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REPRODUCTIVE BIOLOGY AND DEVELOPMENT OF *LIXADMONTIA FRANKI* (DIPTERA: TACHINIDAE), A PARASITOID OF BROMELIAD-EATING WEEVILS

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ABSTRACT

The biology and development of *Lixadmontia franki* Wood and Cave (Diptera: Tachinidae), an endoparasitoid of bromeliad-eating weevils in the genus *Metamasius*, are described. Embryonic development is completed within 8 d post-mating while the egg is held inside the female reproductive system. Neonate larvae actively search for a host and initiate parasitism by penetrating the host's cuticle. Larval developmental time and pupation at 20°C averaged 17 and 25 d, respectively, with no significant differences observed between genders. Adult males live on average 9 d compared to 17 d for females. Females are capable of parasitizing third to sixth instars of *Metamasius quadrilineatus* Chevrolat, but the highest levels of parasitism were observed when third and fourth instars were exposed to flies.

Key Words: parasitism, biological control, weevil

RESUMEN

Se describen la biología y el desarrollo de *Lixadmontia franki* Wood y Cave (Diptera: Tachinidae), un endoparasitoide del picudo de las bromelias del género *Metamasius*. El desarrollo embriónico se completa en un período de 8 d después del apareo, mientras el huevo se mantiene en el sistema reproductivo de la hembra. Larvas neonatas buscan activamente a su hospedero y comienza el parasitismo con la penetración de la cutícula del hospedero. El tiempo de desarrollo de la larva y la pupa a 20° C promedia en 17 y 25 d, respectivamente, sin encontrarse diferencias significativas entre los sexos. Los machos adultos viven en promedio 9 d, comparado con 17 d en las hembras. Las hembras son capaces de parasitar larvas de tercero al sexto estadío de *Metamasius quadrilineatus* Chevrolat, sin embargo, los niveles más altos de parasitismo se observaron cuando se expusieron hospederos de tercero y cuarto estadío a las moscas.

Translation provided by the authors.

Lixadmontia franki Wood and Cave (Diptera: Tachinidae) is native to the tropical montane cloud forests of Honduras and Guatemala, where it attacks the larvae of the bromeliad-eating weevil *Metamasius quadrilineatus* Champion (Coleoptera: Dryophthoridae) (Wood & Cave 2006). The host weevil feeds on epiphytic bromeliads, including species in the genera *Tillandsia*, *Catopsis* and *Vriesea* found between 1600 and 2000 m above sea level (Alvarez del Hierro & Cave 1999). Parasitism by *L. franki* occurs mostly from Jun to Jan and can be as much as 60% in the field during this period.

Laboratory tests have demonstrated that *L. franki* also readily parasitizes the larva of *Metamasius callizona* (Chevrolat) (Frank & Cave 2005). *Metamasius callizona*, a native of southern Mexico and Guatemala, was first detected in Florida in 1989 (Frank & Thomas 1991, 1994). Since then, it has spread throughout southern Florida, destroying much of the native bromeliad flora and threatening populations of rare native bromeliad species (e.g., *Catopsis nutans* Swartz, *Catopsis berteroniana* Schultes, *Guzmania monostachia* L., and *Tillandsia pruinosa* Swartz) (Frank & Cave 2005; http://bromeliadbiota.ifas.ufl.edu). *Tillandsia utriculata* L., once considered common in southern Florida, is now considered endangered due to the extensive damage caused by *M. callizona* (Frank 2000).

Because the only known hosts of *L. franki* are the larvae of bromeliad-eating weevils in the genus *Metamasius*, it offers the possibility of an effective biological control agent of *M. callizona* in Florida (Cave 1997). No other parasitoids of bromeliad-attacking *Metamasius* weevils are known to exist. Information on the developmental and reproductive biology of *L. franki* is of vital importance to understand and maximize parasitism

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under laboratory and field conditions. Alvarez del Hierro & Cave (1999) noted an adult lifespan of 20 d and pupal incubation time of 18-20 d. Virtually nothing else was known about the biology of the fly. Here we provide new information on the biology and behavior of *L. franki* attacking *M. quadrilineatus* under laboratory conditions.

