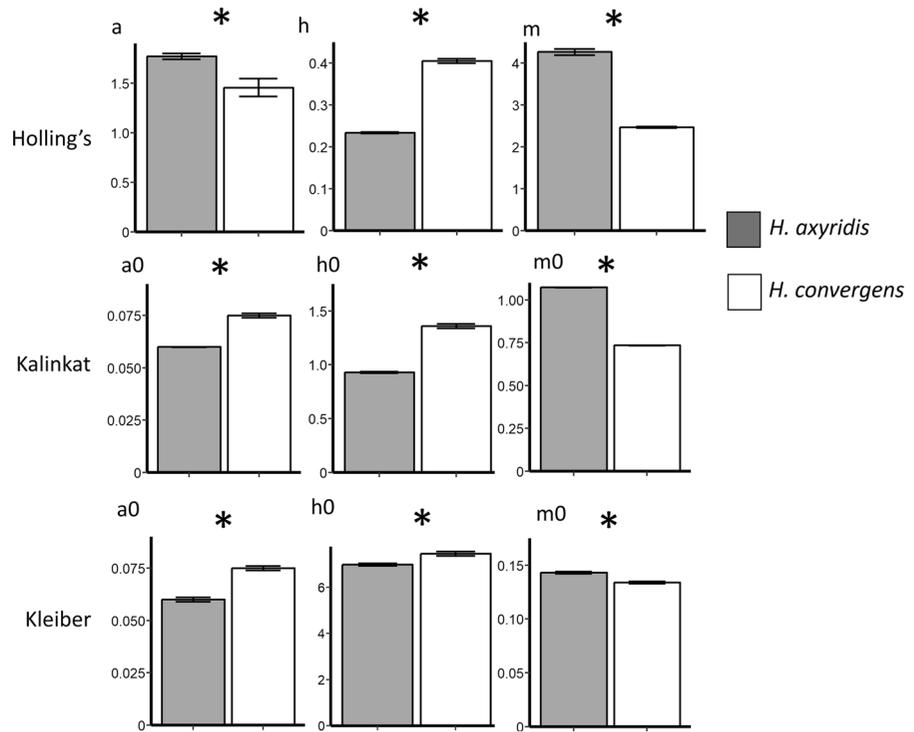
Model	Parameter	<i>Harmonia axyridis</i>		<i>Hippodamia convergens</i>		ANOVA	
		Mean	SE	Mean	SE.	F statistic	P value
Hollings	<i>a</i>	1.770	0.030	1.455	0.090	9.200	< 0.010
	<i>h</i>	0.234	0.002	0.405	0.005	944	< 0.010
	<i>m</i>	4.270	0.075	2.470	0.015	1633	< 0.010
Kalinkat	<i>a0</i>	0.060	< 0.001	0.075	< 0.001	5.480	0.020
	<i>h0</i>	0.931	0.006	1.361	0.021	378	< 0.010
	<i>m0</i>	1.074	0.001	0.735	0.001	542	< 0.010
Kleiber	<i>a0</i>	0.060	< 0.001	0.075	< 0.001	2.200	0.140
	<i>h0</i>	6.970	0.051	7.442	0.102	17.200	< 0.010
	<i>m0</i>	0.143	< 0.001	0.134	< 0.001	3.450	< 0.010

Mean values and standard errors are presented for attack rate (*a*), handling time (*h*) and maximum feeding rate (*m*) (or their scaled equivalents denoted by a zero) for the unadulterated Holling’s model and for the allometric Kalinkat and Kleiber models, respectively

Lenski 1984). The same principle applies in aquatic systems, where small species with low threshold food levels may be capable of outcompeting larger ones with higher food requirements (Stemberger and

Gilbert 1985). Increasing size does not necessarily confer competitive advantage upon non-native species in novel locations unless they possess other physiological or behavioural attributes that enhance

