Interactions Between Adults of Some Species of *Netelia* Gray (Hymenoptera: Ichneumonidae: Tryphoninae) and Their Caterpillar Hosts (Lepidoptera)

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Abstract.—Five species from three subgenera of *Netelia* were observed ovipositing on their hosts under laboratory conditions. Two species of the subgenus *Bessobates* oviposited without a separate insertion of the ovipositor beforehand. One species of the subgenus *Netelia* and two of the subgenus *Paropheltes* employed a venom causing weak (often incomplete) temporary paralysis, administered as a separate action prior to oviposition. The venoms had no long-term adverse effect on hosts and it appears that these taxa, and perhaps all other groups of ectoparasitic koinobiont Ichneumonidae, lack the host-regulating venom systems that have been regarded as instrumental in the evolution of endoparasitism in some koinobiont cyclostome Braconidae. In all species substantial parasitoid development was delayed until the final instar host had constructed its pupation site, wherein it was overwhelmed as a prepupa. Species of all three subgenera dumped eggs in the absence of hosts, and (if kept humid) such eggs subsequently split to reveal a living first instar larva (but not investigated in the subgenus *Paropheltes*). Species of all three subgenera indulged in non-destructive concurrent host-feeding, despite being supplied with honey solution *ad libitum*, making the necessary wounds on the host's body with their mandibles. Occasionally non-destructive host-feeding occurred on hosts that were not also being parasitised.

The main purpose of this study was to investigate the effect of the venom of species of *Netelia* Gray (= *Paniscus* auctt. nec Schrank) (Ichneumonidae: Tryphoninae) on their caterpillar hosts, but in the course of conducting experiments observations were also made on host-feeding, oviposition behaviour, egg dumping, egg hatching and (in one species) copulation.

Many koinobiont parasitic wasps—that is, those in which the host continues to develop after being parasitised—influence the subsequent physiology, behaviour and development of their hosts in various and often profound ways (Vinson and Iwantsch 1980, Beckage 1985, 1991, Lawrence 1986, Barnard and Behnke 1990; see also Quicke 1997). In some, injections of materials ("venoms" in the broadest sense) other than eggs by the female parasitoid during the oviposition sequence are known to be at least partly responsible

(Shaw 1981, Tanaka 1987, Jones 1987, Dover *et al.* 1988, Leluk and Jones 1989). In endoparasitoids the effect on the host of venoms independent of parasitisation as such is usually difficult to investigate directly because the egg is injected concurrently; that is, during a single insertion of the ovipositor. In some koinobiont cyclostome Braconidae, however, venoms initially causing paralysis that is only temporary are injected as a preliminary and separate action prior to oviposition, and in some taxa the venom has been shown to switch the host, which initially recovers to resume feeding, to a prepupal stage in which it is arrested (Shaw 1981, 1983). This includes cocoon formation and the secretion of pupal cuticle, both of which happen precociously (i.e. an instar early) if the host is attacked in its nominally penultimate larval instar, and two koinobiont cyclostome braconid genera, the ectopar-

asitic *Rhysipolis* Foerster (Rhysipolinae) and the endoparasitic *Clinocentrus* Haliday (Rogadinae), were found to employ venoms having identical effects on their hosts. Although these taxa are not regarded as extremely closely related, the suggestion (Shaw 1983) that on at least one occasion the evolution of endoparasitism from ectoparasitoid ancestry within the Exothecinae-Rhysipolinae-Rogadinae group of subfamilies was enabled as a result of these controlling venom systems, which arose originally as adaptations to the host's feeding and pupation biology, has been supported by other evidence (Whitfield 1992).

