The life cycle of *Oressinoma typhla* Doubleday, [1849] (Lepidoptera: Nymphalidae: Satyrinae)

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Abstract: The complete life cycle of *Oressinoma typhla* Doubleday, [1849] and the morphology of its immature stages are described. Biological and ecological information is provided for each stage, and its host plant is identified as *Cyperus involucratus* (Cyperaceae) in the mountains of northern Venezuela.

Key Words. Coenonymphina, Cyperaceae, *Cyperus*, early stages, Euptychiina, host plant, life history, life tables, Satyrini, Venezuela.

INTRODUCTION

The genus *Oressinoma* was erected by Doubleday in 1849 for a single species which he named *O. typhla* based on specimens allegedly from "New Granada" and Colombia (Doubleday, [1849]; Westwood, 1851)[1], but the putative type in the Natural History Museum (London, UK) is labelled "Venezuela", with a phenotype corresponding to populations from the vicinity of Caracas in the Cordillera de la Costa. The genus currently contains just two species, *O. typhla* and *O. sorata* Salvin & Godman, 1868 (Lamas 2004). As observed by Westwood (1851) in his description, *Oressinoma* is notable among Neotropical satyrines principally for the very swollen base of the median and submedian veins of the forewing (not the costa) and its peculiar wing pattern, with a very broad white band across both wings and the absence of ocelli that are so characteristic of most Satyrinae (*Oressinoma* comes from the Greek word for "mountain", alluding to its preferred habitat, while *typhla* means "blind", lacking ocelli).

Although *Oressinoma* has traditionally been placed in Euptychiina (*e.g.*, Miller, 1968; Lamas, 2004), early stage morphology (Murray, 2001; this paper), adult morphology and wing pattern (Doubleday, [1849]; Reuter, 1896), and morphological and molecular analyses (Murray, 2001; Murray & Prowell, 2005) all suggest that it should be placed elsewhere. Recent molecular work indicates that it should be classified in Coenonymphina (Peña *et al*. 2006; Kodandaramaiah *et al*., 2010, 2018).

Oressinoma typhla is distributed from Costa Rica through Colombia to Venezuela, and south through the Andes to Bolivia (DeVries, 1987; Warren *et al*., 2017). It occurs between about 600 and 2,200 m in elevation (most frequently between about 1,200 and 1,800m) on mountain slopes, where it is common and widespread in premontane and cloud forest habitat, especially along road edges (human-altered spaces which its host plant occupies), naturally disturbed areas such as landslides, and frequently close to water bodies (pers. obs.; pers. comm. from A. Aiello in Panama, M. Costa and F. Romero in Venezuela, Y. Gareca in Bolivia, G. Lamas in Peru, and K. Willmott in Ecuador; DeVries, 1987; Petit, 2017). The adults have a slow and somewhat bouncy flight, feed on decomposing fruit and fungi, and males are occasionally attracted to dung and rotting fish bait (pers. obs.; K. Willmott, pers. comm.; DeVries, 1987). We have personally not observed or seen reports of feeding on nectar sources; however, there are some photographs published on the internet of this species feeding on small flowers in Colombia and Ecuador.

Figure 1. *Oressinoma typhla* adult male, dorsal and ventral view (Mérida, Venezuela) (FW length = 24 mm).

[1] According to Gerardo Lamas (pers. comm.), the entries in Lamas (2004) for Doubleday and Westwood are partly wrong, and require correction: authorship of both *Oressinoma* and *typhla* must be credited to Doubleday, as those names were first introduced on plate 62, fig. 5, published on 3 August 1849 in vol. 2 of *Gen. diurn. Lepid*. Since the plate did not bear a date, its publication date should be cited in square brackets ("[1849]"). The text (pp. 363-374) appeared (with a publication date) on 2 April 1851.

The host plants for *Oressinoma* species are only known for *O. typhla* (Beccaloni *et al*., 2008): DeVries (1987) gives *Cyperus luzulae* (Linnaeus) Retzius in Costa Rica, Murray (2001) notes *Cyperus* sp. in Ecuador, while here we report *C. involucratus* Rottbøll from Venezuela (Cyperaceae). This plant family contains mainly herbaceous monocots that look like grasses, and in a few instances, climbers (Steyermark & Huber, 1978: 379).

