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ON THE LIFE CYCLE AND PARASITISM OF JOHNSTONIANA ERRANS (JOHNSTON) 1852
(ACARI: PROSTIGMATA: PARASITENGONAE).

BY A. WOHLTMANN*

SUMMARY: Johnstoniana errans (Johnston) (Acari: Parasitengonae) inhabits the margins of limnic waters in forested areas. The active instars, deutonymph and adult, are nocturnal and found mainly in wet moss covering rotting wood where they prey predominantly on larvae and pupae of Diptera. The larvae, which exclusively parasitize adults of Tipula spp., recognize and rest on the pupa. When the fly emerges from the pupa, the larvae transfer to the fly and begin to feed. The life-cycle of J. errans is usually semiunivoltine, some females may reproduce more than once. Females and the obligatory diapausing eggs are the usually hibernating instars.

SUMMARY: Johnstoniana errans (Johnston) (Acari: Parasitengonae) inhabits the margins of limnic waters in forested areas. The active instars, deutonymph and adult, are nocturnal and found mainly in wet moss covering rotting wood where they prey predominantly on larvae and pupae of Diptera. The larvae, which exclusively parasitize adults of Tipula spp., recognize and rest on the pupa. When the fly emerges from the pupa, the larvae transfer to the fly and begin to feed. The life-cycle of J. errans is usually semiunivoltine, some females may reproduce more than once. Females and the obligatory diapausing eggs are the usually hibernating instars.


RESUME: Johnstoniana errans (Johnston) (Acari: Parasitengonae) habite le bord des mares des aires forestières. Les stades deutonymphaires et adultes actifs sont nocturnes et se rencontrent principalement dans la mousse humide recouvrant le bois en putréfaction où ils chassent essentiellement des larves et des pupes de Diptères. Les larves qui sont exclusivement parasites de Tipula spp. adultes, en reconnaissent les pupes et demeurent sur elles. Lorsque le moustique émerge de la pupe, les larves passent sur le moustique et commencent à se gorger. Le cycle de vie de J. errans est habituellement semiunivoltin, quelques femelles pouvant se reproduire plus d'une fois. Les femelles et les œufs en diapause obligatoire sont habituellement les stades qui hibernent.

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INTRODUCTION

*Johnstoniana errans* (Johnston) is the type-species of the genus *Johnstoniana* George, which is the type-genus for the family Johnstonianidae Newell. Although *J. errans* is known to be widely dispersed throughout Europe, it nevertheless appears to occur in low abundances (COOREMAN, 1949). Reports of this species have been for extremely wet biotopes only (FRANKE, 1940, COOREMAN, 1949, WILLMANN, 1951), and little is known of its biology and phenology (especially its parasitism, life history and seasonal abundance). Moreover, most of the older literature is unreliable because of taxonomic inconsistencies. Larval parasitism and the development from egg to reproducing adult under defined conditions of *J. errans* are described here and compared with other johnstonianid species.

MATERIAL AND METHODS

Mites were captured at two localities in Northern Germany: I. “Osterviertelmoor”, Northern Germany (53°36’30” N, 08°36’00” E): a temporarily flooded fen, about 14,500 m² in area with constantly high humidities and covered with rotting wood. The vegetation of this locality is dominated by *Alnus glutinosa* and *Betula pubescens*. II. “Stoteler Wald”, Northern Germany (53°12’20” N, 08°45’30” E): a forested trough about 150 m² in area and temporarily flooded by a nearby creek. The locality was wet all year round. The dominant species within the vegetation were *Alnus glutinosa* and *Urtica dioica*. The trough is surrounded by a *Quercus-Fagus* forest.

The mites were hand-captured, the parasitic larvae being caught on their hosts with the aid of a sweep-net. For laboratory-rearing experiments, plaster-charcoal filled polystyrene boxes (25 x 25 x 20 mm) were used. Unless otherwise stated, individuals were kept in a light-thermostat at 15°C (± 1°C) and a 12h/12h light/dark cycle. Parasitism experiments were done at 20°C; 5-12 larvae of *J. errans* kept in a rearing box were exposed to 2-3 potential hosts for at least 4 days. All boxes were checked daily.

Hygropreference: Within a circular humidity gradient apparatus (BARLOW & NICHOLLS, 1961, modified) levels of 33 %, 55.5 %, 76 %, 93.5 % and 100 % rh (relative air-humidity) were established. 10 adults were introduced in the chamber with lowest air-humidity (33 %), and the observation started 15 minutes thereafter. Preference was calculated from the actual distributions of the individuals at the respective humidities in 10 min intervals over a period of 4 hours. Experiments were carried out in a light-thermostat at 15°C ± 1°C at darkness and without any food supply.

