

FORUM

# Partial exploitation of host egg patches resulting from a high rejection rate of healthy hosts cautions the mechanistic use of functional response models

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## Abstract

The functional response of parasitoids is a main component of models that describe host–parasitoid interactions. When the functional response assumed in a model (e.g., a population model) is inaccurate, predictions by the model based on the functional response also become unreliable. This study reports that conventional functional response models may commonly fail to capture the actual functional response of parasitoids and discuss its implications. To assist the discussion, an experiment was conducted to describe interactions between the pupal parasitoid *Dirhinus giffardii* (Hymenoptera: Chalcididae) and its host *Bactrocera dorsalis* (Diptera: Tephritidae) in the laboratory. Results showed that the parasitoids typically interacted with all hosts in the environment but parasitised a small fraction of them (e.g., most encountered hosts were rejected), which deviates from the assumption of mechanistic functional response models. An increasing number of published studies on functional response also suggest (although circumstantially) the rejection of unparasitised hosts is common, suggesting that this behaviour is widespread among parasitoid species. By using the experimental results, the study discusses why existing hypotheses are insufficient for the observed behaviour and the implications of this behaviour within the realm of theories surrounding host–parasitoid interactions.

## Introduction

The functional response of a parasitoid describes the per capita parasitism rate as a function of covariates (e.g., host and parasitoid densities). It is a main component of host–parasitoid population models (Hassell 2000), of behavioural models such as the marginal value theorem (Charnov 1976), and of host selection models (Charnov and Stephens 1988; Janssen 1989). For example, the model of the marginal value theorem describes the parasitism behaviour of a parasitoid on patchily distributed hosts, and a functional response model is used to describe within-patch parasitism processes (Wajnberg *et al.* 2006). When the functional response assumed in a model is invalid, the model may produce misleading predictions because of the inaccuracy of the functional response. Due to its importance, an ever-increasing number of studies have characterised the functional responses of diverse parasitoid species (Fernández-arhex and Corley 2003; Uiterwaal *et al.* 2022). However, observed parasitism patterns in published studies suggest that conventional functional response models are insufficient on many occasions, even though the studies may not discuss the issue.

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The issue of functional response considered within the present study can be inferred from published research employing immobile hosts, such as egg and pupal hosts. For example, Mills and Lacan (2004) provided a variable number of egg hosts, *Ephestia kuehniella* (Lepidoptera: Pyralidae), attached on egg cards (1 cm × 3 cm), to individual *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) egg parasitoids for 24 hours. When five eggs were provided, partial exploitation (*i.e.*, parasitism of fewer than five hosts) was frequently observed. However, when 60 eggs were provided, no *T. minutum* parasitised fewer than 20 eggs. The functional response-based explanation for this observation is that parasitoids could not find all five eggs due to the reduced encounter rate at the low density. However, given that all eggs were located on the single egg card, this argument is difficult to make. How unlikely it is for a parasitoid not to encounter all hosts is quantitatively demonstrated in the present paper's Supplementary materials, Appendix 1. Similar results are commonly reported in studies that aimed to characterise the functional responses of parasitoids on immobile hosts (*e.g.*, Jalali *et al.* 2005; Reay-Jones *et al.* 2006; Laumann *et al.* 2008; Kasraee *et al.* 2017; Mi *et al.* 2022; Ray *et al.* 2023).

Empirical studies on the patch-leaving behaviour of egg and pupal parasitoids, motivated by the marginal value theorem, typically used a mass of hosts or a small area (*e.g.*,  $\approx 1.5 \text{ cm}^2$ ) containing hosts as a patch of hosts (Field 1998; Wajnberg *et al.* 2006; Augustin *et al.* 2021; Zhang *et al.* 2022). The marginal value theorem's explanation for partial patch exploitation in these settings is related to functional response because within-patch parasitism is described by a functional response model. That is, parasitoids leave a patch because it becomes more and more difficult to find a useful host as unparasitised hosts are depleted. However, given that hosts were located next to each other, it is difficult to consider that parasitoids left a patch because it was too difficult to find other hosts. In fact, direct observations of parasitoids in these studies revealed that parasitoids left a patch without parasitising healthy hosts that were physically encountered (Wajnberg *et al.* 2006; Augustin *et al.* 2021; Zhang *et al.* 2022).