Study of the immature stages of butterflies has often provided information complementary to studies of the adults (e.g., Freitas & Brown, 2004; Willmott & Freitas, 2006), since morphological divergence among butterfly species can be more constrained, or stronger, in the immature stages than in adults (Aiello, 1984; Heredia & Viloria, 2004). Morphological study, including chaetotaxy, for each stage can therefore potentially contribute to comparative morphology and phylogenetic analyses (Barbosa *et al*., 2010).

MATERIALS & METHODS

Adults were carefully observed in the field until the species' suspected host plant was identified by the close association between females and the plant species. The host plant was identified as *Cyperus involucratus* Rottb. (Cyperaceae) (Fedón, 2007, pers. comm. to MEL), which is a perennial herb with a horizontal hard rhizome, approximately 30 to 150 cm high, with linear leaves and globular inflorescence spikes (Adams, 1994). This plant species, native to tropical and subtropical east Africa, was introduced to many tropical American countries as an ornamental plant. It is now naturalized throughout its American range and is widely distributed, being found mainly in areas of human intervention such as gardens, parks, fields, and road verges, but especially along the banks of water courses (Adams, 1994; Hoyos, 1999).

Field research was carried out in an open area of vegetation in the Venezuelan Cordillera de la Costa. The study site is 11 km SW of Caracas, in Altos de Pipe, in a plot close to the building of the Ecology Center of the Instituto Venezolano de Investigaciones Científicas (IVIC) at 1730 m (10°24'03"N, 66°58'43"W). To rear the butterflies, several host plants together with a total of 17 adult individuals of *O. typhla* were taken to the butterfly house in the "El Pinar" Zoo Insectarium, at 925 m (10°28'52"N, 66°56'15"W) in Caracas.

In the butterfly house, host plant leaves were checked daily looking for the presence of fresh eggs. Eggs were collected daily and placed individually in glass vials. Each container was labelled with the collection date and a voucher number was assigned to each sample. Containers were checked daily for cleanliness and observations were noted regarding hatching and deaths of individuals. When the first larvae emerged (L_1), we fed them by placing fresh pieces of *Cyperus involucratus* leaves into each container, cleaning vials and changing leaves daily to avoid fungal infections. Every molt date (instar change) was recorded for each individual. A little under half the larvae reached the pupal stage (see Table 3). Pupae were also kept in individual glass containers, covered with a piece of netting to allow gas exchange and to avoid the possibility of excessive moisture accumulation inside the jar. Observations were taken until adults emerged. These were sexed and released in the El Pinar butterfly house.

The ecological life table for *Oressinoma typhla* (Table 3) was developed from a cohort of fourteen subcohorts each representing one day of successful egg collection in the butterfly house. These fourteen cohorts were combined into one to improve data analysis (daily egg numbers were limited to one or two).

RESULTS

The adult behavior of *Oressinoma typhla* is potentially sensitive to the presence of observers, since it proved very difficult to observe imagos courting, copulating, or ovipositing. However, DeVries (1987) described these behaviors in some detail based on observations in Costa Rica. Over the course of seven months field work in Venezuela, oviposition was never observed in natural conditions, while in captivity it was observed only twice. Copulation was observed only once in captivity. Adults were solitary and we observed that they always flew alone, only occasionally observing them in pairs during courtship and copulation. Males flew slowly along open trails, while females spent most of their time (several hours per day) flying around the host plants. It was not possible to induce oviposition in plastic bags, unlike in other Neotropical satyrines (see for example, Freitas & Peña, 2006; Kaminski & Freitas, 2008; Montero & Ortiz, 2012, 2013; however Cosmo *et al*., 2014 report only infrequent success using this method), and, in fact, *O. typhla* females did not survive long inside plastic bags, dying in a remarkably short time (between 20 – 120 minutes) even under shaded and cool conditions.

Description of the immature stages

The results presented below were obtained at an average temperature of 24°C (ranging from 23 to 25°C) and an average relative humidity of 82% (ranging from 76 to 85%). Five larval instars were recorded in the life cycle of *Oressinoma typhla*, similar to a large proportion of satyrines (only four larval instars have been recorded in several genera – see references in Cosmo *et al*., 2014). Table 2 shows the morphometry of *O. typhla* immature stages. The nomenclature used for the description of the body arrangement of larval instar setae follows that used by Hinton (1946) (see also Fracker, 1915; Scoble, 1992; Bastidas, 1994).