Phototaxy: Glass tubes 10 cm long and 2.5 cm in diameter were used to test phototactical behaviour by illumination with a light source from alternating positions.

The identification of all instars after clearing and mounting was done according to ROBAUX (1970).

RESULTS

Phenology

In total, 171 larvae and 192 postlarval instars of *J. errans* were found for the period 1990 to 1994 at the locations examined. The capture of the mobile stages, larva, deutonymph and adult proved to be quite effective, but the immobile stages (egg, prelarva, proto- and tritonymph) were difficult to find and only occasional individuals were discovered concealed within moss or some other substratum. The population density was generally low; at the “Stoteler Wald” (150 m²) the number of hibernating adults was estimated to be 90 during March and April 1994.

The substratum where *J. errans* was found was always wet. At less hygric places in the surrounding area with fluctuating humidities, no *J. errans* were found. All ontogenetic instars of *J. errans*, except parasitizing larvae, were found in and beneath moss covering the bark of rotting wood. When temperatures fell below 0°C, adults disappeared into natural cavities within the soil. During this phase, capture proved difficult and only few specimens were found. As soon as the frozen litter thawed out, adults re-entered the moss and were observed to
congregate in groups of 5-17 individuals with their gnathosomata directed against each other. However, during late spring and summer the adults and deutonymphs were solitary.

Although the differences in dispersion of instars clearly influenced the success rate of capture (e.g. the failure to find the hidden adults during December/January), the annual presence of certain instars is evident. In general, the annual occurrence of the active instars was about the same (Fig. 1). Males were prevalent from August to September. Females were prevalent all year round, the maximum abundances being in autumn and spring. Eggs were found in early June. Larvae of *J. errans* appeared simultaneously in May at the same places where the adults were found. They ran about on the bark, examining cavities in the substratum. The larvae aggregated near to or on the body of the pupae of *Tipula* spp. (Diptera: Nematocera). From late May to early July adult crane-flies carried parasitizing *J. errans* larvae attached to the ventral region of the host’s thorax (Table 1). A host carried 1 to 69 larvae. On one occasion 1 larva of *J. errans* was found parasitizing a *Tipula unca unca* Wiedemann adult which was also parasitized by 6 larvae of *Euthyas truncata* (Neum.) (Parasitengonae: Hydragchnidia). Parasitism on other insects or mites was not observed, even though several species of Limoniidae (of which many adults of *Limonia phragmitides* Schrank were parasitized by larvae of *Johnstoniana tuberculata* Schweizer and *Calyptosoma velutinus* (Müller)) and other Diptera were present at that time. Deutonymphs of *J. errans* were collected from June to October. In June, the deutonymphs migrated to locations previously flooded, but now dried up and permanently inhabited by thyasid water mites. In the field, deutonymphs were seen feeding on *Thyas* sp. and larvae of *Tipula* sp., even though the larva was about ten times bigger than the mite. Two deutonymphs found during June/July and one adult found in August were parasitized by larvae of another johnstonianid species identified to be *Johnstoniana parva* Wendt. In August, tritonymphs and males were found. Freshly-emerged females appeared 1-2 weeks after the first males were seen.

**Laboratory results**

*Johnstoniana errans* is one of the larger Parasitengonae, the average fresh body weight of adults being 4.9 mg (n = 15, maximum 7 mg). In tests for hygropreference, adults selected high humidities (Fig. 2), though they avoided flooding. The adults and deutonymphs of *J. errans* were active at night, but hid beneath bark during day-time. When disturbed during day-time, they immediately tried to hide again, but active burrowing was not observed. However, adults used cavities in the soil formed by rotting vegetation or soil dwelling animals. Peristaltic body motions, combined with the backwardly-arranged body setae, promoted forward movement of the mites in such cavities. Deutonymphs and adults fed on larvae and pupae
Abundance in %

Fig. 2: Humidity preference of adult Johnstoniana errans (Johnston) 1852. Bars indicate observations (in percent of total observations) at the respective humidities.

Table 1: Parasitic associations of Johnstoniana errans (Johnston) 1852 larvae. All data obtained from hosts captured in the field.

