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Objektyp: **Article**

Zeitschrift: **Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society**

Band (Jahr): **85 (2012)**

Heft 3-4

PDF erstellt am: **13.07.2024**

Persistenter Link: <https://doi.org/10.5169/seals-403046>

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Choosy polyphagous parasitoids: On the host preferences of *Ichneumon albiger* and *Ichneumon extensorius* (Hymenoptera: Ichneumonidae)

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Polyphagous parasitoids are able to attack different host species, and these often vary in both their availability and suitability. We contribute to a better understanding of the host range structure of the solitary endoparasitoids *Ichneumon albiger* and *Ichneumon extensorius* (Hymenoptera: Ichneumonidae) which parasitise the pupal instar of noctuid moths. Laboratory choice experiments were conducted to test oviposition preferences by offering pupae of different lepidopteran species simultaneously. *Ichneumon albiger* females preferred *Orthosia gothica* (Lepidoptera: Noctuidae) over *O. cerasi*, whereas pupae of the non-host species *Aglais urticae* (Lepidoptera: Nymphalidae) were never attacked. *Ichneumon extensorius* females favoured pupae of *Xestia c-nigrum* (Lepidoptera: Noctuidae) over *Acronicta rumicis* (Lepidoptera: Noctuidae). Additional experiments with already parasitised host pupae suggest that *I. extensorius* avoids superparasitism in young pupae, but even prefers this strategy in old ones. These preliminary results suggest that parasitoid host ranges can be highly structured even in polyphagous parasitoids, and that a complex cascade of criteria determine the final choice made by a female wasp.

Keywords: polyphagous parasitoids, solitary endoparasitoids, host preference, superparasitism, laboratory choice experiments.

INTRODUCTION

Many parasitoid species are generalists and therefore attack different host species, which often vary in their suitability (Godfray 1994; Weisser & Houston 1993). In such polyphagous parasitoids, several questions about their host ranges arise: Are all hosts equally suited, or is the host range structured? What are the consequences for host recognition? Why do parasitoid females prefer some hosts over others? Is there variation at the individual level within one species in host preferences? And does avoidance of superparasitism influence host preference?

Host choice by endoparasitoids can be envisaged as a hierarchical process at three different levels. First, parasitoid females are attracted to a certain type of (micro-) habitat in which they search for hosts (Godfray 1994; Segura *et al.* 2007). Second, parasitoid females need to recognise a potential host species, and then be triggered into oviposition by some host-specific cues (Arthur 1981; Pennacchio *et*

al. 1994). Third, the endoparasitoid egg and larva must be able to develop within the host's physiological environment and overcome its immune defense (e.g. Strand & Pech 1995; Alleyne & Wiedemann 2001; Schmidt *et al.* 2001). While processes at the first level need to be studied directly in the field, processes acting at the second and third level can to a certain extent also be studied under laboratory conditions.

For a large majority of parasitoid wasps, the host range is virtually unknown (Yu *et al.* 2012). This is especially true for parasites of immobile and often well-hidden host stages, e.g. pupal parasitoids, which are difficult and cumbersome to find in the field. We addressed host choice and avoidance of superparasitism in two such species of the genus *Ichneumon* Linnaeus, 1758, *Ichneumon albiger* Wesmael, 1845, and *Ichneumon extensorius* Linnaeus, 1758 (Hymenoptera: Ichneumonidae). Both are solitary, polyphagous parasitoids of different moth species (Lepidoptera: Noctuidae) (e.g. Hinz & Horstmann 1998, 2007). While host records from the field are very scarce (Yu *et al.* 2012), the host ranges of both species became clearer when Rolf Hinz started to extensively breed these parasitoids in the lab and present them with a range of potential hosts (e.g. Hinz 1982, 1983, 1987, 1991; Hinz & Horstmann 1998, 2007). Hinz' data is to date the only information we have about host ranges of many species in this genus. When offered a single potential host at a time, *I. albiger* successfully parasitised five species of two genera of noctuids of the subfamily Noctuinae and nine species of four genera of the subfamily Hadeninae, while *I. extensorius* accepted eleven Noctuinae and one Hadeninae species.