Gauld (1988) envisaged that within the Ichneumonidae idiobiont endoparasitism arose from idiobiont ectoparasitic ancestry, and koinobiont endoparasitism from koinobiont ectoparasitic ancestry. The mechanisms for such transitions remain uncertain but it is possible in principal that the latter route may have involved venom systems similar to those seen in some cyclostome Braconidae. However, evidence for such venom effects in Ichneumonidae has not been directly sought, although it is known that in some endoparasitoid subfamilies (particularly Campopleginae) complex physiological processes ensue from substances injected simultaneously with eggs. Three extant groups of koinobiont ectoparasitoid Ichneumonidae are known: Adelognathinae (most investigated species, parasitoids of sawfly larvae); the *Polysphincta* Gravenhorst genus-group (= Polysphinctini sensu Townes 1969, but see Wahl and Gauld 1998) of the Pimplinae (parasitising spiders); and Tryphoninae (parasitising sawfly and Lepidoptera larvae). At least some members of each group are known to inject venoms causing temporary paralysis as separate actions prior to oviposition (as in *Rhysipolis* and the endoparasitic *Clinocentrus*), offering particularly convenient opportunities to interrupt the oviposition sequence so as to observe any venom effects

in isolation. Indications exist (see Discussion) that in Adelognathinae and the *Polysphincta* genus-group these venom systems are innocuous, in the sense of causing only temporary paralysis rather than exerting lasting control over the host's development, but for the third group, Tryphoninae, essential information is lacking. Because Tryphoninae generally kill the host as a prepupa, the possibility that they employ venoms that disrupt processes normally under endocrine control (as with *Rhysipolis* and *Clinocentrus*) seemed particularly worth examining.

Tryphonines are predominantly (at least at the generic level) parasitic on Symphyta but the family contains the tribe Phytodietini, including the genera *Netelia* and *Phytodietus* Gravenhorst, which attack Lepidoptera larvae. In view of the ease of culturing their hosts, species of *Netelia* were chosen for study. *Netelia* species anchor their highly characteristic stalked black, and typically glossy, eggs externally on the thoracic segments of active exposed Lepidoptera larvae that are normally consumed only after constructing their pupation chambers (i.e. as prepupae). The genus contains species for which temporary paralysis of the host has been reported as well as others that apparently oviposit without having this effect (e.g. Stenton 1910, Shevyrev 1912, Vance 1927). While many observations have been published on the egg structure and larval development of *Netelia* (e.g. Stenton 1910, Cushman 1913, Strickland 1923, Vance 1927, Guppy 1961, Danks *et al.* 1979, Ellis 1998), the possibility that venoms may have arresting effects beyond that of causing temporary paralysis appears never to have been considered.

Yu and Horstmann (1997) recognise eleven subgenera of *Netelia* of which four, *Netelia* s. str., *Paropheltes* Cameron, *Bessobates* Townes, Townes and Gupta, and *Parabates* Foerster, are known to occur in Britain. This paper records the outcome of experiments to investigate possible long-

term venom effects in the first three of these subgenera of *Netelia*, and notes also other aspects of parasitoid behaviour and host development.

The following species were used in experiments (comment on phenology and host range is supported by reared material in the National Museums of Scotland (NMS)): *Netelia (Bessobates) cristata* (Thomson), a plurivoltine and normally solitary parasitoid of various exposed Noctuidae; *N. (B.) latungula* (Thomson), a univoltine, solitary and regular parasitoid of *Operophtera brumata* (Linnaeus), sometimes reared also from other spring-feeding arboreal Geometridae; *N. (Netelia) vinulae* (Scopoli) (= *cephalotes* (Holmgren)), a univoltine, gregarious and regular parasitoid of *Cerura vinula* (Linnaeus) (Notodontidae); *N. (Paropheltes) tarsata* (Brischke), a plurivoltine solitary parasitoid of small Geometridae, especially species of *Eupithecia* Curtis; and *N. (P.) ?thomsoni* (Brauns), in Britain a widespread plurivoltine parasitoid of *Xanthorhoe fluctuata* (Linnaeus) and other similarly small to medium sized Geometridae. The latter comes closer to *N. (P.) inedita* (Kokujev) than to *thomsoni* in Delrio (1975), but Yu and Horstmann (1998) give the latter as a senior synonym. Delrio (1975) records *thomsoni* from Geometridae including *Eupithecia* species.