The results of the published studies discussed above suggest that parasitoids commonly do not parasitise the unparasitised hosts they encounter and that the explanations based on functional response or the marginal value theorem are inappropriate. The purpose of the present study is to discuss the implications of this mismatch between actual parasitism behaviour and the assumed parasitism behaviour in models. Because the arguments noted above may be perceived as circumstantial evidence, an experiment was conducted to describe the parasitism behaviour of a pupal parasitoid to obtain further supporting evidence for our hypothesis. For example, in the functional response studies discussed above, we cannot conclude for sure that parasitoids encountered hosts and did not parasitise them. In the present study's experiment, the behaviour of parasitoids was monitored individually. Similarly, even when a direct observation showed that parasitoids did not parasitise encountered hosts, it may be because of egg limitation or other unknown constraints preventing oviposition. To address this issue, in the present study, two patches were presented to parasitoids and their exploitation of these patches was monitored. For instance, parasitoids departing from one patch after rejecting encountered hosts but proceeding to parasitise hosts in the other patch indicated that the rejection was not due to egg limitation. The experiment is descriptive and is not intended for testing a hypothesis. The parasitism pattern described in the experiment serves as a basis to illustrate the implications of the mismatch that is discussed between the observed parasitism behaviour and the assumed parasitism behaviour in models in the host–parasitoid interaction studies.

## Materials and methods

### Insects

Cultures of the pupal parasitoid *Dirhinus giffardii* Silvestri (Hymenoptera: Chalcididae) and its host *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) were maintained in the laboratory.

*Bactrocera dorsalis* larvae were raised on an artificial diet comprising a blend of wheat bran, sugar, yeast, citric acid, and water, with a weight ratio of 25:10:5:1:50. Adult flies were provided with a mixture of sucrose, yeast powder, and peptone in a ratio of 6:1:1, along with sugar and water. *Dirhinus giffardii* populations were maintained by providing pupae of *B. dorsalis* to adult wasps along with sugar and water. Both species were kept in a room where the temperature was set at 28 °C, with natural light coming in through windows.

The experiment was conducted in a plastic container (area: 96 mm × 137 mm; height: 76 mm). Sifted dried peat moss (Euflor, Munich, Germany) filled the bottom 17 mm of the container. Each patch consisted of hosts that were in physical contact with each other. Two patches containing the same number of hosts (two or six hosts per patch) were created at two diagonal corners of the container. The number of *B. dorsalis* eggs found in an individual fruit can vary from a few to hundreds (Xu *et al.* 2012; Yang *et al.* 2023). Larvae ready for pupation may leave fruits and pupate on or under the ground (Alyokhin *et al.* 2001; Hou *et al.* 2006), and variable numbers of pupae may be aggregated by chance. To examine the effect of the depth of pupae on parasitism behaviour, two levels of depth (0 and 5 mm) were examined. *Dirhinus giffardii* may excavate hosts located near the surface (Chung and Okuyama 2021), which also occurred in the present study. The present study used the shallow depth because the parasitism rate was very low for deeper depths (e.g., no parasitism was common in trials of a few days). Pupae at 0 mm and 5 mm are referred to as “exposed hosts” and “buried hosts”, respectively. Pupae from 1 to 6 days old were used in the experiment, but all pupae used in the same trial were equivalently sized by visual inspection and were of the same age. Thus, parasitoids did not experience variability in host quality in terms of size and age within a trial. The mortality rate of pupae is less than 5% (Fang *et al.* 2011), and it is unlikely that rare unviable pupae affected the conclusions of the present study. One female parasitoid was introduced into the container for a period, as described below, and the number of resulting eggs was counted by removing the puparium. The presence of at least one egg indicates parasitism and of two or more eggs indicates superparasitism.