Materials and Methods

Biological Material

Collections of host plants, weevils, and flies were taken in 5 cloud forests in south-central Honduras. These included the biological reserves of Cerro Monserrat (N13°56' W86°54') in El Paraíso department, and Cerro Uyuca (N14°00' W87°09'), El Chile (N14°30' W86°51'), La Montañita (N14°03' W87°10'), and Cerro de Apalagua (N14°02' W87°04') (all 1400-1800 m elevation) in Francisco Morazán department. Plant material consisted of live bromeliad plants knocked down from trees by natural causes and which could be found in groups on the forest floor. The leaves from these plants were removed and the stems used as feeding material for the weevil colony. Stems collected in such manner were placed in plastic bags and stored at 4°C until needed. These plants were primarily *Tillandsia standleyi* L.B. Smith (approximately 90%), one of the most common species in these ecosystems, with *Tillandsia ponderosae* L. B. Smith and *Catopsis hahnii* Baker making up the rest.

Metamasius quadrilineatus eggs, larvae, and pupae were collected from field infested plants, brought to the laboratory, placed individually in 30-mL (1-oz) plastic cups with screened lids, and used to start a weevil colony. A slice of bromeliad stem was provided for each weevil larva as needed to ensure a constant supply of fresh food. Early instar weevils were determined not to be parasitized in the field, therefore field-collected first and second instar weevils were used to supplement the laboratory colony. Some of these larvae also were raised to the third and fourth instars and exposed to adult flies.

Lixadmontia franki reared from field-parasitized weevil larvae were used to initiate a fly colony. This colony was continually supplemented with field material, but by the end of this project it had turned into a self-sustaining laboratory population. Forty fly pupae were placed between layers of moistened paper towels in a 10-cm diameter Petri dish within 2 d after formation and incubated at 21°C with 70% RH. Petri dishes with fly pupae were placed in a screen cage ($1.5 \times 1.5 \times 1.2$ m) where adults were allowed to emerge. Adult flies were provided with water and artificial hummingbird nectar (Perky-Pet Instant Nectar, Perky-Pet Products Co., Denver, CO) in 30-mL plastic cups fitted with cotton wicks through the lid to prevent flies from drowning. For parasitism, thirty 30-mL plastic cups, each containing a third or fourth instar weevil and 5-cm piece of bromeliad stem, were placed on a tray and simultaneously placed inside the fly cage (Suazo et al. 2006). A new tray with 30 larvae was introduced into the fly cage every other day. All larvae on the same tray were exposed to adult flies for 12 consecutive days. For experimental purposes, newly emerged flies were placed in smaller cages ($35 \times 35 \times 35$ cm) and provided with food and water as described above. Flies were sexed based on dimorphism in the abdominal region: females are usually larger and have a rounder, darker abdomen, contrasted with that of males, which is more triangular and reddish colored.

Development Time, Mating Behavior, Female Fecundity, and Longevity

Development time of fly larvae at 21°C was estimated by artificially parasitizing 3rd instar weevils. Ready-to-hatch pharate 1st instars, recognizable by the presence of a well developed cephalopharyngeal skeleton, were collected by dissecting the abdomen of six 8-10-d-old mated females, exposing their reproductive system, and gently opening the oviduct where the pharate larvae were located (Fig. 2B). Dissections were made in sterilized water with the aid of a stereomicroscope. Artificial parasitism was accomplished by using a fine bristle brush to place a 1st instar on the weevil host. After placing the maggot on the weevil larva, the penetration time for the maggot to enter the host was recorded. The elapsed time between host penetration and exit of the fully developed fly larva from the host was deemed the development time. Data for penetration time were obtained from 14 fly larvae and, for development time, from 20 fly larvae.

The period from pupal formation until adult emergence was studied under 4 constant temperature regimes: 15, 20, 25, and 30°C, all with 70% RH. Minimum and maximum temperatures were chosen based on average day and night temperatures at Cerro Uyuca. Newly formed pupae within their puparium were weighed and placed between layers of moistened paper towel in a 92-mL (25-dram) plastic vial. Pupae were added to each of the incubators daily for 4 d until a total of 20 pupae was attained at each temperature. Fiberglass screen was used to cover both ends of the vial to allow for proper ventilation. Fly emergence was checked daily and the date of emergence was used to determine pupal development time. The gender of each emergent fly was determined and the number of emergent flies per cohort at each temperature was used to determine percent emergence. Pupae from which emergence did not occur after an additional 2 weeks from the expected emergence time (21 d, based on preliminary obser-

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vations) were examined under the microscope. Pupae which appeared to be alive and healthy were left and checked daily for an additional 2 weeks until fly emergence or death. Causes of death were dehydration, characterized by a scaly and dry appearance, partial emergence (only head out of the puparium), fungal or bacterial infection, or physical damage.