METHODS

All livestock originated from England. Adult parasitoids were identified by reference to Delrio (1975), and voucher specimens are deposited in the NMS.

Netelia (Bessobates) cristata. One female (unmated) reared from *Cosmia trapezina* (Linnaeus) from Hartslock, Oxfordshire, was used in experiments. The experimental host, *Lacanobia oleracea* (Linnaeus), was reared from the previous generation in culture and fed on leaves of *Taraxacum* Weber and *Crataegus* Linnaeus.

Netelia (Bessobates) latungula. Adults used in experiments were collected by sweeping *Corylus* Linnaeus at Hell Cop-

pice, Buckinghamshire (two females), and reared from *O. brumata* from Gait Barrows NNR, Lancashire (one female, unmated). Experimental hosts were wild-collected larvae of *O. brumata* (*Corylus*, Hell Coppice; *Corylus*, Pamber Forest, Hampshire; and *Salix* Linnaeus, Otmoor, Oxfordshire), and cultured *O. brumata* and *Theria primaria* (Haworth) from the previous generation. All hosts were fed on leaves of *Crataegus*. Some *O. brumata* larvae bearing eggs of *N. latungula* when collected were also investigated.

Netelia (Netelia) vinulae. Parasitised larvae of *C. vinula*, collected at Druridge Bay, Northumbria, were received from H. A. Ellis (cf. Ellis 1998) and provided the adult *N. vinulae* used the following year. Five females (at least two mated and at least two virgin) were involved in experiments. Larvae of the experimental host, *C. vinula*, were obtained from livestock dealers (ex culture) and fed on leaves of *Salix*.

Netelia (Paropheltes) tarsata. One female (unmated) reared from *Eupithecia absinthiata* (Clerck) from Sheffield, Yorkshire (received from T. H. Ford) was used in experiments. The experimental host, *Eupithecia vulgata* (Haworth), was cultured from the previous generation and fed on leaves of *Crataegus*.

Netelia (Paropheltes) ?thomsoni. One female (unmated) reared from *Xanthorhoe fluctuata* from Hampstead Heath, London (received from R. A. Softly) was used in experiments. *Eupithecia nanata* (Hübner), cultured from the previous generation and fed on *Calluna* Salisbury, and *Eupithecia* sp. collected wild from *Quercus* Linnaeus at Pamber Forest, Hampshire were experimental hosts.

All female parasitoids were seen to feed on honey: water (ca 1:3), with which they were kept at all times in corked glass tubes or clear plastic boxes (see below) apart from the brief periods of experimental manipulation. Lepidoptera larvae were fed in ca 16 × 8 × 6cm closed clear plastic boxes lined with copious absorbent tissue

paper. All livestock was kept in an un-heated, detached and fully shaded out-door shed under conditions of natural temperature and daylength except during experiments under observation.

Experimental exposures of hosts to par-asitoids were done under observation (ex-cept for some with N. (B.) cristata—see Re-sults) in 2.5 × 7.5 cm corked glass tubes (N. (B.) latungula and the two N. (Paro-pheltes) species), or in ca 16 × 8 × 6 cm clear plastic boxes (N. (B.) cristata and N. (N.) vinulae).

RESULTS

Netelia (Bessobates) cristata.—Eggs were mature by the twelfth day after adult emergence. Egg dumping was not seen, probably because the single parasitoid ob-served was never deprived of hosts for long. This species is almost completely nocturnal and only four parasitisations (one with successful non-destructive con-current host-feeding—see Jervis and Kidd 1986 for explanation of these terms) and one further non-destructive but non-con-current host-feeding event were observed directly. For oviposition the female grasped the late final instar host with all six legs, oriented head to tail, and moved backwards along the host's body towards its head, then rapidly oviposited on a tho-racic segment without separately stinging the host. In three cases the female then tried to bite the host mid-dorsally, pre-sumably in order to host-feed, but in each case the host writhed furiously and she was thrown off. In the only other ovipo-sition sequence observed the parasitoid laid a second egg, without releasing the host, before successfully host-feeding on haemolymph via a wound made with the mandibles. Host-feeding without oviposi-tion was observed on one host (earlier in its final instar)—as in oviposition sequenc-es the host was grasped tightly with all six legs, and the female chewed a wound at which she fed midway along the host's dorsum, at the same time curling the tip of her abdomen towards the host's thorac-ic segments but without ovipositing.