Egg (Figs. 2a, 2b). The eggs are sub-spherical, light green with a metallic sheen, and have an average diameter of 1.98 mm (n=5) (SD=0.014). The micropyle is located in the apical pole, and it shows an appreciable concavity. Eggs are decorated with vertically-oriented longitudinal ridges from the dorsal to the ventral pole in a radial arrangement. Upon maturity, the epicranium of the larva was visible through the chorion (two days before its hatching). Duration: 5 days (n=68) (SD=1.08).

First instar. (Figs. 2c, 2d) The body of the larva (L_1) is a yellowish green color with a shiny black head capsule. The head is wider than the body, with a mean length of 0.51 mm (n=3) (SD=0.009) and an average width of 0.66 mm (n=3) (SD=0.042). The head has two very small scoli (0.002 mm) (n=3) (SD=0.016). The mean body length is 1.98 mm (n=3) (SD=0.103) with a mean width of 0.50 mm (n=3) (SD=0.010) upon emergence. The body ends in a barely developed bifid tail. Legs and prolegs have the same color as the body. Mouthparts are black. Spiracles are a very light brown color, and only on segments T1 and A8.

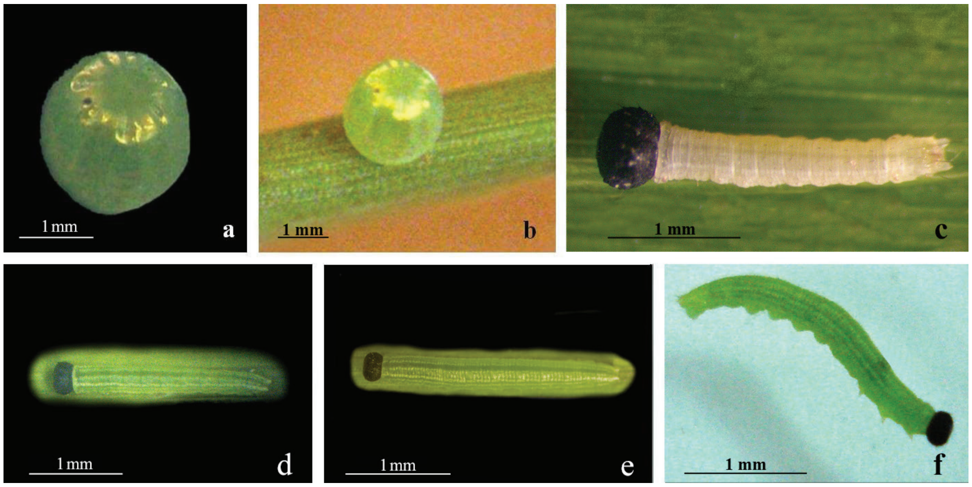

Figure 2. *Oressinoma typhla* immature stages: (a, b) Egg; (c, d) First instar; (e, f) Second instar.

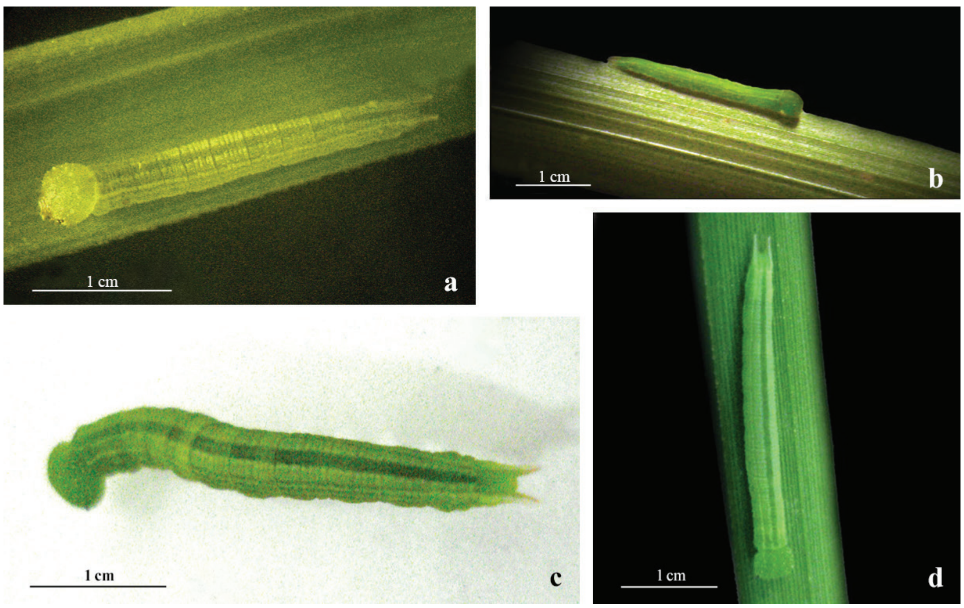

Figure 3. *Oressinoma typhla* immature stages: (a, b) Third instar; (c, d) Fourth instar.