<table>
<thead>
<tr>
<th>Date</th>
<th>Host</th>
<th>No. infected/No. of all Tipula spp.</th>
<th>No. larvae/host</th>
<th>Attachment site on host</th>
</tr>
</thead>
<tbody>
<tr>
<td>22.05</td>
<td>Tipula m. maxima</td>
<td>3/5</td>
<td>31</td>
<td>Thorax I, ventral</td>
</tr>
<tr>
<td>22.05</td>
<td>Tipula m. maxima</td>
<td>3/3</td>
<td>69</td>
<td>Thorax I, ventrolateral</td>
</tr>
<tr>
<td>28.05</td>
<td>Tipula m. maxima</td>
<td>3/5</td>
<td>2</td>
<td>Thorax I, ventral</td>
</tr>
<tr>
<td>28.05</td>
<td>Tipula m. maxima</td>
<td>2/4</td>
<td>29</td>
<td>Thorax I, ventral</td>
</tr>
<tr>
<td>08.06</td>
<td>Tipula m. maxima</td>
<td>1/1</td>
<td>4</td>
<td>Thorax I, ventral</td>
</tr>
<tr>
<td>10.07</td>
<td>Tipula u. unca</td>
<td>1/2</td>
<td>1</td>
<td>Thorax I, ventral</td>
</tr>
</tbody>
</table>

of ants, Tipulidae and other Diptera, and the pupae of Rhagonycha sp. (Coleoptera: Cantharidae). Occasionally they also prey on adults and deutonymphs of Trombidium holosericeum (L.), Calyptostoma velutinus and Thyas spp. (all Parasitengonae). However, they did not attack mobile arthropods like aphids, collemboles, woodlice and adults of several Diptera, Cantharidae and Miridae. Starved J. errans regularly cannibalised various conspecific instars, but never eggs. Before or during the reproductive phase, adults survived without food on average for 16 days (20°C, max. 31 days, n = 10 specimens). However, females which had completed oviposition survived for up to 60 days under the same conditions.

Males captured in the field deposited spermatoaphores in the laboratory from August to December at 20, 15 and 10°C, as described by Witte (1984). Males reared in the laboratory started spermatoaphore deposition 10-18 days after emergence, but only if they had contacted a female before. Males kept isolated since the protonymphal instar sometimes produced signal stalks, but did not deposit spermatoaphores (n = 10). Two males exposed 46 days after emergence to a female started spermatoaphore deposition shortly thereafter. Females captured in the field in spring or in autumn usually laid eggs in the laboratory a few days after capture. Laboratory-reared females took up sperm a few days after their emergence and at 15°C some
started oviposition 20 days after their emergence. Most females began laying eggs only after an incubation at 10° C for a period exceeding 2 months. Oviposition took place at 20, 15 and 10° C, mostly in darkness, the eggs preferably being pressed into the mud or some other substratum. The average oviposition period lasted 45 days, during which time 62 eggs (n = 33, max. 115, egg diameter 375 μm) were deposited singly. The reddish coloured eggs had a smooth surface. Females sometimes survived their first oviposition period and, in three cases, females that had laid eggs in June started a second oviposition in September/October after being inseminated again.