Otherwise parasitised hosts were ob-tained by keeping the single female over-night with 5–7 hosts in a cardboard shoe box (ca 23 × 13 × 10 cm) closed with a sheet of glass, and removing the contents the following morning. Penultimate instar hosts, and those early in their final instars, never received eggs, but over a thirteen day period the female laid 54 eggs (50 of them in the last nine days) on late final instar larvae until the experiment was cur-tailed for want of further host larvae, al-though the female parasitoid lived for about another 55 days (ca 80 as an adult in all). At the end of a night, sixteen hosts had received one egg; nine had received two; two had received four; and one had received twelve eggs (generally, some hosts had also received no eggs, but as the smaller hosts were clearly less attractive there is no scope to analyse egg distribu-tion). The host with twelve eggs was reared and five parasitoid cocoons result-ed; the two hosts with four eggs similarly each resulted in two cocoons; two of four hosts reared with two eggs yielded two cocoons and the other two a single cocoon each; and all seven hosts reared with sin-gle eggs duly yielded the single parasitoid cocoon expected. This suggests that com-petition causes some mortality but that broods of two will regularly be fully via-ble.

Nine hosts from which eggs were man-ually removed, and also one host bearing an egg that failed to hatch, produced pu-pae and then adult moths, apparently nor-mally. Two eggs on one host were allowed to hatch (which occurred two and five days after oviposition) and on the sixth day after oviposition the two larvae (four and one days old) were destroyed, after which the host pupated and became an adult moth. Two other hosts each bearing one parasitoid were reared for eight days after oviposition, by which time parasitoid larvae were ca six days old and ca three

times as long as the egg, before the parasitoid larvae were killed. Both hosts became prepupal within two days, but died without pupating, apparently in an arrested state.

In all wild and experimental rearings permitted to reach such a state, the host was consumed as a prepupa in its prepared pupation site, in which the parasitoid cocoon is constructed. The generation that overwinters does so in the cocoon.

Netelia (Bessobates) latungula.—Eggs were mature five days after adult emergence, and started to be dumped ca ten days after emergence in the absence of hosts. If kept humid dumped eggs later split to reveal a living first instar larva, just as did eggs laid on hosts. Penultimate instar hosts (both *O. brumata* and *T. primaria*) were rejected consistently, although sometimes investigated. Oviposition attacks on final instar hosts are evidently provoked by movement: hosts remaining still when contacted by the female were ignored. There was no pre-oviposition sting, the adult parasitoid rapidly pouncing on the host and ovipositing singly on one of the host's thoracic segments (very rarely at the host's caudal end: the two eggs laid in this position were quickly lost, possibly because the host could reach them with its mouthparts). After all seven ovipositions witnessed the host was then released, without the parasitoid attempting to host-feed. Some interactions, however, took a different course: in five cases the female parasitoid grasped a final instar *O. brumata* larva, jabbing it once with its ovipositor midway along its dorsum. Four of these larvae were then released and abandoned, but the parasitoid chewed a wound on the other from which it fed on haemolymph. No paralysis was evident.

Eggs were cut off eleven parasitised *O. brumata* larvae and two *T. primaria,* all of which pupated and produced adult moths. The five *O. brumata* which had been possibly stung but not oviposited onto also pupated and produced adult moths apparently normally.

In a heavily parasitised field sample of final instar *O. brumata* larvae collected from *Corylus* on 7.vi.1979 at Hell Coppice, Buckinghamshire, 15 bore no eggs, 19 had one egg, and nine carried two eggs of *N. (B.) latungula.* Five of the latter nine produced single *N. (B.) latungula* cocoons (the other four produced other parasitoids preemptively), showing that this species is probably strictly solitary but apparently incapable of rejecting already parasitised hosts.