Partial patch exploitation is defined as an abandonment of a patch containing unparasitised hosts, followed by parasitism of one or more hosts in another patch. For example, given that a total of  $x$  hosts ( $x > 1$ ) are parasitised in the two patches combined, if all  $x$  parasitised hosts are from the same patch, it is not an indication of partial patch exploitation. If hosts from both patches are parasitised (i.e.,  $z$  parasitised hosts in one patch, and  $x - z$  parasitised hosts in the other patch where  $z = 1, \dots, x - 1$ ), it indicates an occurrence of partial patch exploitation by the time  $x$  hosts are parasitised, provided that not all hosts are parasitised in the patches. When only one host is parasitised ( $x = 1$ ), it was not included in the analysis because the presence or absence of partial patch exploitation cannot be concluded. In the case of six-host patches, when  $x = 2$  to 6, and in the case of two-host patches, only when  $x = 2$ , can the tendency of partial patch exploitation be examined.

To introduce variability in the number of parasitised hosts ( $x$ ) in the present study, variable durations of experimental trials were employed. Specifically, longer durations resulted in a higher number of hosts being parasitised on average. Additionally, the trials for buried hosts had a longer duration compared to those for exposed hosts. The difference in duration was due to the lower parasitism rate observed for buried hosts as compared to for exposed hosts.

For two-host patches, four levels of experimental durations were used: 4 hours ( $n = 106$  (exposed) + 2 (buried)), 1 day ( $n = 22$  (exposed) + 5 (buried)), 2 days ( $n = 0$  (exposed) + 9 (buried)), and 3 days ( $n = 0$  (exposed) + 18 (buried)). In sum, the total number of replications was 128 for exposed hosts and 34 for buried hosts in the two-host patches.

For six-host patches, five levels of experimental durations were used: 4 hours ( $n = 128$  (exposed) + 39 (buried)), 8 hours ( $n = 43$  (exposed) + 0 (buried)), 1 day ( $n = 8$  (exposed) + 30 (buried)), 2 days ( $n = 3$  (exposed) + 7 (buried)), and 3 days ( $n = 0$  (exposed) + 11 (buried)). In sum, the total number of replications was 182 for exposed hosts and 87 for buried hosts in the six-host patches.

## Video recording

The parasitism experiment described above can reveal only the presence and absence of partial patch exploitation, but the mechanism remains unknown. To capture details on the individual movements of parasitoids, a subset of the aforementioned trials involving exposed hosts was video recorded. Thirty-four of the 128 trials involving two-host patches were recorded for 4 hours. Similarly, 41 of the 182 trials involving six-host patches were recorded for 8 hours. Specifically, it was noted whether or not parasitoids made physical contact with each host. Patch residence times were also recorded. A patch was considered aborted when a parasitoid physically left the patch (*i.e.*, had no physical contact with hosts). Parasitoids were considered to have left a patch even if they returned to the same patch within a short period (the shortest period being 45 seconds).