The laboratory experiments showed a varying success of the parasitoids to develop in different host species. However, developmental success does not necessarily mirror the oviposition preference (Henry *et al.* 2005). Complementing these experiments with choice experiments provides further insight into the structure of the host ranges of these polyphagous parasitoids. We thus simultaneously offered the pupae of two or three different lepidopteran species. Having a sufficient number of host individuals available, we furthermore tested if *I. extensorius* is able to distinguish between parasitised and unparasitised hosts, and whether it showed avoidance of superparasitism.

MATERIALS AND METHODS

Parasitoid sampling

Forty females of *I. albiger* and 29 females of *I. extensorius* were collected in March 2009 at three different localities of Central Switzerland, all canton Luzern (Luzern: 47°01'54" N, 08°18'35" O; Horw: 46°59'57" N, 08°17'06" O; Hergiswil 46°59'25" N, 08°17'06" O). The collected specimens were found hibernating aggregated with additional Ichneumoninae species. The microhabitats were under the bark of *Pyrus* sp. and *Quercus* sp., respectively (Luzern and Horw), and under a moss-layer on top of a heap of earth (Hergiswil). Each wasp female was kept separately in a jam jar (9 cm in height x 6 cm in diameter) closed by gauze in the climate chamber (photoperiod of L12: D12, 8°C: 3°C). The bottoms of the glasses were prepared with a calcium sulphate layer of one centimetre in order to sustain a constantly high humidity. The glasses were watered every third day and the parasitoids fed on a pudding as described by Hinz (1987).

The females were grouped into morphospecies, and after their death identified with the aid of Hilpert's determination key (1992). On April 27th, conditions

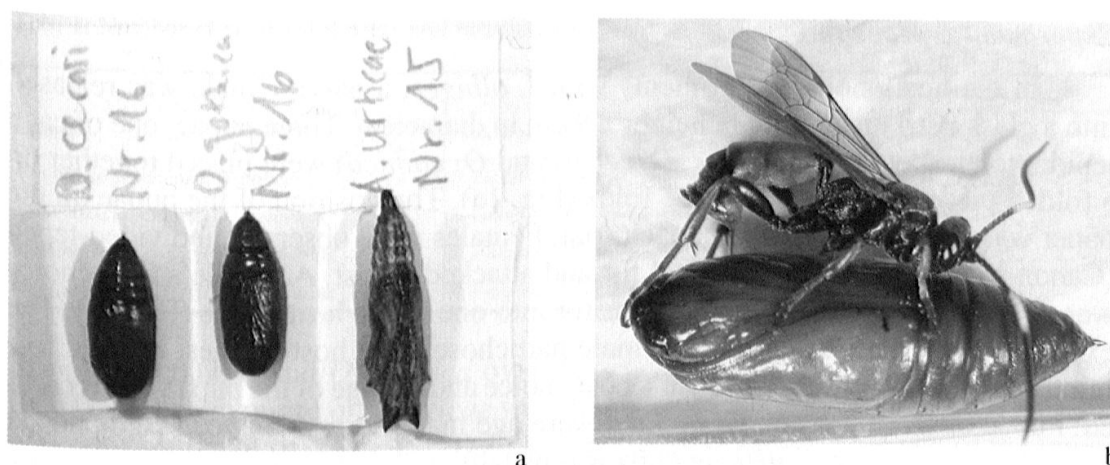


Fig. 1. a) Setup used for the host choice experiments with *Ichneumon albiger*, b) *Ichneumon extensorius* female ovipositing into the pupa of *Xestia c-nigrum*. When the ovipositor was inserted into the pupa, we treated the attacked species as the preferred one.

in the climate chamber were changed to long-day (L16: D8, 17°C: 6°C) so that the females could complete the development of their ovaries (Hinz & Horstmann 2007). The wasps were kept under these climatic conditions for two to three weeks in the case of *I. albiger* and fifteen to sixteen weeks in the case of *I. extensorius* before they were used in the choice experiments.