In all wild and experimental rearings permitted to reach such a state, the host was consumed as a prepupa in its prepared pupation site, and the parasitoid overwintered there in its own cocoon.

Netelia (Netelia) vinulae.—Two copulations each of about four minutes duration were observed: in both cases the male climbed on the dorsum of the female, which was standing on a horizontal surface, so that the copula was orientated head to head. This contrasts with the account of copulation given by Vance (1927) for *N. (N.) spinipes* (Cushman).

Female parasitoids contained mature eggs from about the eighth day after their emergence, and by the eleventh day females having had no access to hosts started to dump eggs on the sides of the container. Such eggs, if kept humid, later split to reveal the first instar larva, just as eggs placed on hosts. The females were offered both penultimate and final instar larvae, attacking the former (including those in proecdysis/apolysis between these instars) very much more readily. They advanced on hosts at first rather cautiously, making repeated stinging attacks with brief (rarely as long as a second) insertions of the ovipositor, usually in central positions along the host's body. The hosts, which at first attempted to defend themselves by thrashing and sometimes daubing oral secretions, were gradually subdued; those in the penultimate instar in

particular becoming markedly incapacitated, though not fully paralysed. The female then sometimes rejected hosts (in both penultimate and final instars) in which she had invested considerably (as many as ten stinging attacks) without ovipositing, or else she climbed onto the host and commenced oviposition onto thoracic segments. Each site for anchoring an egg appeared to be chosen with some deliberation. After the ovipositor tip was inserted through the host's cuticle it took approximately half a second for the egg to slide down the outside of the ovipositor to be anchored into the epidermis by its stalk, which travels down the ovipositor shaft internally. Host movement as it recovered during the egg-laying process greatly inhibited the female, and this may impose a strong limit to brood size (about 4–8 eggs seems usual). Following oviposition, the female usually fed on host haemolymph through a wound which it chewed with its mandibles mid-way along the host's dorsum. Hosts that were stung but then rejected were not fed on in this way, and haemolymph oozing from stinging sites was not imbibed. The behaviour of females towards hosts before their penultimate instar was not investigated. During host ecdysis eggs anchored into the epidermis of penultimate instar hosts easily tear through the cuticle being sloughed and losses are normally extremely low.

Three penultimate instar hosts that had suffered stinging attacks without oviposition, and three penultimate instar hosts on which oviposition had also occurred but the progeny was destroyed, were reared to investigate the effects of venom. All six pupated and produced adult moths contemporaneously with controls.

In all wild and experimental rearings permitted to reach such a state, the host was consumed as a prepupa in its prepared pupation site, and the parasitoids overwinter there in their own cocoons.

Netelia (Paropheltes) tarsata.—The female parasitoid lived as an adult from 5.vi until 24.ix, a period of 111 days. Hosts were not offered until the parasitoid's 60th day of adult life. An unknown number of eggs had been dumped but, once experiments commenced, further egg dumping was not seen, probably because the female was not then deprived of hosts. Indeed, on one occasion an egg that was clearly immature (greenish grey rather than the usual black in colour) was laid on a host, but this and also several others of the eggs laid failed to anchor adequately and were lost, presumably because the chorion had not sufficiently hardened. The eggs are more or less coriacious and matt, unlike the shiny eggs seen in the species of the subgenera *Netelia* and *Bessobates* here studied. Final instar hosts were greatly preferred, though some ovipositions occurred on penultimate instar hosts (including one in the proecdysis/apolysis preceding the final instar). Hosts were stung once, with an insertion of the ovipositor into an abdominal position, causing partial temporary paralysis. The parasitoid then oviposited once onto a thoracic segment, and subsequently nearly always chewed a wound midway along the host's back from which it fed on haemolymph. In one case host-feeding commenced before oviposition and continued during it and for a time afterwards. Host-feeding was often so heavy (green fluid greatly distending the parasitoid's metasoma) that the female was unable to move with agility and did not attack further hosts until the following day. A limited capacity to deal with more than two hosts per day was also evidenced by her laying immature eggs (see above) and sometimes failing to produce enough venom to subdue hosts to the point that she was willing to oviposit on them.