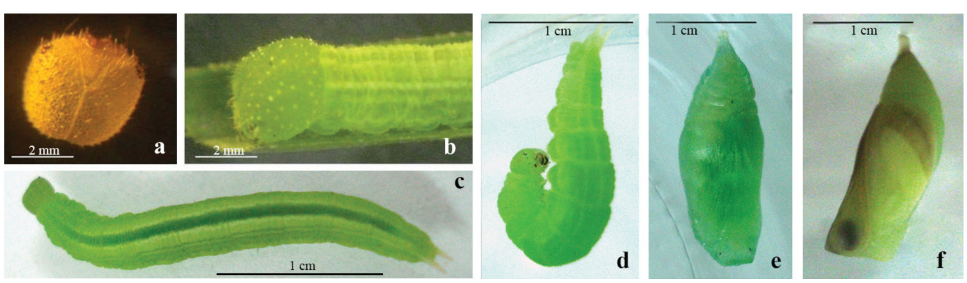

Figure 4. *Oressinoma typhla* immature stages: (a) Head capsule exuvia in fifth instar; (b, c) Fifth instar; (d) Prepupa; (e, f) Pupa.

Setae are small and black (except the ones present on the last segment that are greater in length). Segments T1-T3 present D1, D2, SD1 and L_1 setae, while T1 also has a single XD1 seta. Segments A1-A9 present D1, D2, SD1, L_1 and SV1 setae. Segment A10 presents D1, D2 and SD1 setae. The prolegs (segments A3-A6 and A10) present P2 and P4 setae. During this instar the larvae exhibited very little activity. The setae arrangement and chaetotaxy described above are shown in figures 5a and 5b. Duration: 4 days (n=67) (SD=0.69).

Second instar (Figs. 2e, 2f). This instar is morphologically similar to the previous, presenting only variations in size. The head has an average length of 0.53 mm (n=3) (SD=0.024) and average width of 0.80 mm (n=3) (SD=0.024), while the scoli remain unchanged. The body presents an average length of 2.00

Table 1. Life cycle of *Oressinoma typhla* under laboratory conditions. Standard Deviation (SD); Coefficient of Variation (CV).

Instar	Average duration (days)	SD	CV	Individuals
Egg	5	1.08	0.13	68
Larva I	4	0.69	0.08	67
Larva II	4	1.74	0.27	43
Larva III	6	1.45	0.23	41
Larva IV	8	1.08	0.18	36
Larva V	12	1.48	0.25	34
Pupa	9	0.78	0.15	29

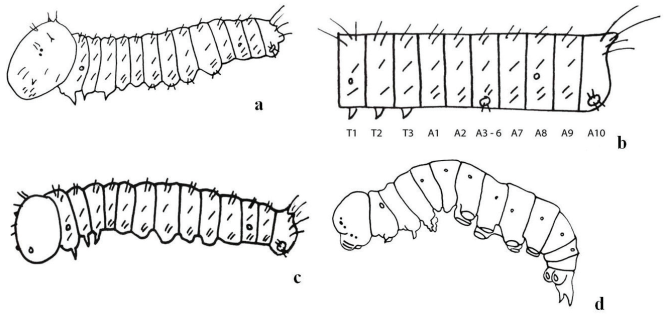

Figure 5. Schematic drawings of *Oressinoma typhla* larvae: (a) Setae arrangement of first instar (50x); (b) Chaetotaxy of first instar; (c) Setae arrangement of second instar (15x); (d) Setae arrangement of fifth instar (1.25x).