Fig. 4 Mean parameter estimates (attack rate: $a/a0$; handling time: $h/h0$; maximum feeding rate: $m/m0$) derived from bootstrap re-sampling of the non-scaled Holling's model (upper row), the Kalinkat allometric scaled model (middle row) and the Kleiber scaled model (lower row) for *H. axyridis* (grey) and *H. convergens* (white). Statistically significant differences (Tukey's post hoc test) are indicated by an asterisk. Bars show standard errors



competitive ability. Limiting similarity among sympatric native coccinellid beetles may offset any disadvantages conferred by energetically-demanding body mass maintenance, resulting in an enhanced ability to compete for resources independent of allometric scaling relationships through the evolution of covarying phenotypes. Furthermore, this competitive advantage may only become realized when the surrounding biotic or abiotic environments change, as for example might be the case when a species is introduced into a new region.

The FR analysis indicates that the elevated FR of *H. axyridis* is a result of shorter handling times, i.e., it either physically manipulates or consumes aphids much more quickly than the native species or it possesses higher digestive functioning (Jeschke et al. 2002). The higher FR explains the higher *per capita* maximum feeding rate and overall consumption by *H. axyridis* across all aphid densities. That the attack rate was not consistently significantly elevated in the non-native over the native beetle across all FR models (and the relationship is reversed in this study) is not unexpected, as similar findings have been observed with other non-native taxa (e.g., Alexander et al. 2014) and any hitherto inferred elevated attack rates may

need to be reassessed with allometry in mind. Also, the rate at which both beetle species encountered aphids did not vary across prey densities across the entirety of the 3 h experimental time period. This was not surprising as the antennae-based olfactory sense, which they use to detect food and potential mates (e.g., Acar et al. 2001), is likely of limited utility in the small, closed arenas of our study. The closed petri dish experimental design likely approximates the real world in degree, rather than in kind, as differences in the immediate environment that each organisms in a trial encounters may modify the predator's—and/or prey's—responses. Therefore, these results need to be caveated with the realisation that the experimental design, bound by the spatial limitations of the petri dish environment, approximates real-life (Murdoch 1983), but remains a useful model in which to evaluate comparative modes of resource consumption by predators (Dick et al. 2014).

Although supported by bootstrapping, the best-supported Type II FR model is only marginally better supported than the Type III FR model. It is conceivable that a Type III response may be shown by coccinellids under other circumstances (different ontogenetic stages, variant resource(s), or under

alternate trophic scenarios, etc.) and, therefore, cannot be ruled out for these taxa. As a corollary, the expected positive density-dependent response of resources to less efficacious predation at low resource densities may afford some populations of prey items a chance to stabilize in some habitats when predated by Type III coccinellids, presumably impacting higher-level trophic intraguild competition among sympatric coccinellid populations, including between indigenous and non-indigenous species.

The correlated decline of North American native coccinellids with increasing abundance of *H. axyridis* (and the European seven-spot ladybird *Coccinella septempunctata*) is consistent with asymmetric competition whereby the introduced species become established at the expense of a native one. Asymmetric competition is twice as common as equilibrium competition in insects (Lawton and Hassell 1981). However, theoretical and experimental work shows that limiting resources at the lowest densities is the arena in which competitive exclusion is most efficacious (Tilman 1982). Whilst not a direct measure of competition, comparing FR curves gives an indication of the potential impact for unequal resource utilisation, particularly at lowest resource densities (see also Tilman 1977). The higher absolute and scaled maximum feeding rate of *H. axyridis* over *H. convergens* is consistent with an interpretation that the former may reduce aphid prey resources available to the latter at the lowest prey densities. More efficient *H. axyridis* have the potential to drive asymmetric competition in an intraguild coccinellid community in which resources (e.g., aphids) are not spatially or temporally homogeneously distributed. Numerous studies have found that ladybird beetles can significantly reduce aphid abundance in controlled cage experiments (e.g., Thiess et al. 2011). Further, a decline in wild aphid populations correlates with the presence of aphidophagous predators (e.g., Zhao et al. 2013) thus aphids may be a limiting resource both to coccinellid beetles and other intraguild predators.