To study mating behavior, 4-6 pairs of newly emerged flies were placed within a screen cage (35 × 35 × 35 cm). Five cages were set up over a 1-week period. In preliminary observations, it was determined that flies mated only during the day, so observations were made daily from 7:00 am to 7:00 pm at 2-h intervals for 4 consecutive d. Mating time and date were recorded and courtship and mating behavior was noted. Data were obtained from 22 mating pairs.

To estimate fecundity, newly emerged females were allowed to mate and then moved to a separate cage supplied with hummingbird food but no hosts. Flies were dissected (as described above) 2, 4, 6, and 8 d after mating; unmated flies housed in a similar cage with hummingbird food but no hosts also were dissected. At least 3 flies were dissected for each treatment. The number of eggs with developing embryos and number of pharate 1st instars were counted and recorded. Measurements of the length and width (mm) of fifteen 1st instars were taken.

The post-mating preoviposition period of female flies was determined by exposing weevil larvae to flies 2, 4, 6 and 8 d after mating. Mating pairs were separated from a large colony and placed in a small cage (35 × 35 × 35 cm). Four cages, each with 3 mating pairs and 6 weevil larvae in bromeliad stems, were prepared. Weevil larvae fed on *T. standleyi* stems for 3 d before being exposed to the flies and were exposed to the flies for only 1 d. Exposed weevil larvae were subsequently reared on bromeliad stems until pupation or emergence of fly larvae. The experiment was repeated twice. Twelve weevil larvae were exposed in each of the treatments. The number of parasitized larvae was recorded and these data were used to calculate percent parasitism for each of the fly maturity periods.

Adult longevity was determined by placing flies of both sexes that emerged within a 24-h period in screen cages (35 × 35 × 35 cm) and recording the number of dead flies and their gender daily. Cages contained variable numbers (8-12) of mixed gender flies. Five cages were set up over a period of 1 week, based on fly availability. Data were collected until all flies died.

Susceptibility of Host Instars to Parasitism

To determine the preferred host instar for parasitism, each of the 6 weevil instars was exposed to three 10-d-old fly pairs for 5 consecutive d. Weevil instars were determined by head capsule width (Alvarez del Hierro 1997). Weevils were exposed to flies in cages (35 × 35 × 35 cm) containing hummingbird nectar and water. Data were collected in 3 trials consisting of 6 larvae/instar, which yielded 18 observations per instar.

Statistical Analyses

Analysis of variance (ANOVA) (Proc GLM, SAS Institute, 1996) was used to evaluate the effect of temperature on pupation period, pupal weight and survivorship, reproductive maturation time on the number of eggs and pharate 1st instars produced, and preferred host instar parasitized. Significant ANOVAs were followed by a Duncan's mean separation test. Comparison of adult longevity between genders was tested for significance by a *t*-test ($\alpha = 0.05$) (Proc GLM, SAS Institute, 1996). Means are given with their standard error.

Results

Developmental Time, Mating Behavior, Female Fecundity, and Longevity

When placed on a host, 1st instars of *L. franki* were observed penetrating the weevil larva by cutting the cuticle with their mandibles (Fig. 1), usually through an intersegmental membrane. Average elapsed time from placement on the host to penetration was 7.8 ± 7.5 min with a range of 3-30 min. The time to pass through the host's integument was about 1 s.

Larval development time inside the host lasted on average 17.0 ± 0.7 d with a range of 13-21 d (Table 1). After completion of development within the host, the mature fly larva exited the host car-

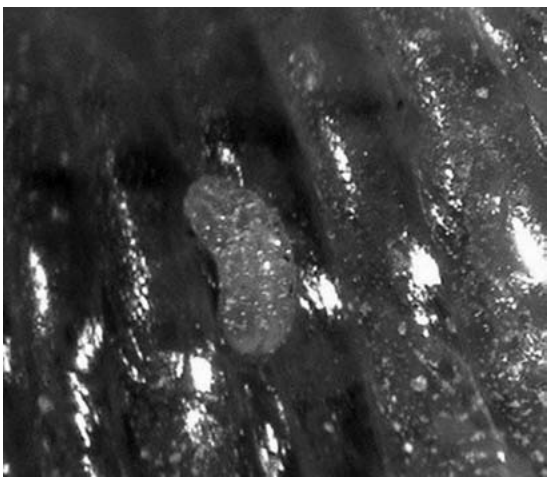


Fig. 1. First instar *Lixadmontia franki* on the integument of a 3rd instar *Metamasius quadrilineatus*.