Host rearing

For the host choice experiments with *I. albiger*, we used two known host species, *Orthosia cerasi* (Fabricius, 1775), and *O. gothica* (Linnaeus, 1758) (Lepidoptera: Noctuidae), and a species which is clearly outside of the host range, *Aglais urticae* (Linnaeus, 1758) (Lepidoptera: Nymphalidae) (Hinz & Horstmann 2007). Females of *O. cerasi* and *O. gothica* were captured by light trapping near La Lurette (Valais, Switzerland, 46°09'44" N, 07°26'57" O), and made to oviposit on moist tissue (Friedrich 1975). The caterpillars were kept in a terrarium (69x40x40 cm) at room temperature and provided with leaves of *Quercus* sp. (Carter & Hargreaves 1986) *ad libitum* until they pupated.

First, second and third instars of *Aglais urticae* were collected (on *Urtica* spp.) near Mazembroz (Valais, Switzerland, 46°09'22" N, 07°08'48" O). They were reared in a terrarium (69x40x40 cm) in the dark at 16±2°C in order to slow down their metabolism, so the individuals of the other two host species were able to compensate for their developmental lag. Until pupation, *A. urticae* caterpillars were kept on *Urtica dioica* (Carter & Hargreaves 1986) *ad libitum*.

For the choice experiments with *I. extensorius*, we used the host species *Xestia c-nigrum* (Linnaeus, 1758) (Lepidoptera: Noctuidae) (Hinz & Horstmann 2007) and *Acrionicta rumicis* (Linnaeus, 1758) (Lepidoptera: Noctuidae), which is not a known host. Females of *Xestia c-nigrum* and *Acrionicta rumicis* were caught by light trapping in July 2009 near Kriens (Lucerne, Switzerland, 47°02'34" N, 08°16'11" O), and made to oviposit. Twenty caterpillars of each species were transferred together into a plastic box (21.5x14.5x4.5 cm), kept at room temperature, and kept on *Taraxacum* spp. (Ebert 1998) *ad libitum* until pupation.

Experimental procedures

In the host-choice experiments with *I. albiger*, a naïve female was released into a glass Petri dish (2 cm in height x 9 cm in diameter). Three pupae, one of each lepidopteran species (*A. urticae*, *O. cerasi* and *O. gothica*) were placed together on a folded piece of paper with three folds (Fig. 1a). The position of the pupae on the paper was chosen randomly for each trial. Females were observed and video-taped (Canon MV500i) as they searched for and attacked a host. A female's host choice was defined by insertion of the ovipositor into one of the host pupae (Fig. 1b). The experiment either ended when a female had chosen one host species, or after five minutes without an attack. Female's host choice and the age of the pupa were recorded. Pupae of *O. cerasi* and *O. gothica* were age matched and between zero and six days old, whereas the *A. urticae* pupa was usually of the same age, but in five cases, we had to use pupae which were up to three days younger or older.

I. extensorius females had the choice between a *X. c-nigrum* pupa and an *A. rumicis* pupa of the same age, and the experimental procedure was the same as outlined above. In order to investigate whether *A. rumicis* could represent a hitherto undocumented host of *I. extensorius*, we also conducted 29 non-choice trials where *I. extensorius* females were presented with this host only.

To assess whether superparasitism is avoided by *I. extensorius*, we conducted two additional experiments. In the first test, two *X. c-nigrum* pupae were presented to an *I. extensorius* female which already had the oviposition experience of at least one previous experiment on a previous day. One of the *X. c-nigrum* pupae had already been used for oviposition by a different *I. extensorius* female some minutes before. In the second test, the female had the choice between two pupae of different lepidopteran species (*A. rumicis* and *X. c-nigrum*) as in the previous experiment, but the *X. c-nigrum* pupa had already been attacked. In all tests with *I. extensorius* female's host choice, age and weight of host pupae at experimental use were recorded.