## Statistics

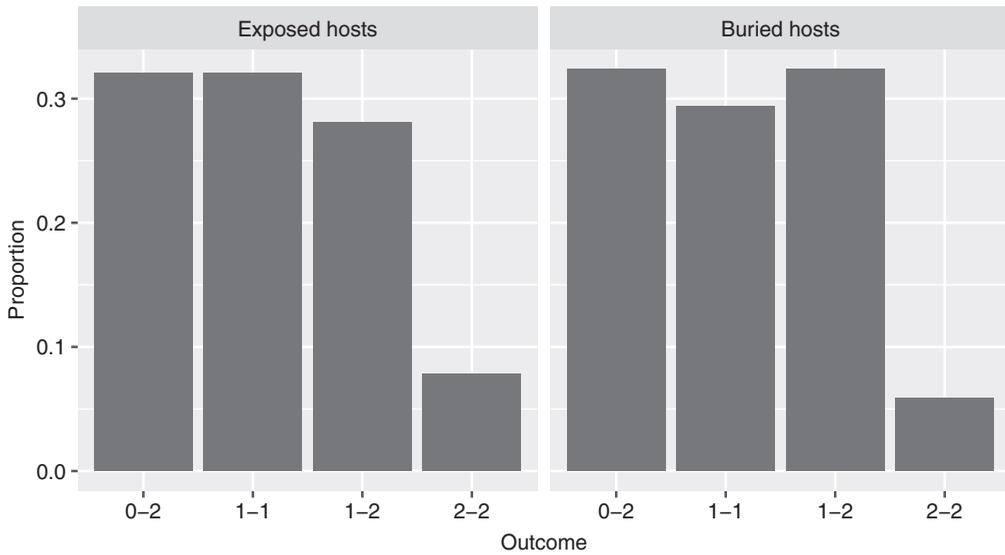
For a given number of parasitised hosts  $x$  in a trial, the probability ( $P$ ) of partial patch exploitation as a binary outcome (described above) was modelled with a binomial generalised linear model with a logit link. In particular, the model was defined as  $\text{logit}(P) = a + bx + cy$  for buried hosts ( $y = 1$ ) and exposed hosts ( $y = 0$ ), where  $a$ ,  $b$ , and  $c$  are the maximum likelihood estimates. The parameter  $b$  (*i.e.*, the coefficient of  $x$ ) represents the relationship between the number of parasitised hosts ( $x$ ) and the probability of partial patch exploitation ( $P$ ). As explained above,  $x$  ranged from 2 to 6 for six-host patches, whereas  $x$  was fixed at 2 for the two-host patches. Therefore, for the two-host patches, the model is simplified as  $\text{logit}(P) = a + cy$ . Because  $x = 2$  is a possible outcome in both two-host and six-host patches, the probability of partial patch exploitation was compared between two-host and six-host patches given  $x = 2$ :  $\text{logit}(P) = a + du$  for  $u = 0$  (two-host patches) and  $u = 1$  (six-host patches). When the parameter  $d$  differs significantly from 0, it indicates that patch size influences the tendency of partial patch exploitation. The patch residence times were compared between the cases for two-host patches and six-host patches using Welch's  $t$ -test.

## Results

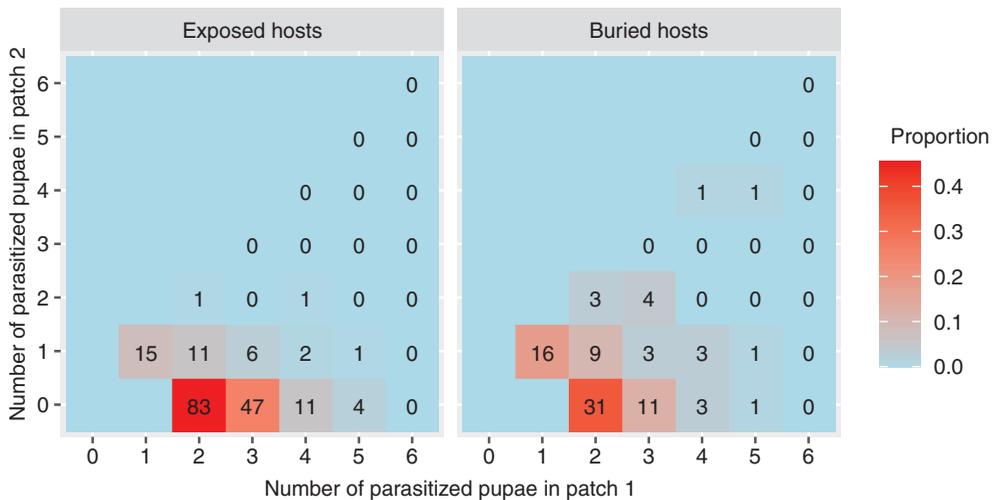
In the case of two-host patches, parasitism patterns were similar for exposed and buried hosts (Fig. 1). When two hosts were parasitised ( $x = 2$ ), the probability of partial patch exploitation ( $P$ ) was described by  $\text{logit}(P) = 8.57 \times 10^{-17} - 9.53 \times 10^{-2}y$  for exposed ( $y = 0$ ) and buried ( $y = 1$ ) pupae. Both parameters are not significantly different from 0 (Wald test,  $P > 0.05$  for both), indicating that given that a parasitoid had parasitised two hosts, the probability that the two hosts are from different patches is 0.5 for both buried and exposed hosts. Among all hosts parasitised in the two-host patches, the proportion of self-superparasitism (two or more eggs in one pupa) was 0.067.