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TABLE 1. DEVELOPMENTAL PARAMETERS FOR *LIXADMONTIA FRANKI* PARASITIZING *METAMASIUS QUADRILINEATUS*.

Variable	*n*	Mean ± SE	Min	Max	*P*-value (*t*-test)
Larval developmental time (d)	20	17.0 ± 0.7	13	21	
Pupation period (d)					
15°C					
Male	7	43.4 ± 0.4	42	44	>0.05
Female	8	43.6 ± 0.2	43	44	
20°C					
Male	9	24.7 ± 0.2	20	29	>0.05
Female	5	25.0 ± 0.5	24	27	
Adult longevity (d)					
Male	14	9.0 ± 1.8	3	24	0.025
Female	16	16.9 ± 3.1	3	54	

cass, usually from the caudal end of the host. Pupation occurred 1-2 d after exiting the weevil carcass. Pupation normally occurred under decomposing bromeliad tissue or inside the feeding tunnels or pupal chambers made by the weevils in the plastic rearing cups.

Weights of pupae were significantly different between males and females ($F_{2,26} = 4.83$; $P = 0.016$) with females weighing 37.3 ± 2.4 mg compared to 28.4 ± 1.7 mg for males. Pupation period did not differ significantly between males and females at 15 and 20°C (Table 1). However, duration of the pupal stage was significantly longer at 15°C (43.5 ± 0.2 d) than at 20°C (24.8 ± 0.6 d) ($F_{2,26} = 475.33$; $P < 0.0001$). Similarly, survival at 15°C was 75%, contrasting with 65% at 20°C. No fly emergence was observed when pupae were incubated at 25 and 30°C. Dehydration of pupae was characterized by a scaly, brittle appearance of the contents with no distinguishable adult anatomical structures, the lack of a foul smell and no visible mycelia after opening the pupal case. Dehydration accounted for only 10% of pupal mortality at 20°C, whereas 85% and 100% died from dehydration at 25 and 30°C, respectively. Some flies died while exiting (partially emerged flies) and had only their heads out of the puparium; this type of mortality accounted for approximately 10 and 20% of mortality at 20 and 25°C, respectively. Death by bacterial or fungal infection was determined after breaking the puparium open and noticing a mushy consistency and foul smell (bacteria) or dry consistency and visible mycelia (fungi). This factor accounted for 15% of mortality and was observed only at 15°C.

Mating by *L. franki* occurred within 48 h after adult emergence. On average, female flies mated 1.7 ± 0.2 d after emergence. During courtship, males moved in circles around the female, constantly moving their wings in a forward/backward motion. After this courtship period, which lasted less than a min, mating took place. Copulation lasted an average of 58.9 ± 7.1 min with a range of 20-105 min.

Unmated females did not have any eggs within the oviduct (Fig. 2A). Eggs with developing embryos within the reproductive system of mated females were evident at 2 d post-mating and the number increased significantly ($F_{3,13} = 8.13$; $P = 0.026$) with time after mating, reaching a maximum at 6 d (Table 2). Eggs with pharate 1st instars were not seen within the oviduct of gravid flies until 8 d post-mating (Table 2), at which time they were packed side by side within the median oviduct (Fig. 2B). Active, fully formed 1st instars were apparently still contained within the egg chorion inside the oviduct, but neonate larvae were observed moving without restriction, as they would within a chorion, when they exited the ovipositor of freshly killed females (Fig. 3). First instars averaged 0.88 ± 0.22 mm long and 0.19 ± 0.01 mm wide.

No weevil larvae exposed to adult flies 2-6 d after mating were parasitized, whereas more than half of the weevil larvae exposed to adult flies 8 d post-mating were parasitized (Table 2). Adult female flies lived significantly longer than males ($t = 1.71$; $df = 24$; $P = 0.025$), averaging 16.4 ± 3.1 d compared to 9.0 ± 1.8 d for males (Table 1).