Statistical analysis

Fisher's exact test was used to analyse both the host choice and superparasitism experiments. This test was chosen due to small sample sizes. To test for confounding factors which could have affected host choice, we applied a logistic regression model by forward selection. Pupal age (Tab. 1) and the locality where the female wasps were collected were analysed for the host-choice experiments conducted with *I. albiger*, whereas for *I. extensorius* wasps, pupal weight differences were also included, as they showed a considerable variation. All analyses were carried out with SPSS software (Version 17.0, SPSS Inc., Chicago, IL, USA).

RESULTS

Host choice experiments

In the host-choice experiment with *I. albiger*, 25 out of 40 females attacked one of the three offered host pupae (Tab. 1). Naïve females did not choose the pupae of *O. gothica*, *O. cerasi* and *A. urticae* equally (Fig. 2a, $n = 25$, $\chi^2 = 26.0$, $df = 2$, $P < 0.001$), but showed a clear preference for *O. gothica* over *O. cerasi* ($n = 25$, $\chi^2 = 9.0$,

Tab. 1. Number of successful trials and host pairs (at a given age) used in the different experiments.

Experiments	Parasitoid species	successful trials	Pairs of host species pupae	# host pairs with pupal age in days											
				0	1	2	3	4	5	6	7	8	9		
1. Host-choice experiment	<i>I. albiger</i>	25	<i>O. cerasi</i> / <i>O. gothica</i>	4	14	3	-	-	2	2	-	-	-	-	-
2. Host-choice experiment	<i>I. extensorius</i>	21	<i>X. c-nigrum</i> / <i>A. rumicis</i>	2	6	8	5	-	-	-	-	-	-	-	-
1. Superparasitism	<i>I. extensorius</i>	16	<i>X. c-nigrum</i> / <i>X. c-nigrum</i> parasitised	-	4	-	1	1	2	3	2	2	1	-	-
2. Superparasitism	<i>I. extensorius</i>	10	<i>X. c-nigrum</i> parasitized / <i>A. rumicis</i>	-	3	2	5	-	-	-	-	-	-	-	-

$df = 1$, $P = 0.004$) and *O. gothica* over *A. urticae* ($n = 20$, $\chi^2 = 20.0$, $df = 1$, $P < 0.001$). Although pupae of *A. urticae* were never attacked, the difference to *O. cerasi* was not significant ($n = 5$, $\chi^2 = 5.0$, $df = 1$, $P = 0.063$). Neither the age of the pupae nor the collection locality of the wasp had a significant impact on the outcome of the choice experiment. In the host-choice experiment conducted with *I. extensorius*, *X. c-nigrum* was strongly preferred over *A. rumicis* (Fig. 2b, $n = 21$, $\chi^2 = 17.19$, $df = 1$, $P < 0.001$). Again, this strong preference cannot be explained by the collection locality, pupal age or pupal weight differences. Only in a single trial, an *I. extensorius* female chose an *A. rumicis* pupa. In no-choice trials, three females out of 29 accepted *A. rumicis* for oviposition.

Avoidance of superparasitism

In the test with two pupae of the same species, there was no significant difference of preference between already parasitised and unparasitised *X. c-nigrum* pupae when the data was pooled (Fig. 3a, $n = 16$, $\chi^2 = 0.0$, $df = 1$, $P > 0.05$). This test was not significantly affected by the locality of parasitoid females and host weight differences, but the host age had a significant influence on host preference (Fig. 4, $\chi^2 = 4.67$, $df = 1$, $P = 0.031$), which motivated us to further investigate the interaction