The eggs had little drought resistance, since they dried out in an hour when exposed to humidities of 55% rh. Saturated air was necessary to keep the eggs alive. Eggs kept submerged in water developed like those kept at 100% rh. No egg development took place when kept at constant 10° C (n = 50), 15° C (n = 100) or 20° C (n = 33) for up to 266 days regardless of whether the eggs were deposited in autumn or spring. The same happened when incubated at 10° C for 176 days and thereafter exposed to 20° C (n = 90). Eggs kept at constant 5° C (n = 36) developed to prelarvae only 328 days later, larvae hatched another 60 days later. Eggs incubated at 5° C for 104 days and then exposed to 10, 15 or 20° C developed to prelarvae and later on to larvae, which emerged almost simultaneously 15-25 days after temperature change. Different light conditions (0, 8, 12, 16 hours light/day) did not influence egg development. The hatched larvae reacted negatively to light and survived without hosts for up to 29 days at 15° C (Table 2). Predation or parasitism was not observed on any instars of conspecifics, nor did they attack adults of other Parasitengonae (Calypostoma velutinus, Johnstoniana spp., Trombidium holosericeum). Adults of Tipula unca unca, Limonia phragmitides and other Tipulidae were each offered to 5 J. errans larvae and, once again, no parasitism took place (n = 6) even when the mite larvae contacted the wings, legs or the abdomen of the nematocerans. Only on one occasion, when a single J. errans larva was placed on the dorsal site of the abdomen of an adult Tipula unca unca (by means of a needle), did it start sucking. A fraction of J. errans larvae (n = 12) placed in a box with larvae of T. unca unca, however, responded to the nematocerans only when they entered the pupal phase. When this happened, J. errans larvae carefully examined the whole body of the pupa with their palps. The next day 6 J. errans had formed a cluster on the soil beneath the area of the tipulid pupa where the legs of the adult became visible within the pupal skin. Three days after the pupal phase began, some J. errans larvae climbed onto the T. unca unca pupa and clustered on the ventral region of the thorax. No parasitism or feeding by the mite larvae took place during this phase. After 7 days the anterior part of the pupa split to open a longitudinal slit reaching from dorsal site to the ventral part near to the legs. As the T. unca unca adult emerged from the pupa, the mite larvae moved from the pupa and attached themselves ventrally between coxae I of the tipulid adult where they started sucking. This experiment was repeated thrice (at 20 and 15° C) and the mite larvae always behaved in the same way. When waiting motionlessly on the tipulid pupa, larvae survived up to 40 days (15° C). During the parasitic phase, which lasted 5 days in the laboratory, the larvae increased in size about 10 times. Engorged larvae dropped off their hosts and, once again, reacted negatively to light. Both observed hosts survived parasitism (like most parasitized tipulids captured in the field). The duration of the post-parasitic mobile larva depended on the availability of cavities. If no such cavities were present, the calyptostatic protonymph was found after a maximum of five days of searching, as opposed to a 24 hours period when cavities were available. Like other Johnstonianidae, the first pair of legs extended upwards at the end of the mobile phase of the larva. The protonymph lasted, on average, 16 days at 15° C (Table 2). The protonymphal skin split at the proximal end and first the gnathosoma, then legs I and II of the deutonymph became visible. Finally, the peristaltic body motions pushed the deutonymph free. Deutonymphs were fed Drosophila melanogaster larvae and various ant larvae and pupae. For one to two weeks, 1-2 Drosophila melanogaster larvae were consumed each day, then the apparently well-fed deutonymphs became less
Table 2: Johnstoniana errans (Johnston) 1852: Duration of development (in days) in the laboratory. Asterisk: data obtained on hosts kept parasitized in the field.

<table>
<thead>
<tr>
<th>Egg</th>
<th>Larva</th>
<th>Protonymph</th>
<th>Deutonymph</th>
<th>Tritonymph</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>maximal lifespan</td>
<td>parasitic phase</td>
<td>range</td>
<td>range</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20°C</td>
<td>15°C</td>
<td>20°C</td>
<td>15°C</td>
</tr>
<tr>
<td>diapause</td>
<td>max.</td>
<td>max.</td>
<td>n=10</td>
<td>n=10</td>
<td>n=80</td>
</tr>
<tr>
<td></td>
<td>20°C</td>
<td>29°C</td>
<td>5°C</td>
<td>5.5°C</td>
<td>13°C</td>
</tr>
</tbody>
</table>

active. Rather than beginning the calyptostatic tritonymph the deutonymphs fed irregularly (only 1-2 Drosophila larvae each week), until the deutonymph was, on average, 63 days old (Table 2). Food and cavities for hiding were always available. Attempts to shorten the deutonymphal phase by raising the temperature to 20°C one month after emergence failed. After 93 days 66% of the deutonymphs had reached the tritonymph at 15°C. Six of the remaining individuals were transferred to 10°C (8/16 light/darkness) where three deutonymphs started the tritonymph 25 days thereafter. Another six deutonymphs were exposed to 4°C (darkness, n=6) for 122 days. These specimens reached the tritonymph 27-72 days after re-exposure to 15°C (12/12 light/darkness). In order to start the calyptostatic tritonymph, hidden places were sought and, again, the first legs were stretched upwards.

**DISCUSSION**

The adult of Johnstoniana errans was described by Johnston (1852). For 100 years there was much confusion concerning this species, since several authors introduced new names for the species or subsumed different species under the name J. errans. Robaux (1970) cleared up the taxonomical situation by redescribing all active instars of the species, aided by laboratory-rearing. My rearings of J. errans from northern Germany confirmed his description. A comparison of reared larvae of J. errans with the larva described as Rohaultia ban- gulum Oudemans (Mus. Leiden, Cat. No. 7) verified the synonymy of these species-names.

The laboratory and phenological data support previous reports that Johnstoniana errans requires high air humidities all year round (Johnston, 1852, Franke, 1940, Cooreman, 1949, Willmann, 1951). This restriction is a general characteristic for Johnstonianidae (Newell, 1957, Schweizer & Bader, 1963, Wendl, in press). J. errans is clearly not as rare as previously believed. It is a species found only in small populations occupying wet biotopes in forested areas, containing rotting wood.