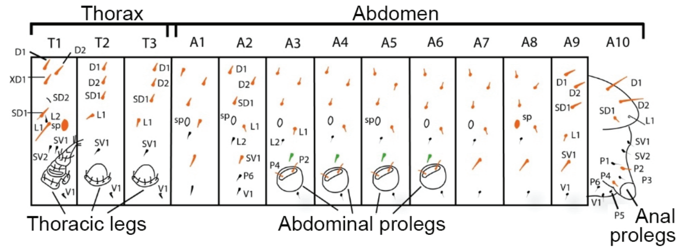

Figure 6. Schematic diagram of setae distribution pattern comparing first instar larvae of typical nymphalids with those of *Oressinoma typhla* (setae common to both taxa in orange; setae unique to *O. typhla* in green). (Modified from Scott, 1986).

mm (n=3) (SD=0.551) and an average width of 0.50 mm (n=3) (SD=0.577). The internal body coloration is a little more saturated than L_1. A dark green line lies along the dorsum from the head to the anus (segments T1-A10), surrounded by two thinner and paler lines on each side. The mouth parts maintained the black coloration of L_1. The setae arrangement is as for L_1 (Fig. 5c). These larvae ate their exuvia and head capsule completely. Duration: 4 days (n=43) (SD=1.74).

Third instar (Figs. 3a, 3b). The head capsule changes in coloration to light green, similar to the body. The head is covered with more yellowish-green granulations and the scoli are less visible in this instar. Larvae maintain the longitudinal dorsal lines as described for L_2. The head presents an average length of 0.81 mm (n=3) (SD=0.062) and an average width of 1.03 mm (n=3) (SD=0.179). The body has an average length of 20.7 mm (n=3) (SD=0.577) and an average width of 1.20 mm (n=3) (SD=0.058). This larval instar shows a greater development of the caudal filaments, the bifid tail becoming more evident. All setae with putative taxonomic importance disappear completely while several small setae of a very light yellow color cover certain areas of the body. In this instar the larvae show more activity, movement and voracity. Duration: 6 days (n=41) (SD=1.45).

Fourth instar (Figs. 3c, 3d). This instar is morphologically similar to L_3, differing mainly in body size. The head presents an average length of 1.38 mm (n=3) (SD=0.043) and an average width of 1.80 mm (n=3) (SD=0.029). Head scoli are not present. The body has an average length of 23.0 mm (n=3) (SD=0.938) and an average width of 1.63 mm (n=3) (SD=0.217). Spiracles are present with a light brown coloration on segments T1 and A1-A8. A greater number of small light yellow setae cover the body. There are no setae with taxonomic importance. Duration: 8 days (n=36); (SD=1.08).

Fifth instar (Figs. 4a, 4b, 4c, 4d). The larvae closely resemble L_3 and L_4, but with a substantial increase in body size. The head has an average length of 1.80 mm (n=3) (SD=0.029) and an average width of 3.50 mm (n=3) (SD=0.289). The body has an average length of 25.0 mm (n=3) (SD=2.309) and an average width of 3.97 mm (n=3) (SD=0.058), but may be up to 40.0 mm in length. There are no setae of taxonomic importance (Fig. 5d). Larval activity increased considerably, with larvae spending most of the time feeding. The inactive prepupa stage has an approximate duration of one day, and the pupation process has an approximate duration of three minutes. Duration: 12 days (n=34) (SD=1.48).

Pupa (Figs. 4e, 4f). The pupa is light green, elongate, smooth and translucent, with an average length of 13.9 mm (n=3) (SD=0.006) and average width of 4.43 mm (n=3) (SD=0.116). The cremaster is the same color as the pupa, with an average length of 0.75 mm (n=3) (SD=0.015). It possesses two small ocular capsules, separated by an average of 2.37 mm (n=3) (SD=0.002). From the sixth day the pupa body becomes more translucent and all adult morphological structures can be better observed. Two days before the emergence it is possible to distinguish the imago inside the capsule. The wings are clearly visible with an average length of 8.00 mm (n=3) (SD=0.020) and an average width of 3.88 mm (n=3) (SD=0.002). Duration: 9 days (n=29) (SD=0.78).

A scheme for comparing the generalized distribution pattern of setae of the family Nymphalidae and the specific pattern found in *Oressinoma typhla* is presented in Figure 6. The setae shared between both taxa are highlighted in orange, while additional setae found in *O. typhla* are in green.

Table 2. Morphometric table for life cycle stages of *Oressinoma typhla*.