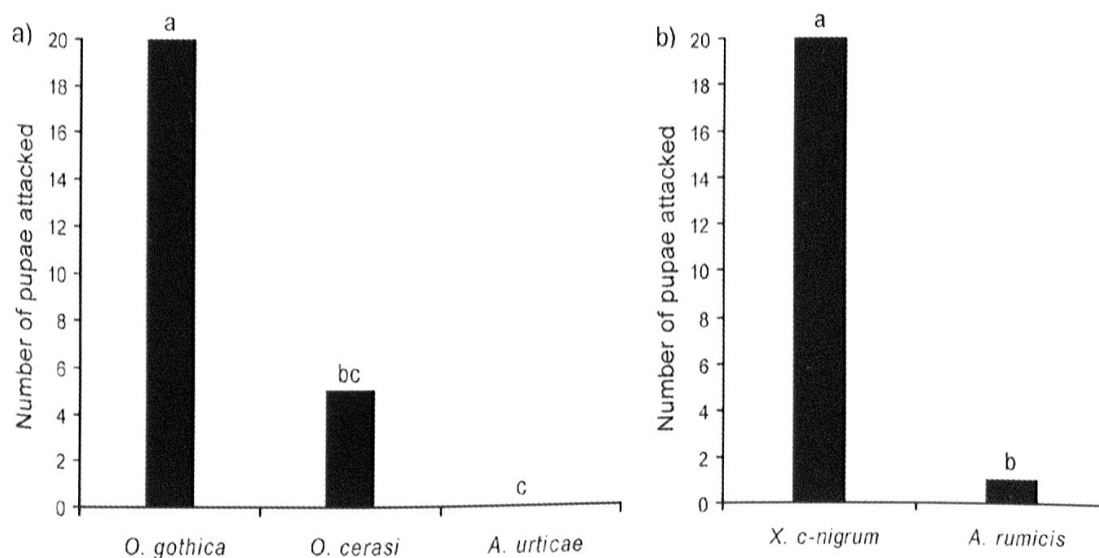


Fig. 2. Host choice trials: Number of pupae attacked by a) naïve *Ichneumon albiger* females that had the choice between two *Orthosia* species and *Aglais urticae* (total $n = 25$, $P = 0.001$) b) naïve *Ichneumon extensorius* females that had the choice between *Xestia c-nigrum* and *Acronicta rumicis* ($n = 21$, $P = 0.004$). Bars with different letters are significantly different.

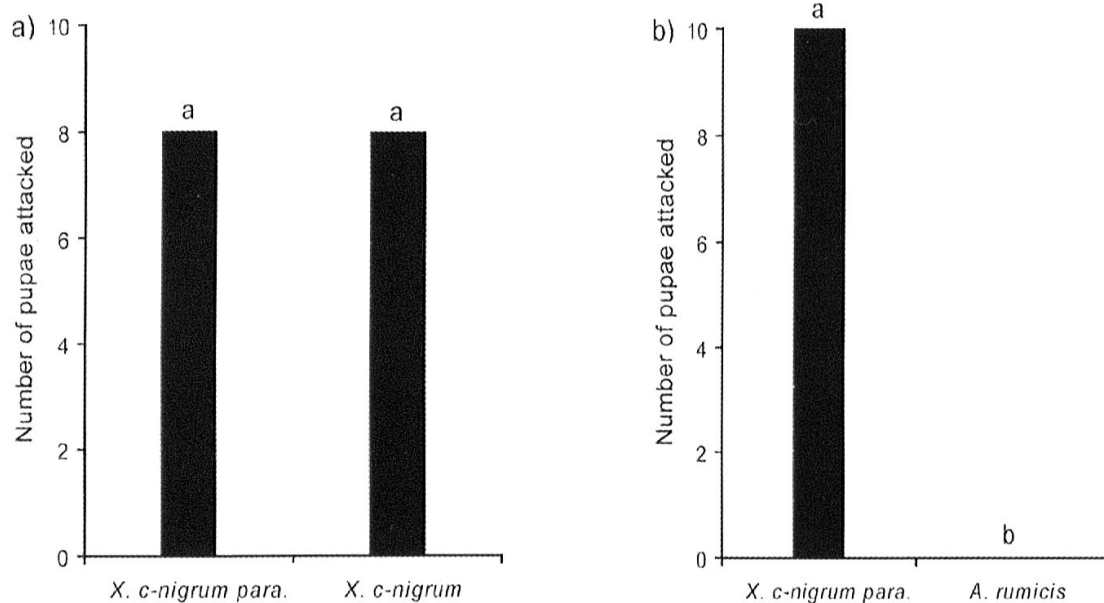


Fig. 3. Superparasitism avoidance: Number of pupae attacked by *Ichneumon extensorius* females that had the choice between a) parasitised (*Xestia c-nigrum para.*) and unparasitised pupae of *Xestia c-nigrum* (n = 16, P > 0.05) b) *Xestia c-nigrum para.* (= parasitised) and *Acronicta rumicis* (n = 10, P = 0.02). Bars with different letters are significantly different