For six-host patches, the number of hosts parasitised in each patch varied substantially (Fig. 2). The probability of partial patch exploitation ( $P$ ) occurring by the time  $x$  hosts were parasitised was described by a binomial generalised linear model:  $\text{logit}(P) = -3.19 + 0.66x + 1.22y$  for exposed ( $y = 0$ ) and buried ( $y = 1$ ) hosts. The positive coefficients, 0.66 (Wald test,  $z = 4.264$ ,  $P = 2.01 \times 10^{-5}$ ) and 1.22 (Wald test,  $z = 4.074$ ,  $P = 4.63 \times 10^{-5}$ ), respectively, indicate that partial exploitation is more likely to be observed as the number of parasitised hosts increases and for buried hosts. Among all hosts parasitised in the six-host patches, the proportion of self-superparasitism was 0.018.

Given that two hosts are parasitised, the occurrence of partial patch exploitation for exposed hosts was  $\text{logit}(P) = -3.85 \times 10^{-6} - 1.71u$  for two-host patches ( $u = 0$ ) and six-host patches ( $u = 1$ ). The negative coefficient for patch size ( $-1.71$ : Wald test,  $z = -4.79$ ,  $P = 1.66 \times 10^{-6}$ ) indicates that partial patch exploitation is less likely to occur in six-host patches than in



**Figure 1.** Parasitism patterns in two patches each containing two hosts. The outcomes are represented by two numbers, where the first and second numbers represent the count of parasitised hosts in each respective patch. For instance, “1-2” denotes one parasitised host in one patch and two parasitised hosts in the other patch. The numbers of replications are 128 for exposed hosts and 34 for buried hosts.



**Figure 2.** Parasitism patterns in two patches each containing six hosts. The number of observed outcomes is shown as numbers, in addition to the proportion of occurrence in the colour key. When an unequal number of hosts were parasitised in two patches, patch 1 was designated to be the patch in which a greater number of hosts were parasitised.

two-host patches when hosts were exposed. The estimated model for buried hosts was  $\text{logit}(P) = -0.095 - 0.57u$ . The coefficient of  $u$  did not differ significantly from 0 ( $-0.57$ : Wald test,  $z = -1.059$ ,  $P = 0.29$ ), indicating that the probability of partial patch exploitation did not differ between two-host patches and six-host patches when hosts were buried.

Video recordings indicated that partial patch exploitation resulted from a high rejection rate on unparasitised hosts. For two-host patches, the number of video recordings for the outcomes “0-2”, “1-1”, “1-2”, and “2-2” ( $x$  and  $y$  in “ $x-y$ ” are the numbers of hosts parasitised in the two patches), respectively, was 10 (29.4 %), eight (23.5 %), 13 (38.2 %), and three (8.8 %). For the six-host