Susceptibility of Host Instars to Parasitism

Parasitism was observed only in 3rd to 6th instar weevils, never in 1st and 2nd instars. Levels of parasitism were significantly different ($F_{5,126} = 5.8$, $P < 0.0001$) between the different host instars and ranged from 40.9% in 3rd instars to 4.3% in 6th instars (Fig. 4). Female flies hovered around the pieces of bromeliad stem containing weevil larvae until landing on the plant material. It is yet uncertain whether the females deposited one or more neonate larvae or eggs with a fully developed embryo on the host plant material. Observations during the dissection of gravid, recently killed females indicate that the first instars may hatch from the egg while still in the mother's ab-

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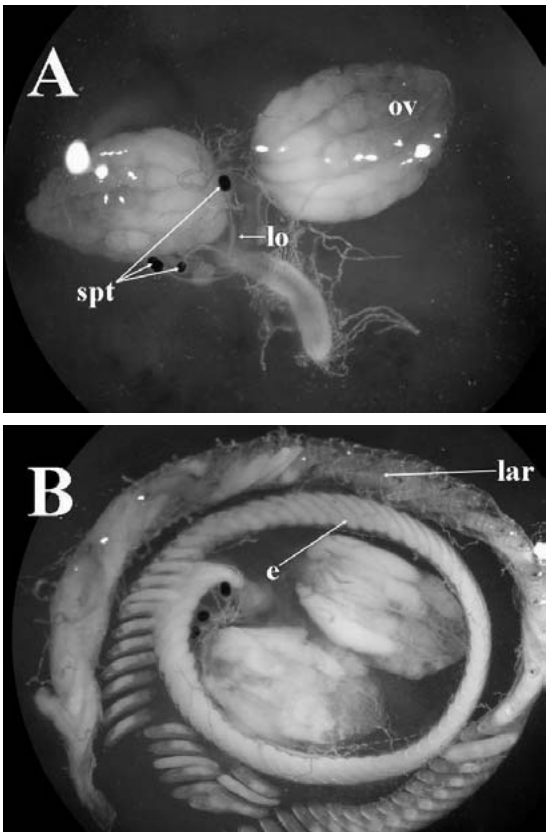


Fig. 2. Reproductive system of an unmated female *Lixadmontia franki* immediately after emergence (A) and of a mated female fly 8 d after mating (B). Ovaries and ovarioles (ov); spermatheca (spt); lateral oviduct (lo); pharate 1st instar (lar); eggs (e).

domen. Whichever the case, these were placed close to the entrance point where the weevil larva burrowed into the plant stem.

Discussion

In its natural habitat, *M. quadrilineatus*, the native host of *L. franki*, feeds on fallen bromeliads found on the forest floor of tropical montane cloud forests (Alvarez del Hierro & Cave 1999). These plants are normally found in large groups on their side, a condition that prevents water accumulation among the bases of the leaves, which apparently favors feeding and development of weevil larvae. Weevil larvae burrow and feed inside the stems of these plants, providing a seemingly difficult environment for *L. franki* to find and parasitize its host. However, *L. franki* has adapted to these conditions by either laying eggs containing pharate larvae that hatch from the egg immediately after deposition or by possibly larvipositing neonate 1st instars; in either case, the young larvae immediately burrow through the macerated plant tissue and weevil frass to locate and contact a host. This is an adaptation in tachinid flies to parasitize hosts within well-protected and concealed areas and to minimize search and handling time (Stireman et al. 2006). The ability of first instars to survive before finding a host is impressive. Neonate larvae left in distilled water overnight at room temperature (~22°C) successfully penetrated the host when placed on the larvae of *M. callizona* (AS, personal observation). This suggests that, given the right conditions, a first instar *L. franki* can survive for a long period before finding a host.

Duration of the pupal stage at 15°C was almost twice that at 20°C, but the mortality was lower. This may be a reflection of the environmental conditions within the fly's native cloud forest habitat and is an important factor to consider when developing mass-rearing methods of *L. franki*.