Three penultimate instar and two final instar hosts that had received paralysing venom but no eggs, and three further final instar hosts that had also received eggs which were then removed, all pupated and produced adult moths apparently

normally. An additional four final instar and one penultimate instar hosts from which eggs had been removed died of a fungal disease that also affected some unexposed control larvae.

In all wild and experimental rearings permitted to reach such a state, the host was consumed as a prepupa in its prepared pupation site, and the generation that overwinters does so in the cocoon.

Netelia (Paropheltes) ?thomsoni.—Eggs (which are similar to those of *N. (P.) tarsata*) were dumped after several days of host deprivation. Two similar ovipositions were observed, on a final instar *Eupithecia nanata* and on a final instar *Eupithecia* sp. The female stung the host (10–20 seconds insertion) in an abdominal position causing rather full temporary paralysis; she then oviposited singly onto a thoracic segment, when the body of the egg was seen to slide down the outside of the ovipositor during ca 1 second; and subsequently she chewed a wound midway along the host's back from which she fed on haemolymph. The cultured host (*E. nanata*) died of a fungal disease and the other (wild collected) host proved to be already parasitised. No further trials could be conducted.

In all wild rearings the host was consumed as a prepupa in its prepared pupation site, and the generation that overwinters does so in the cocoon.

DISCUSSION

Pre-ovipostion venoms causing a degree of temporary paralysis have been reported in several species of the subgenus *Netelia* previously (Shevyrev 1912, Cushman 1926, Vance 1927) and studies on species of the subgenus *Bessobates* have either stated that no paralysis is caused (Shevyrev 1912) or been reported without mention of it (Stenton 1910, whose account of his parasitoid of *O. brumata* almost certainly refers not to *N. (B.) virgata* but to *N. (B.) latungula*, as it is clear from material in NMS that C. Morley, who had determined Stenton's specimens, regularly mis-

identified *latungula* as *virgatus*). The present study concurs with these earlier findings, but the biology of the subgenus *Paropheltes* does not seem to have been previously studied even to this extent.

The main finding of the present work is that no substances controlling host development are injected during the oviposition process in any of the three subgenera investigated, since hosts from which eggs had been removed developed normally. Thus the venoms injected prior to oviposition in the subgenera *Netelia* and *Paropheltes* have no effect on the host other than to subdue it, simply allowing the female parasitoid to place eggs accurately using its appreciably exserted ovipositor. Species of the subgenus *Bessobates*, which have markedly shorter ovipositors, oviposit more rapidly without immobilising the host other than physically by grasping it. Oviposition has been described for one species in the genus *Phytodietus*, the putative sister genus to *Netelia*, and a venom causing temporary paralysis, often requiring several insertions of the ovipositor as in *N. (N.) vinulae*, was observed (Simmonds, 1947). This may suggest that the use of a paralysing venom is plesiomorphic in *Netelia* (see also Kasparyan 1973 [1981:49]).

In all tribes of Tryphoninae other than Idiogrammatini and Phytodietini eggs ready for oviposition are commonly carried externally on the ovipositor until a host is found (pers. obs.; but for Ankylophonini and Sphinctini, A. Bennett pers. comm.). In the studied subgenera of *Netelia* (Phytodietini) this behaviour is not approached: in all three subgenera the egg did not start to issue from the parasitoid's genital opening until the ovipositor was inserted for attaching the egg to the host. Although observations of oviposition in the tribes carrying eggs on the ovipositor are rather sparse, only the exenterine *Exenterus abruptorius* (Thunberg) has been reported to cause temporary paralysis (Morris 1937). This observation would indicate