patches, the number of video recordings in which hosts in both patches were parasitised was 15 (36.6 %), and the number of video recordings in which hosts in only one of the two patches were parasitised was 26 (63.4 %). In three cases in two-host patches (8.8 %) and in five cases in six-host patches (12.2 %), parasitoids visited only one of the two patches. In all other cases, parasitoids initially chose one patch and then eventually moved to the other patch. Most individuals (77% in two-host patches and 83% in six-host patches) did not return to the initially chosen patch after visiting the other patch within the recording durations, although the initially chosen patch may have been visited multiple times before reaching the other patch. For two-host patches, the patch residence times (mean  $\pm$  standard error) for the first visit of parasitoids to the initially chosen patch and the other patch, respectively, were  $75.26 \pm 9.38$  minutes and  $48.18 \pm 6.41$  minutes. For six-host patches, they were  $188.23 \pm 19.9$  minutes (initially chosen patch) and  $63.00 \pm 13.71$  minutes (the other patch). When a parasitoid was still in the middle of exploiting the other patch at the end of the recording, the corresponding patch residence time could not be determined, and such results were treated as missing data. The average patch residence time for the initially chosen patch was greater in six-host patches than in two-host patches (Welch two sample *t*-test,  $t = 5.13$ ,  $df = 55.05$ ,  $P = 3.82 \times 10^{-6}$ ), and no difference was found for the patch residence time for the other patch (Welch two sample *t*-test,  $t = 0.98$ ,  $df = 36.98$ ,  $P = 0.33$ ). Given that a parasitoid visited a patch, the probability that a host in the patch was physically contacted by the parasitoid was 1 for two-host patches and 0.94 for six-host patches. Parasitoids inserted the ovipositor into 91% of physically contacted hosts in two-host patches and into 52% of physically contacted hosts in six-host patches (Supplementary materials, Video 1).

## Discussion

The results show that partial patch exploitation is common in *D. giffardii*. Although the probability of partial patch exploitation naturally increases as the number of parasitised hosts increases, the probability was already substantially high even after the first host was parasitised. The data in which exactly two hosts were parasitised indicate that the probability that parasitoids abandon the initially chosen patch after parasitising only one host and parasitise the second host from the other patch (*i.e.*, partial patch exploitation) was 0.5 for two-host patches (Fig. 1) and 0.153 for six-host patches (Fig. 2) for exposed hosts. Furthermore, video recordings of individual parasitoids verified that the abandonment of a patch is not based on the parasitoid's inability to locate other hosts in the patch, indicating that partial patch exploitation is caused by a high rejection rate of unparasitised hosts.

Partial exploitation of a patch of hosts is not an artefact of laboratory experiments. It was also described by direct observation of the egg parasitoid *Anagrus delicatus* in the field (Cronin and Strong 1993). One hypothesis for partial patch exploitation is that parasitoids cannot perfectly discriminate parasitised and unparasitised hosts and therefore abandon useful hosts to avoid superparasitism (Rosenheim and Mangel 1994; Outreman *et al.* 2001). To solitary parasitoids (including *D. giffardii*), self-superparasitism is likely a waste of an egg (but see van Alphen and Visser 1990). However, *D. giffardii* parasitised multiple hosts in the same patch, mostly without committing self-superparasitism. How well the hypothesis applies to species that can distinguish parasitised and unparasitised hosts needs further investigation. A second hypothesis is "bet-hedging", in which parasitoids distribute their eggs into multiple patches to spread risk (Cronin and Strong 1993). However, that hypothesis cannot explain why *D. giffardii* is more likely to abandon a small patch than a large patch. In addition, *D. giffardii* interacted a substantial number of times with hosts without parasitising them, which this hypothesis cannot explain. A third hypothesis is that the rejection of healthy hosts is based on an attribute of hosts not yet described (*e.g.*, an expression of host selection). However, designing an experiment to test whether a healthy host rejected by one parasitoid is independently more likely to be rejected by other parasitoids is

difficult because the interaction between a parasitoid and a host may irreversibly change the attribute of the host (Takasu and Hirose 1991; Castelo *et al.* 2003).

As mentioned in the Introduction section, the rejection of healthy hosts has been reported in various studies in which the behaviour of parasitoids was directly observed (Boivin *et al.* 2004; van Baaren *et al.* 2005; Wajnberg *et al.* 2006; Robert *et al.* 2016). Therefore, the observation itself may not be surprising although it may have not been acknowledged as extreme as what is shown in the present study (*i.e.*, parasitoids interact with all hosts in a conventional experimental setting and parasitise only a small fraction of them). The importance of high rejection rates of hosts has been neglected in research, particularly if it is considered a well-known result. When actual parasitism processes deviate from the mechanistic assumptions of functional response models, estimated parameters such as the attack rate and handling time cannot be mechanistically interpreted. Therefore, publishing those parameters as if they are mechanistically interpretable parameters (*e.g.*, labelling them as attack rate and handling time) can cause problems. For example, a meta-analysis study may use estimated parameters from published functional response studies to test ecological hypotheses (*e.g.*, Englund *et al.* 2011). However, when published parameters cannot be mechanistically interpreted, the inclusion of those studies can make a meta-analysis unreliable.