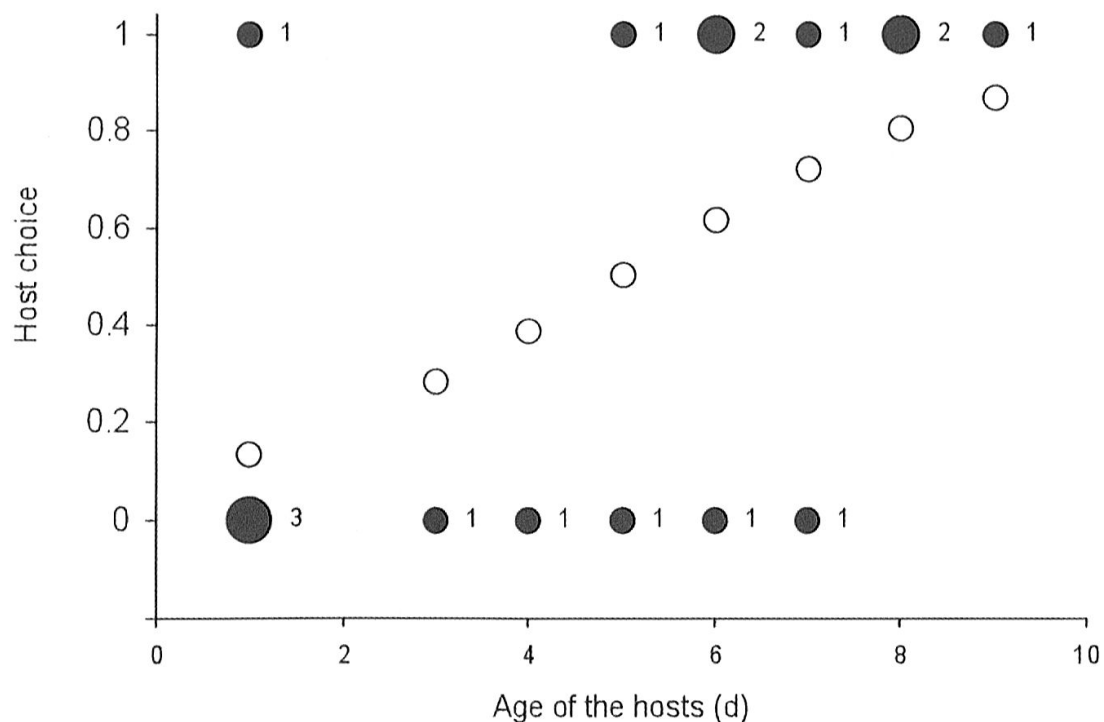


Fig. 4. Superparasitism avoidance by *Ichneumon extensorius* females is affected by the age of hosts (days). Real values (closed circles) follow a linear approximation after transformation into estimated values (open circles). A host choice value of 0 means that an unparasitised *Xestia c-nigrum* pupa was attacked, a host choice value of 1 indicates that a parasitised *Xestia c-nigrum* pupa was attacked. Sizes of circles and numbers next to them reflect the number of trials for a given host pupal age at a certain host choice outcome (n = 16). The model indicates a significant influence of host age on superparasitism strategy (P = 0.031).

host weight – parasitoid choice. If the offered two *X. c-nigrum* pupae were young, *I. extensorius* females preferred the unparasitised pupa, but the older the pupae were, the more wasp females chose the already parasitised pupa. In the second test for avoidance of superparasitism, already parasitised *X. c-nigrum* pupae were preferred in all cases to unparasitised *A. rumicis* pupae (Fig. 3b, $n = 10$, $\chi^2 = 10.0$, $df = 1$ $P = 0.02$). The result of this test was not significantly affected by the locality of parasitoid females, host weight differences and pupal age. 94 % out of 31 *I. extensorius* females were willing to attack one of the offered host pupae.