	Egg	Larva L_1	Larva L_2	Larva L_3	Larva L_4	Larva L_5	Pupa
Egg	n = 5						
Diameter	1.98 mm	---	---	---	---	---	---
Epicranium		n = 3	n = 3	n = 3	n = 3	n = 3	
Length	---	0.51 mm	0.53 mm	0.81 mm	1.38 mm	1.80 mm	---
Width	---	0.66 mm	0.80 mm	1.03 mm	1.80 mm	3.50 mm	---
Scoli		n = 3	n = 3				
Length	---	0.002mm	0.002mm	---	---	---	---
Body		n = 3	n = 3	n = 3	n = 3	n = 3	n = 3
Length	---	1.98 mm	2.00 mm	20.70 mm	23.00 mm	25.00 mm	13.90 mm
Width	---	0.50 mm	0.50 mm	1.20 mm	1.63 mm	3.97 mm	4.43 mm
Cremaster							n = 3
Length	---	---	---	---	---	---	0.75 mm
Ocular capsules							n = 3
Separation	---	---	---	---	---	---	2.37 mm
Wings							n = 3
Length	---	---	---	---	---	---	8.00 mm
Width	---	---	---	---	---	---	3.88 mm
Duration (days)	5	4	4	6	8	12	9

Survivorship and comments

An ecological life table was compiled for *Oressinoma typhla* (Table 3) to indicate how the population of individuals and the proportion of survivors decreases over time. The most critical stage is apparently the second larval instar (L_2), followed by the first larval instar (L_1). Mortality and survival curves are also presented (Figures 7a, 7b). It can be observed that the mortality rate increases over time while survival rate decreases, with a critical stage being the change from larva L_1 to larva L_2.

In natural and captive conditions *Oressinoma typhla* females lay individual eggs on the upperside of leaves towards their distal end. This habit has been reported for several species of the Neotropical subtribe Pronophilina (DeVries, 1987; Heredia & Viloria, 2004). From the 92 eggs collected in the insectarium only 68 reached larval instar L_1. Among the 24 eggs that did not reach L_1, one died, eight were parasitized and 15 were unfertilized. From each parasitized egg there emerged between one to two parasitic Hymenoptera of the family Encyrtidae.

Table 3. *Oressinoma typhla* ecological life table. (x) Life cycle stage; (N_x) Individual numbers per stage; (I_x) Survival proportion at stage x; (d_x) Mortality proportion between stages x and x+1; (D_x) Mortality numbers per stage; (q_x) Probability of dying between x and x+1.

x	Nx	lx	dx	Dx	qx
Egg	77	1	0	0	0
Larva I	68	0.883	0.130	10	0.132
Larva II	43	0.558	0.324	25	0.581
Larva III	41	0.532	0.026	2	0.049
Larva IV	36	0.468	0.065	5	0.139
Larva V	34	0.442	0.026	2	0.059
Pupa	29	0.377	0.065	5	0.172
Adult	25	0.325	0.052	4	0.160

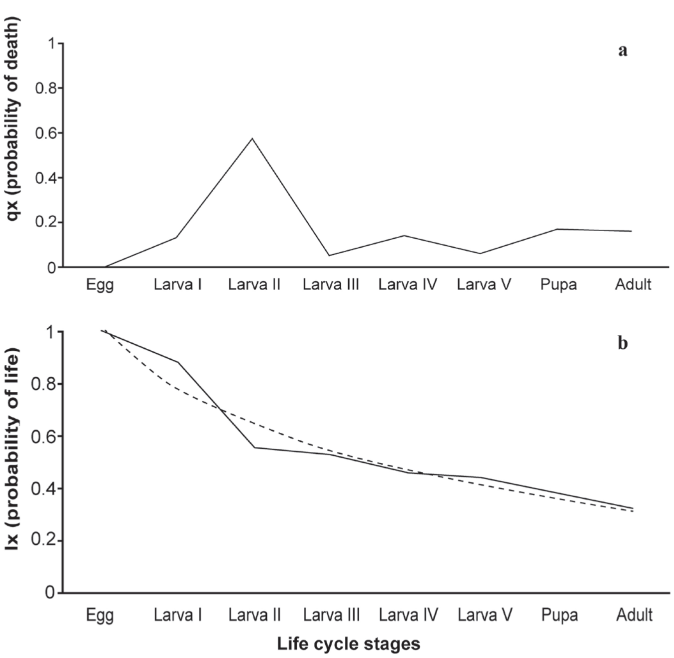

Figure 7. *Oressinoma typhla* life cycle: (a) Mortality Curve; (b) Survival curve.