We compared only adults of both species, though *H. axyridis* exhibits a Type II FR at all stages of larval development (Lee and Kang 2004); therefore, the combined functional response across all life stages may be higher than other coccinellids. However, while it was observed that under laboratory settings single individuals of *H. axyridis* outperform *H. convergens* in the consumption of a single prey type, ladybird size is

positively correlated with size of their prey (Dixon and Hemptinne 2001). Future FR experiments may test whether smaller *H. convergens* proactively choose smaller aphid nymphs or smaller species, and whether larger *H. axyridis* may prefer bigger prey from a mixed prey field. Moreover, interference among intraguild species may modulate FRs. Furthermore, the *H. convergens* population used in this study may differ from wild populations in FR due to the differing ontogenetic circumstances in which commercial populations—even those buttressed by wild-caught individuals—and wild populations experience during development. Therefore, our results should be interpreted cautiously until wild-caught populations of native coccinellids are subject to replicated experimentation. However, catching enough native individuals for a robust analysis will become more difficult as numbers of natives continue to decline.

The most significant finding of this study is the elevated comparative resource utilisation efficiency of *H. axyridis* compared to *H. convergens*. The causative basis for this increased ability is not clear. Temperature affects metabolism, which, in turn, affect functional responses (Sentis et al. 2012). Feeding mode (sucking or chewing) can alter predation pressure calculated for macroinvertebrate predators on aquatic prey (Klecka and Boukal 2013). While both ladybird species chew their prey, we observed that the time allotted to cleaning mouthparts with their forelegs was lower for *H. axyridis* (DeRoy, pers. observ), increasing time available for hunting. This may be related to mouthpart polymorphism in ladybird beetles (Minelli and Pasqual 1977). A greater capacity for passing food through the digestive system suggests that *H. axyridis* has higher digestive or metabolic efficiency. *H. axyridis* likely has increased gut efficiency—allowing better manipulation and processing of food through the gut—and higher faecal production (E. DeRoy, pers. observ.) relative to *H. convergens*, even though it has lower metabolic efficiency at 20 °C (Acar et al. 2005). By processing and clearing food quickly, *H. axyridis* may be expected to be less readily sated than *H. convergens* and will engage in further foraging behaviour.

In conclusion, data from our FR experiments suggests that the Asian multicoloured ladybird possesses a greater ability to process aphid prey than a native counterpart, inclusive of scaling. This ability provides a platform by which it may successfully

compete with and suppress native coccinellid beetles in urban, agricultural and undisturbed habitats of North America. Other coccinellid taxa have already become established in North America or threaten to do so (e.g., *C. septempunctata* and *Harmonia variegata*). It is not clear whether these species also possess physiological and behavioural mechanisms that confer invasiveness. We encourage greater use of FRs and their parameters in the understanding and prediction of invasive species impacts through predation and competition.

Acknowledgements We thank Drs. Dan Pritchard and Steven Marshall for analytical and field advice and Dr. Trevor Pitcher with experimental setup and execution. We are also indebted to the comments made by two referees that enhanced the manuscript. We are grateful for funding from an NSERC Discovery Grant and Canada Research Chair to HJM.