DISCUSSION

Polyphagous, but choosy

Our experiments reveal that both polyphagous parasitoids were very choosy when presented with different lepidopteran pupae in the laboratory. In the case of *I. extensorius*, the strong preference for *X. c-nigrum* over *A. rumicis* might show that the latter noctuid species is not part of the host range at all, or that it is only a minor host. When offered individually, it was accepted for oviposition by more than 10 % of the females, but as long as no successful rearing of *I. extensorius* from *A. rumicis* has been reported, it cannot be excluded that the observed ovipositor insertions were mere probings and not actual oviposition attempts. This interpretation is also in agreement with the findings of Hinz & Horstmann (2007); based on nonchoice experiments in the laboratory, they list as potential hosts only species of the subfamilies Hadeninae and Noctuinae, while *A. rumicis* belongs to Acronictinae. Furthermore, *A. rumicis* pupates on the ground in a cocoon (Carter & Hargreaves 1986), while all the known hosts of *I. extensorius* pupate in the soil (Hinz & Horstmann 2007). *A. rumicis* might thus not be considered a suitable host species by *I. extensorius* in nature because it occupies a niche where the parasitoid would never search for potential hosts (Shaw 1994).

In *I. albiger*, the preference behaviour involved two very closely related, known host species, i.e. *O. gothica* and *O. cerasi*. The clear preference for one of two host species of the same genus is quite surprising given the comparatively wide host range of the species which includes representatives of at least six different genera and two different subfamilies (Hinz & Horstmann, 2007). Moreover, both host species have a fairly similar phenology, similar food plants and can be found in similar habitats (cf. Carter & Hargreaves 1986; Ebert 1998).

If different potential host species are available, polyphagous parasitoids should choose an optimal host depending on its profitability, as claimed by optimal host-selection theory (Iwasa *et al.* 1984). Differences in profitability between hosts might arise from several factors, including host size, defense behaviour, and of course the suitability of the physiological environment for an endoparasitoid to develop (Gross 1993; Godfray 1994; De Farias & Hopper 1999). Although not investigated in detail, differences in host size and defense behaviour were at least not obvious in our setting, and both *Orthosia* species are probably suited for successful development by *I. albiger*. Hinz & Horstmann (2007) observed that 48 % of *I. albiger* embryos developed successfully within the (not preferred) *O. cerasi* pupae under laboratory conditions; comparable data about developmental success in the here preferred *O. gothica* are unfortunately not available. We unfortunately

could not rear any *Ichneumon* individuals from our laboratory experiments, so we cannot be certain whether any eggs were actually laid, and cannot quantify the physiological suitability of the hosts. The reason for this strong preference behaviour thus remains to be elucidated.

Although laboratory choice experiments are by no means sufficient to investigate the realised host range of a parasitoid in nature (Hinz & Horstmann 2007), it is likely that the strong preferences that we observed have some correspondence in nature, where a female might be able to detect a host at some distance by chemical cues. Choice experiments as conducted by us are furthermore a valuable complement to experiments in which only a single host is offered. Although the latter approach can demonstrate that a host might be accepted by a female wasp if no other species are available, it does not allow investigation of the structure of the host range. Despite the limited sample size and restricted choice of hosts offered in our experiments, we believe that they provide valuable insights into these wasps' preference behaviours (Sathe & Shantkumar 1992; Mansfield & Mills 2004; Brotdjojo & Walter 2006; Gitau *et al.* 2007).