DISCUSSION

During this research eggs were only found and collected on *Cyperus involucratus* (Cyperaceae), both in nature and in captivity, despite searching several other common Cyperaceae in the field. This leads us to conclude that the butterfly may be locally monophagous, an hypothesis reinforced by other host reports for this genus (DeVries, 1987; Murray, 2001; Beccaloni *et al*., 2008). As *C. involucratus* is an invasive, exotic plant species in South America, *O. typhla* presumably also has a local native species as its original host plant in Venezuela.

With very few exceptions, the subfamily Satyrinae is restricted to feeding as larvae on monocotyledons, within which the majority of species feed on Poaceae (grasses and bamboos) (Beccaloni *et al*. 2008), and a few more poorly studied groups on Arecaceae and Cyperaceae (Murray, 2001). The last family is closely related to Poaceae, thus potentially facilitating host plant switches between the families (Clifford, 1970), as appears likely to have happened in the case of *Oressinoma typhla*.

Oressinoma typhla's life cycle in captivity extended over a total of 48 days at an average temperature of 24°C and an average relative humidity of 82% (egg 5 days, L_1 4 days, L_2 4 days, L_3 6 days, L_4 8 days, L_5 12 days, and pupa 9 days). These figures are comparable to other Neotropical satyrine butterflies, such as *Manataria maculata* (Hopffer, 1874) (48 days) (Murillo & Nishida, 2004), *Taydebis peculiaris* (Butler, 1874) (54 days) (Freitas, 2003) and *Magneuptychia libye* (Linnaeus, 1767) (59 days) (Kaminski & Freitas, 2008), when the life cycle occurs at a similar temperature. The examples mentioned represent species that are relatively distantly related to *O. typhla*, being in different subtribes.

A number of eggs remained unfertilized (n=15) in captivity. We surmise that captive-bred adults (of both sexes) released in the insectarium were unable to achieve full fertility due to the absence of certain proteins and salt nutrients from the butterfly house. Adult females are known to require these essential nutrients for their eggs to reach maturity, and for that reason they visit flower nectar (rich in polysaccharides), as well as, rarely, other sources that provide them with nutrients such as amino acids and nitrogen – these include mineral salts, animal secretions, organic matter in decomposition, and excrement. Adult males are much more common visitors to the latter kinds of food sources, enabling them to provide nitrogen to females for vitellogenesis and egg maturation via the spermatophore (Chew & Robbins, 1984). In the insectarium, however, butterflies only had access to flower nectar, fruit and water.

In the case of egg parasitization (n=8), this was caused entirely by encyrtid hymenopterans. Almost all members of the Encyrtidae are primary endoparasitoids of other arthropods, mainly species of various insect orders. In the case of butterflies they are usually egg endoparasites (Trjapitzin *et al*., 2004), as we witnessed with *Oressinoma typhla.*

Studies of life tables are of great importance as they elucidate aspects of population dynamics (Rabinovich,1978), especially critical stages in the life cycle and mortality rates. The highest mortality rate was found in the change from L_1 to L_2, when only 43 of 68 L_1 larvae successfully transitioned to L_2. This is the most critical stage of the cycle since over 60%

of the L_1 population can be lost, resulting in a decrease of more than half of the total population by L_2. During rearing, it was observed that several conditions influenced survival of the first instar. During this instar, larvae were easily dehydrated, as bodies dried out frequently, while conversely several wild L_1 caterpillars were found drowned in water droplets on the host plant (n=14 to n=18).

Survival rates are also important data, as they reflect the probability of life for each state within the cycle (Rabinovich, 1978). The larval instars of *Oressinoma typhla* with the highest probabilities of survival are those between L_2 and L_5, since they show a smaller population decrease when they are changing stage. A modified Type II survival curve was obtained (with a slight tendency to a Type III curve), in which organisms maintain a constant mortality rate throughout the remaining cycle after a notable initial increase during the first stages. This pattern is very common in almost all insect life cycles (Price, 1997). This curve type is a direct result of the reproductive strategy used by this butterfly species: it lays single eggs, using a type K reproduction strategy (low number of eggs with a high survival rate).

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