References

- Acar EB, Medina JC, Lee ML, Booth GM (2001) Olfactory behaviour of convergent lady beetle (Coleoptera: Coccinellidae) to alarm pheromone of green peach aphid (Hemiptera: Aphididae). *Can J Entomol* 133:389–397
- Acar EB, Mill DD, Smith BN, Hansen LD, Booth GM (2005) Comparison of respiration in adult *Harmonia axyridis* (Pallas) and *Hippodamia convergens* Guérin-Manville (Coleoptera: Coccinellidae). *Environ Entomol* 34:241–245
- Alexander ME, Dick JTA, Weyl OLF, Robinson TB, Richardson DM (2014) Existing and emerging high impact invasive species are characterised by higher functional responses than natives. *Biol Lett* 10(2):20130946. <https://doi.org/10.1098/rsbl.2013.0946>
- Coderre D, Lucas E, Gagné I (1995) The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in Canada. *Can Entomol* 127:609–611
- Dick JTA, Alexander ME, Jeschke JM, Ricciardi A, MacIsaac HJ, Robinson TB, Kumschick S, Weyl OLF, Dunn AM, Hatcher MJ, Paterson RA, Farnsworth KD, Richardson DM (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biol Invasions* 16:735–753
- Dick JTA, Laverty C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Britton JR, Medoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy FE, Banks PB, Dodd JA, MacNeil C, Penk MR, Aldridge DC, Caffrey JM (2017) Invader relative impact potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *J Appl Ecol* 54:1259–1267
- Dixon AFG, Hemptinne J-L (2001) Body size distribution in predatory ladybird beetles reflects that of their prey. *Ecology* 82:1847–1856
- Dreistadt SH, Flint ML (1996) Melon aphid (Homoptera: Aphididae) control by inundative convergent lady beetle (Coleoptera: Coccinellidae) release on chrysanthemum. *Environ Entomol* 25:688–697
- Elton CS (1958) *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago
- Emery SM (2007) Limiting similarity between invaders and dominant species in herbaceous plant communities? *J Ecol* 95:1027–1035
- Gordon RD (1985) The Coleoptera (Coccinellidae) of America north of Mexico. *J N Y Entomol Soc* 93:1–912
- Hassell M, Lawton J, Beddington J (1977) Sigmoid functional responses by invertebrate predators and parasitoids. *J Anim Ecol* 46:249–262
- Hesler SL, McNickle G, Catangui MA, Losey JE, Beckendorf EA, Stellweg L, Brandt DM, Bartlett PB (2012) Method for continuously rearing *Coccinella* lady beetles (Coleoptera: Coccinellidae). *Open Entomol J* 6:42–46
- Hinkleman TM, Tenhumberg B (2013) Larval performance and kill rate of convergent ladybird beetles, *Hippodamia convergens*, on black bean aphids, *Aphis fabae*, and pea aphids, *Acyrtosiphon pisum*. *J Insect Sci* 13:46
- Hoebeke ER, Wheeler AG (1996) Adventive lady beetles (Coleoptera: Coccinellidae) in the Canadian Maritime provinces, with new eastern U.S. records of *Harmonia quadripunctata*. *Entomol News* 107:281–290
- Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European sawfly. *Can Entomol* 91:298–385
- Ingels B, van Hassel P, van Leeuwen T, de Clercq P (2015) Feeding history affects intraguild interactions between *Harmonia axyridis* (Coleoptera: Coccinellidae) and *Episyrrhus balteatus* (Diptera: Syrphidae). *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0128518>
- Jeschke JM, Kopp M, Tollrian R (2002) Predator functional responses: discriminating between handling and digesting prey. *Ecol Monogr* 72:95–112
- Juliano SA (2001) Nonlinear curve-fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) *Design and analysis of ecological experiments*. Oxford University Press, Oxford, pp 178–196
- Kalinkat G, Schneider FD, Digel C, Guill C, Rall BC, Brose U (2013) Body masses, functional responses and predator-prey stability. *Ecol Lett* 16:1126–1134
- Klecka J, Boukal DS (2013) Foraging and vulnerability traits modify predator-prey body mass allometry: freshwater macroinvertebrates as a case study. *J Anim Ecol* 82:1031–1041
- Kleiber M (1932) Body size and metabolism. *Hilgardia* 6:315–353
- Lamana ML, Miller JC (1998) Temperature-dependent development in an Oregon population of *Harmonia axyridis* (Coleoptera: Coccinellidae). *Environ Entomol* 27:1001–1005
- Lamb RJ, MacKay PA, Gerber GH (1987) Are development and growth of pea aphids, *Acyrtosiphon pisum*, in North America adapted to local temperatures? *Oecologia* 72:170–177
- Lawton JH, Brown KC (1986) The population and community ecology of invading insects. *Philos Trans R Soc Lond B* 314:607–616