that carrying the egg on the ovipositor (which it is here presumed to be the case in *E. abruptorius*, though it is not explicitly stated to be so by Morris) does not preclude the use of a paralysing venom, but the lack of records of paralysis by Exenterini and Tryphonini stemming from other studies (see Kasparyan 1973 [1981:49]) suggests that it is not usual in these tribes. The situation is uncertain in Idiogrammatini: despite some speculation by Cushman (1937) and an erroneous citation by Kasparyan (1973 [1981: 49]), the process of oviposition in *Idiogramma* Foerster seems not to have been reported, but eggs have not been found to be carried externally on the ovipositor (A. Bennett pers. comm.).

Thus there remains no evidence that Tryphoninae deploy venom systems that have effects other than to subdue the host while oviposition takes place, although egg-removal experiments have been conducted only for *Netelia* and should be carried out for other tribes. Furthermore the other two known groups of koinobiont ectoparasitic Ichneumonidae, i.e. some Adelognathinae and the *Polysphincta* genus-group, appear to employ pre-oviposition venoms that, as in two of the subgenera of *Netelia* studied here, have only this subduing effect. Adelognathinae consists of the single genus *Adelognathus* Holmgren. One species, *A. chrysopygus* (Gravenhorst) (= *granulatus* Perkins), is a typical idiobiont, employing venom for the permanent paralysis of its host (Rahoo and Luff 1987, confirmed by F.D. Bennett pers. comm.). However, most *Adelognathus* species appear to be koinobionts (Fitton *et al.* 1982), and one thoroughly investigated but undescribed species employs a venom causing temporary paralysis, facilitating oviposition, but which has no other apparent effect: hosts intercepted after paralysis but before oviposition, as also hosts from which eggs were removed, recover to develop to the adult stage normally (Shaw unpublished). In the *Polysphincta* genus-group temporary paralysis of the

host prior to oviposition is probably common to all genera and has been described by Cushman (1926) for *Zatypota parva* (Cresson) and by Eberhard (2000a) for *Hymenoepicnemis argyraphaga* Gauld. In the latter species Eberhard (2000a) found that the venom appears to have no long term effect on host development. This appears to be generally true of the *Polysphincta* genus-group: I have on several occasions reared to adulthood immature spiders bearing parasitoid larvae at the time of collection that for one reason or another subsequently died young, to check that host development was unimpaired, and in every case (involving the parasitoid genera *Polysphincta*, *Dreisbachia* Townes, *Schizopyga* Gravenhorst, *Zatypota* Foerster and *Acrodactyla* Haliday) it was found to be so. Thus, although more investigation of Tryphoninae is warranted, it appears that none of the extant groups of koinobiont ectoparasitic Ichneumonidae employs a venom system with an effect remotely similar to that seen in the cyclostome Braconidae, which seems to have been so important in the evolution of endoparasitism within at least one lineage (Shaw 1983, Whitfield 1992).

Whereas the two studied species of the subgenus *Bessobates* will normally oviposit only on final instar larvae, and one species clearly avoided inactive hosts, the single species studied in the subgenus *Netelia*, *N. (N.) vinulae*, which is unusual in both the subgenus and the genus as a whole for being fully gregarious, preferred hosts in the penultimate instar (see also Ellis 1998) and was very willing to attack them when they were inactive in the proecdysis/apolysis between that and the final instar. Other studied species of the subgenus *Netelia* are solitary, and, although apparently preferring final instar hosts, also commonly oviposit on penultimate instar hosts (Guppy 1961, Danks *et al.* 1979). At least one of the species of the subgenus *Paropheltes* investigated here also seems to be somewhat plastic in this respect.