Avoidance or preference of superparasitism

When *I. extensorius* females were presented with already parasitised pupae of *X. c-nigrum* and unparasitised *A. rumicis* pupa as an alternative, they did not change their preference, no matter how old the pupae were. Because *X. c-nigrum* obviously is a very suitable host for *I. extensorius*, as shown by the high developmental success in the laboratory (Hinz & Horstmann 2007), it might still be more attractive than the at the most peripheral host *A. rumicis*, even when already parasitised. When presented with a parasitised and an unparasitised pupa of *X. c-nigrum*, however, our results suggest that *I. extensorius* females avoid superparasitism in fresh pupae, while the opposite is true if the host pupa was older than five days. Superparasitism as a strategy to overcome the host's immune defence might explain this result, if the potency of this defence changes with the age of the pupa (e.g. Sagarra *et al.* 2000, Khafagi & Hegazi 2008). Given the extensive reorganisation taking place during the pupal stage, this seems quite likely.

Our relatively small sample size ($n = 16$) does not allow to definitely answer this question. Nevertheless, if we assume that our results mirror a plasticity in the preference depending on host age and parasitisation status, this implies that *I. extensorius* is able to discriminate between parasitised and unparasitised hosts, as it is recognized for a wide variety of different parasitoid species (van Lenteren 1981). Furthermore, it implies that *I. extensorius* females use this information to oviposit into the most profitable host. This phenomenon deserves further attention; our experiments should be repeated with larger sample sizes, and complemented with an investigation of the strength of the immune responses of pupae of different ages.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge the support of Peter Sonderegger, Rudolf Bryner, and Markus Fluri (all Entomologischer Verein Bern, Switzerland) with the host capturing and host rearing. We also thank Dik Heg, Universität Bern, Switzerland, and Hannes Baur, Naturhistorisches Museum Bern, Switzerland (NMBE), for help with statistics, and Stefan Bachofner (NMBE) for technical support. Mark Shaw (National Museums Scotland, Natural Sciences, Edinburgh) and Klaus Horstmann (Würzburg) provided numerous helpful comments on a previous version of this manuscript.

ZUSAMMENFASSUNG

Polyphage Parasitoide nutzen verschiedene Wirtsarten, welche oft in ihrer Verfügbarkeit und ihrer Eignung variieren. Gegenstand unserer Arbeit ist die Strukturierung des Wirtsspektrums der solitären Endoparasitoiden *Ichneumon albiger* und *Ichneumon extensorius* (Hymenoptera: Ichneumonidae, Ichneumoninae). Beide Arten parasitieren die Puppen verschiedener Eulenfalterarten. Durch Wahlexperimente wurde getestet, inwiefern die Parasitoide bei der Eiablage eine Präferenz zeigen, wenn unterschiedliche Nachtfalter-Arten zeitgleich angeboten werden. Die Weibchen von *I. albiger* bevorzugten *Orthosia gothica* (Lepidoptera: Noctuidae) über *Orthosia cerasi* (Lepidoptera: Noctuidae), wobei die Puppen der wirtsspektrumsfremden Art *Aglais urticae* (Lepidoptera: Nymphalidae) nie angestochen wurden. *I. extensorius* Weibchen favorisierten *Xestia c-nigrum* Puppen (Lepidoptera: Noctuidae) vor *Acrionicta rumicis* (Lepidoptera: Noctuidae). Wir diskutieren verschiedene Gründe, welche zum Präferenzverhalten dieser beiden *Ichneumon*-Arten führen können. Auch wurde das Vermeiden von Superparasitismus getestet. Im Fall von *I. extensorius* scheint das Vermeiden von Superparasitismus nur bei jungen Wirtspuppen vorhanden zu sein; während er bei älteren Puppen sogar bevorzugt angewendet wurde. Diese vorläufigen Resultate zeigen, dass auch die Wirtsspektren von breit polyphagen Parasitoiden stark strukturiert sein können, und dass eine komplexe Kaskade von Einflüssen das Wahlverhalten eines Parasitoidenweibchens beeinflussen können.

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(received June 29, 2012; accepted October 16, 2012; printed December 31, 2012)