- Lawton JH, Hassell MP (1981) Asymmetrical competition in insects. *Nature* 289:793–795
- Lee J-H, Kang T-J (2004) Functional response of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) to *Aphis gossypii* Glover (Homoptera; Aphididae) in the laboratory. *Biol Control* 31:306–310
- Lenski RE (1984) Food limitation and competition: a field experiment with two *Carabus* species. *J Anim Ecol* 53:203–216
- Matzek V (2012) Trait values, not trait plasticity, best explain invasive species' performance in a changing environment. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0048821>
- Minelli A, Pasqual C (1977) The mouthparts of ladybirds: structure and function. *Bolletino di Zool* 44:183–187
- Murdoch WW (1983) The functional response of predators. *J Appl Ecol* 10:335–342
- Poling TD, Hayslette SE (2006) Dietary overlap and foraging competition between mourning doves and Eurasian collared-doves. *J Wildl Manag* 70:998–1004
- Pritchard DW (2014) frair: functional response analysis in R. R package version 0.4. <http://CRAN.R-project.org/package=frair>
- Roy HE, Brown PMJ, Adriaens T, Berkvens N et al (2016) The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. *Biol Invasions* 18:997–1044
- Sentis A, Hemptinne JL, Brodeur J (2012) Using functional response modelling to investigate the effect of temperature on predator feeding rate and energetic efficiency. *Oecologia* 169:1117–1125
- Smith CA, Gardiner MM (2013) Biodiversity loss following the introduction of exotic competitors: does intraguild predation explain the decline of native lady beetles? *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0084448>
- Snell-Rood EC, Swanson EM, Young RL (2015) Life history as a constraint on plasticity: developmental timing is correlated with phenotypic variation in birds. *Heredity* 115:378–388
- Snyder WE, Clevenger GM, Eigenbrode SD (2004) Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia* 140:559–565
- Stemberger RS, Gilbert JJ (1985) Body size, food concentration, and population growth in planktonic rotifers. *Ecology* 66:1151–1159
- Thiess C, Haenke S, Scherber C, Bengtsson J, Bommarco R, Clement LW, Ceryngier P, Dennis C, Emmerson M, Gagic V, Hawro V, Liira J, Weisser WW, Winqvist C, Tschamntke T (2011) The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecol Appl* 21:2187–2196
- Tilman D (1977) Resource competition between plankton algae: an experimental and theoretical approach. *Ecology* 58:338–348
- Tilman D (1982) Resource competition and community structure. Princeton University Press, New York
- Vilcinskas A, Stoecker K, Schmidtberg H, Röhrich CR, Vogel H (2013) Invasive harlequin ladybird carries biological weapons against native competitors. *Science* 340:862–863
- Wells ML, McPherson RM (1999) Population dynamics of three coccinellids in flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). *Environ Entomol* 28:768–773
- Wheeler AG Jr, Hoebeke ER (1995) *Coccinella novemnotata* in northeastern North America: historical occurrence and current status (Coleoptera: Coccinellidae). *Proc Entomol Soc North Wash* 97:701–716
- Yodzis P, Innes S (1992) Body size and consumer-resource dynamics. *Am Nat* 139:1151–1175
- Zhao Z-H, Hui C, Ouyang F, Liu J-H, Guan X-Q, He D-H, Ge F (2013) Effects of inter-annual landscape changes on interactions between cereal aphids and their natural enemies. *Basic Appl Ecol* 14:472–479