Female *L. franki* emerge from the puparium without eggs in their oviduct. Egg maturation and embryonic development require about 8 d to complete. The presence of pharate larvae within the egg chorion inside the oviduct and the apparent exit of free-moving larvae from the female's abdomen indicate that *L. franki* larvae may hatch from the egg just before exiting the female's reproductive system. This is similar to the ovoviviparous reproduction observed in *Lydella jalisco* Woodley, which parasitizes stem borers (Lauzière et al. 2001). *Lixadmontia franki* has a low fecundity level compared to that reported for ovolarviparous tachinid species (Stireman et al. 2006). Species with indirect oviposition strategies generally

Table 2. Fecundity of and parasitism by *L. franki* at 4 adult ages.

Days post-mating	*n*	Eggs w/ developing embryos (Mean ± SE)	Pharate 1st instars (Mean ± SE)	Total	Parasitism (%)
2	4	20.0 ± 3.5 a	0	22.5	0 a
4	3	81.6 ± 8.5 b	0	81.7	0 a
6	4	103.5 ± 17.9 b	0	103.5	0 a
8	6	84.3 ± 11.6 b	53.8 ± 9.9	138.1	57 b

Values in the same column with the same letter are not significantly different (Duncan's mean separation test; $P > 0.05$).

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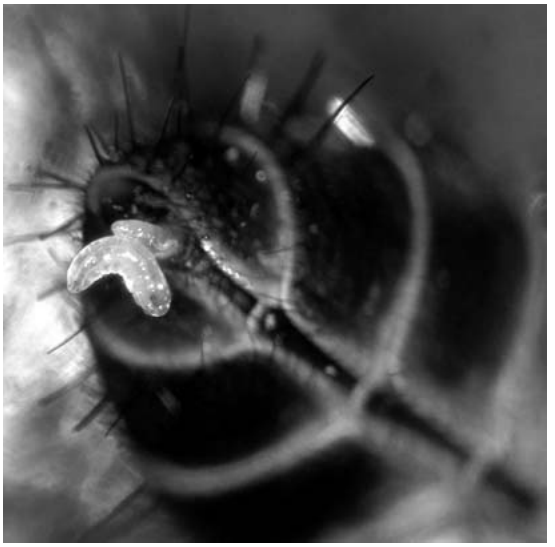


Fig. 3. First instar *Lixadmontia franki* exiting the adult female ovipositor.

have a low probability of successful parasitism and low survival of their offspring, and, therefore, high fecundity as opposed to those that oviposit directly on the host (Stireman et al. 2006). Larviparity in *L. franki* needs to be substantiated by closer examination of the median oviduct to find free roaming 1st instars and empty chorions.

The difference observed between male and female longevity in *L. franki* concurs with evidence in other tachinid species of short male longevity compared to female counterparts (Cardoza et al. 1997).

Control of *M. callizona* has been largely limited to commercial ornamental bromeliad operations by chemicals (Short 1992). However, chemical control in southern Florida's protected areas where weevils have large populations is not an option because of the difficulties of applying chemicals to plants found high in the trees, environmental contamination, and the negative effects on non-target organisms. *Lixadmontia franki* parasitizes only bromeliad-eating weevils in the genus *Metamasius*. The potential of *L. franki* in a biological control program of *M. callizona* largely depends on the fly's adaptability to the climatological conditions of southern Florida ecosystems and the establishment of self-sustaining populations in these habitats. Although *L. franki* originates from cool, shady, moist montane tropical forests and its reproduction in the laboratory is best at around 20°C, we have observed flies survive temperatures of upwards to 28°C when adequate moisture is available. We expect the adult flies will be able to escape from Florida's high summer temperatures by seeking the cooler refuges within water-laden tank bromeliads under shady tree canopies.

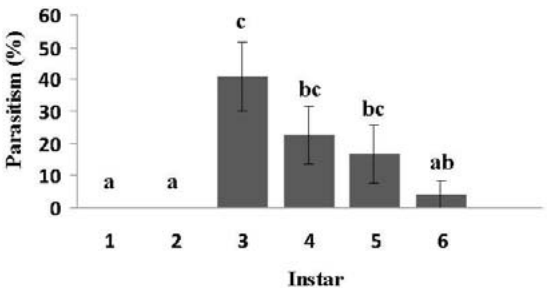


Fig. 4. Parasitism by *Lixadmontia franki* in 6 instars of *Metamasius quadrilineatus*. Vertical lines indicated 1 SE above the mean. Values of bars with the same letter are not significantly different (Duncan's means separation test, $P > 0.05$).

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