The life cycle of J. errans, based on field data and laboratory results, is shown in Fig. 3. Like other Johnstonianidae (Eggers, in press, Wohltmann & Wendl, 1996), eggs are deposited individually. The egg-diapause is obligatory and set by internal mechanisms. A chilling phase is necessary to induce the development to prelarva and larva. This type of diapause greatly resembles a hyperpause according to Müller (1992). It leads to simultaneous larval emergence in spring when tipulid pupae are abundant. The synchronization of larval emergence with host abundance by means of diapausing eggs is known from some other parasitengonids (Robaux, 1971, Wendl et al., 1994, Wohltmann et al., 1994) and seems to be common for all species of Johnstoniana (Eggers, in press).

The freshly-emerged larvae recognize only preimaginal instars of the hosts and parasitism starts only on the adults. This is known to be the case for some other parasitengonid larvae (Smith & Oliver, 1986, Wohltmann et al., 1994, Wohltmann & Wendl, 1996). It allows for host recognition of
immobile instars that are more easily discovered, recognized and occupied by the mite larvae. Moreover, this type of behaviour allows for many larvae to attach to one host, thereby increasing the chances of dispersal to new localities by the adult tipulid. Beginning the parasitic phase on a freshly-emerged adult host is advantageous especially if the adult host is short-lived like most Nematocera.

Only adult *Tipula* spp. were parasitized by the larvae of *J. errans*, which seem to be specific for the genus. The parasitized *Tipula* species are reported as restricted to wet, wooded areas (Freeman, 1967) and offer good chances for distribution of the *J. errans* larvae between such habitats. The findings confirm earlier reports of Oudemans (1912) and Cooreman (1949). Other data in the literature are in all probability erroneous, probably due to the fact that *J. errans* (syn. *Rohaultia biungulum* Oudemans) constituted the only *Johnstoniana* species described at that time for the central and northern parts of Europe. *Johnstoniana* larvae reported as parasites of several *Limonia* spp. (Rack, 1976; material deposited at Zool. Mus. Hamburg), revealed that all specimens are not *J. errans*, but *Johnstoniana tuberculata*, a smaller species recently described as a parasite of Limoniinae (Wohltmann et al., 1994). Reports of *J. errans* larvae parasitizing conspecific adults (Franke, 1940, Willmann, 1951) seem to be of the species *Johnstoniana parva* which is known to exclusively parasitize other parasiten gonids (preferably *Johnstoniana* species) (Wendt et al., 1994). Lastly, the parasitism of *Tipula longicornis* larva by *J. errans* larvae (Oudemans, cited after Willmann, 1939) is obviously wrongly cited by Willmann. However, dipteran larvae are known to be parasitized by larvae of *Johnstoniana rapax* Wendt, 1994, which also occurs in northern Germany (Eggers, in press).

The duration of the deutonymphal instar of *J. errans* in the laboratory and the field is similar and takes much longer than other species of *Johnstoniana* in the laboratory (Wendt et al., 1994, Wohltmann et al., 1994, Eggers, in press). *J. parva*, *J. rapax* and *J. tuberculata* have similar development times for the three nymphal instars (with the mobile deutonymph varying as a function of feeding success). Although the deutonymph is not diapausing (as in *Leptus beroni* Fain 1991, Wohltmann, in press), one must assume that internal factors prolong the development of the deutonymph in *J. errans*. The deutonymph can hibernate, although deutonymphs were not found.
in the field during winter and spring. Probably most individuals reach the adult instar before spring.

Unlike other *Johnstoniana* species, which deposit spermatophores without contacting females (WITTE, 1991, WENDT et al., 1994, WOHLTMANN et al., 1994, EGGERS, in press), *J. errans* males deposit spermatophores only after an initial contact with females. The variable development times of the deutonymphs makes male/female contacts necessary to ensure that spermatophores are released only when females are abundant.

In general, *J. errans* males do not survive winter. Some females may start laying eggs during autumn of the year they developed, but most females begin oviposition in the spring and may oviposit a second time after a new insemination in autumn. Thus *J. errans* has a mainly semiunivoltine life cycle. A combination of 1) the obligatory diapause of eggs, 2) the different ovipositions periods and 3) at least some iteroparous females, can result in females of one generation depositing eggs that hatch during May in three successive years.

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**References**