The standard host–parasitoid population models describe the proportion of host escaping from parasitism as  $e^{-fPT/H}$ , where  $f$  is the functional response, and  $P$  and  $H$ , respectively, are the densities of parasitoids and hosts (Hassell 2000).  $T$  is a discrete time-step of the population model that describes the longevity of adult parasitoids, and it is conventional to set  $T = 1$  without a loss of generality. When a model uses a type II functional response ( $f = aH/(1 + ahH)$ ) in which  $a$  and  $h$ , respectively, are attack rate and handling time, the quantity becomes  $e^{-aP/(1 + ahH)}$ . When the time unit of the handling time,  $h$ , is in hours, the corresponding handling time in a population model is rescaled as  $h/T$ , where  $T$  is the longevity of adult parasitoids in the unit of hours. Because handling time is usually very short (*e.g.*, less than an hour) compared to the longevity of adult parasitoids (many days corresponding to a large number of hours), the value of  $h/T$  is negligibly small for many parasitoid species (Hassell 1978). For this reason, important results of host–parasitoid population models have used a type I functional response ( $e^{-aP}$  as the proportion of unparasitised hosts; May 1978; Chesson and Murdoch 1986; Pacala *et al.* 1990). That is, even if an empirical study shows that a type II functional response is the appropriate model, the population model predicts that the effect of handling time is negligible. However, as discussed above, the mechanistic interpretation of functional response models may not be warranted. Therefore, results from population models must be interpreted with reservation.

The main problem is not that the estimated parameters such as the attack rate and handling time are biased when the assumption is violated. Rather, the high rejection rate of healthy hosts indicates that functional response itself is changing over time in ways we do not yet understand. For example, published functional response studies typically used an experimental duration of one day or less (Mills and Lacañ 2004; Jalali *et al.* 2005; Reay-Jones *et al.* 2006; Laumann *et al.* 2008; Kasraee *et al.* 2017; Mi *et al.* 2022; Ray *et al.* 2023). However, it is also possible to conduct the same experiment for different durations (*e.g.*, a few to several days). If the rejection of healthy hosts such as shown in the present study is expressed for prolonged durations, the extrapolation of a functional response model based on a one-day experiment will overestimate parasitism occurring over two days or longer. In other words, models based on different experimental durations will be inconsistent (and such verification is encouraged in future empirical studies). If the extrapolation of a functional response based on a one-day experiment fails to predict parasitism occurring in two days in a simple controlled condition, it is inappropriate to use it to predict the parasitism occurring in a duration of the longevity of adult parasitoids as happens in population models.

Mechanistic models such as functional response models and the marginal value theorem often are validated qualitatively. For example, the marginal value theorem predicts that patch residence time is longer when the number of hosts in each patch is higher, which has been verified by several studies (Wajnberg 2006). The present study also found a result consistent with the prediction, with

the patch residence time being longer in six-host patches than in two-host patches, but this qualitatively consistent result does not indicate that the theorem is correct under its basic interpretation. For example, in the present study, *D. giffardii* interacted with nearly all hosts in a patch before leaving the patch. Similarly, a good fit (e.g.,  $R^2$ ) in a functional response model does not indicate that the assumption of the model is valid because the same parasitism pattern can result from many different mechanisms (Okuyama 2012). The high rate of rejection of healthy hosts demonstrated in the present study raises questions about existing theories that are based on mechanistic parasitism processes. Regardless of whether the rejection behaviour is a behavioural error (including unexplainable stochastic variability) or an adaptive strategy of parasitoids, its implication for host–parasitoid interactions is substantial and should not be neglected.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.4039/tce.2024.1>.

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**Competing interests.** The author declares no competing interests.

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