Species of all three subgenera dumped eggs in the absence of hosts, as has been observed before in the subgenera *Netelia* (Vance 1927) and *Bessobates* (Stenton 1910). This presumably happens because embryonic development is independent of the host, contrary to Stenton's (1910) view, and eggs in these two subgenera (not investigated for *Paropheltes*) can "hatch" even if dumped. The degree of maturity of eggs that are laid on hosts varies considerably and this may have a bearing on the time that elapses before they hatch, although, as dumped eggs tend to dry up without hatching unless kept humid, prevailing humidity is clearly also important and may explain why, in the wild, eggs of many Tryphoninae typically hatch only after the host has constructed its pupation chamber (cf Clausen, 1932). An egg-hatching/larval development response to the conditions of high humidity developing in the host cocoon thus may be the principle means of ensuring the commencement of parasitoid development at the appropriate host stage in Tryphoninae, in contrast to koinobiont ectoparasitoid taxa such as *Rhysipolis* (Shaw 1983) and the eulophid *Eulophus ramicornis* (Fabricius) (Shaw 1981, as *E. larvarum* (Linnaeus)) which achieve this through their venoms. Hosts parasitised by *Netelia* collected while they are still feeding in the wild almost invariably bear only unhatched eggs (pers. obs.), though once brought under captive conditions involving the high humidity of closed containers the eggs frequently hatch, and the larvae start to develop, before the host constructs its pupation chamber. In extreme cases (cf. that illustrated by Ellis 1998 for *N. (N.) vinulae*) this can lead to the host being overwhelmed prematurely and a failure of the parasitoids to survive. The extent to which larval development *per se* may depend on high humidity would be worth investigating.

Guppy (1961) and, possibly following him, Danks *et al.* (1979), writing on species in the subgenus *Netelia*, have stated that the host's development is "arrested" as a prepupa as the parasitoid starts to feed, but without giving reasons for that conclusion. In one case for one species of the subgenus *Bessobates* studied, two parasitoid larvae on one host were allowed to feed for up to 4 days before they were killed, and the host then went on to pupate normally. In two further cases involving this host and parasitoid species the parasitoid larvae were killed after 6 days, when they were still too small to have caused much damage to the larval hosts, and both hosts then burrowed for pupation but died as prepupae in what seemed to be an arrested state. The interesting possibility that the larva of *Netelia* species does indeed inhibit host development, other than by causing damage merely in the course of feeding, is worthy of further investigation, though it appears not to be capable of this in the earliest days of its feeding. Eberhard (2000a, b) gives evidence of control over the host, apparently through chemicals produced by the parasitoid larva, in *Hymenoepimecis argyraphaga* of the *Polysphincta* genus-group.

The use of mandibles, rather than the ovipositor, to make the wound necessary for non-destructive host-feeding has been noted before in the subgenus *Netelia* (Vance 1927), and was common to all three of the subgenera studied. In one subgenus, *Bessobates*, it appears sometimes (or possibly usually) to involve host individuals other than those used for oviposition, perhaps because a different grip on an unsubdued host is required. In contrast, in the subgenera *Netelia* and *Paropheltes* non-destructive host-feeding is concurrent (cf. Jervis and Kidd 1986) and normally occurs following each oviposition. The behaviour in *Netelia* s.l. is in marked contrast to that recorded by Simmonds (1947) for *Phytodietus rufipes pulcherrimus* (Cresson), in which feeding was said to take place on the fluids that exuded from the puncture wound (or wounds) made by the ovipos-

itor in the course of injecting venom, and furthermore if the adult fed from the host it did so before ovipositing on it, rather than afterwards as in the subgenera *Netelia* and (normally) *Paropheltes*. Remarkably, Zinnert (1969) noted that *Erromenus calcator* (Müller) (Tryphonini) wounds the host with its mandibles but does not then feed on the exuding haemolymph. Other Ichneumonidae known to make feeding wounds with their mandibles include the tryphonine *Eridolius rufonotatus* (Holmgren) (Exenterinae) (Carl 1976), the pimpline *Exeristes roborator* (Fabricius) (Fox 1927) and an undescribed species of *Adelognathus* (Shaw unpublished). Elsewhere in the Hymenoptera it is known in Eulophidae, Scelionidae and particularly in parasitoid aculeate groups (cf. Jervis and Kidd 1986).

ACKNOWLEDGMENTS

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