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ANIMAL SCIENCE

Immature stages of the limnephilid caddisfly *Verger lutzi* (Navás 1918) (Trichoptera: Limnephilidae): description and larval life-history traits in seasonal forested wetlands of Northwestern Patagonia

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Abstract: The genus *Verger* Navás 1918 (Trichoptera: Limnephilidae), is a Neotropical genus exclusive to the Andean region, with most of its species distributed from Tierra del Fuego to north central Chile and Argentina. Currently, 20 species of the genus have been described from adults and only six larvae have been associated and diagnosed. The ecology of the species is completely unknown. In this work, we describe and illustrate the immature stages of *Verger lutzi* (Navás 1918) and study its breeding phenology, larval growth and adult emergence. The main characters that enable the separation of this species are the coloration the body, shape of the anterior ventral apotome, shape and distribution of metanotal setal areas, distribution of tracheal gills and number of accessory teeth in the anal prolegs. Reproduction occurs during the summer and females lay their eggs on the wetland basin formed by humid leaf litter and organic debris, covered by herbaceous vegetation. Larvae hatch after flooding and overwinter in the wetland. Larvae develop fast during spring and emergence begins in December before the wetland dries up. Description of the immature stages is helpful for use of macroinvertebrates biomonitoring, ecological studies and understanding their ecosystem services in seasonal-lentic habitats.

Key words: caddisfly larvae, dry resistance, morphology, pupal stage, Trichoptera.

INTRODUCTION

The family Limnephilidae is one of the most diverse caddisfly families in the North Temperate Zone of North America and Eurasia, especially in high elevations (Holzenthal et al. 2007). Limnephilidae is ecologically diverse, as larvae inhabit a variety of habitats such as lakes, streams and wetlands (Holzenthal et al. 2007). Limnephilid larvae reach large sizes, around 30 mm long, and construct cylindrical cases formed mainly by plant detritus and minerals (Wiggins 1996). In general, larvae that inhabit cool running waters use rock material, while those living in warmer lentic habitats use plant material (Wiggins 1996). South America has a significant number of limnephilids represented by several endemic genera and species in the subfamily Dicosmoecinae (Flint 1982, Holzenthal & Calor 2017). The genus *Verger* Navás (1918a), is a Neotropical representative of the family Limnephilidae exclusive to the Andean region. It is the most diverse genus within the subfamily Dicosmoecinae, with most of its species distributed in the Cordillera region from Tierra del Fuego to north-central Chile and Argentina (Flint 1982, Angrisano & Korob 2001, Angrisano & Sganga 2009). Of the 20 known species of the genus *Verger*, only 6 have been formally described from its immatures (Angrisano 1983, 1986, Flint 1968, 1982, Jacquemart 1980, Ulmer 1904). Description of immature stages is crucial, not only to have better knowledge of the diversity of the group, but also to understand the functionality of assemblages and their role in freshwater habitats.

In Patagonia, species of Limnephilidae are common in lotic freshwater systems (streams and rivers) with a permanent or temporal flow, and show variation in species composition along altitudinal gradients (Miserendino 1999, Brand & Miserendino 2014, Mariluan et al. 2015). Some species (e.g. *Verger vespersus*) are adapted to live in lentic temporary waters with hydroperiods that extend from autumn to early summer. Prior research has found *Verger vespersus* to be a major contributor to detrital decomposition in lentic freshwaters (Diaz Villanueva & Trochine 2005), similar to other caddisfly larvae whose main function is leaf litter breakdown (Mariluan et al. 2015).

Breeding season, egg hatching, larval development and metamorphosis is unknown for several caddisflies species, particularly for species that reach the southern areas of Argentina characterized by harsh climate conditions and low temperatures (e.g. 0° C) during autumn and winter (Jara & Perotti 2018). *Verger lutzi* (Navás) is a species endemic to the Andean Region (southern Chile and adjacent Argentina). It was originally described by Navás (1918b) from Santa Cruz province (Argentina) in the genus *Nostrafilla*, and nowadays it is known from other Argentinean provinces such as Río Negro, Chubut and Neuquén (Brand 2009, Cohen 2004, Flint 1974, Navás 1918b, 1929, Schmid 1949, 1955). *Verger lutzi* larvae are abundant during autumn to early summer in temporary ponds and pools and serve as food for several aquatic insect predators and also for birds (Jara 2014, 2016). Currently, only the adult stage of *V. lutzi* has been described, but none of its immature stages (larvae and pupae) have been associated. Therefore, the objectives of this work were: (1) to describe the immature stages of *V. lutzi* (2) to determine other species that co-occur with *V. lutzi* and (3) to describe their life cycle and phenology of the larval stage in relation to hydroperiod and temperature in wetlands located within a protected area in Northwestern Patagonia (Argentina).

MATERIALS AND METHODS

Study area

The climate in the area is humid-temperate (Paruelo et al. 1998), with more than 60% of the precipitation (rain and snow) concentrated between May and August, which dictates the austral summer as the dry season (Mermoz et al. 2009). There is marked seasonality in temperature, with cold winters (below 0 °C) and summers with moderate temperatures (Paruelo et al. 1998). The study sites included different types of wetlands such as ponds, pools, meadows and floodplains. These wetlands differed in size and hydroperiod regimens (Table I). All the wetlands were surrounded by forest with dominant *Nothofagus* species (Nothopagaceae) and localized within a protected area (Llao Llao Municipal Park) or in relatively impacted areas, close to Bariloche city (Río Negro province, Argentina, Table I and Fig. 1). The substrates of these water bodies were composed mainly by fine sediment and gravel with scarce or abundant aquatic vegetation, sometimes covered by abundant leaf litter coming from the forest dominated by coihue (*Nothofagus dombeyi*), arrayan (*Luma apiculata*), pitra or patagua (*Myrceugenia exsucca*) and maiten (*Maytenus boaria*) (Table I). The aquatic vegetation was represented by *Juncus balticus*, *J. involucratus*, *Schoenoplectus californicus*, *Carex niederleiniana*, and *Agrostis leptotricha* (Jara & Perotti 2018, Jara 2019, Cuassolo & Díaz Villanueva 2019) (Table II).

Caddisflies sampling for identification

Collection of specimens and environmental characterization

All sampled wetlands were georeferenced with a GPS (©Garmin) and in each case the dominant forest species surrounding the wetland were registered, as well as the light condition as a qualitative variable. We classified the light condition as: 1- full sun, when 80 % of the wetland is sunny during daytime, 2- partially shaded, when at least 50 % of the wetland is sunny during daytime, and 3- completely shaded, when less than 20 % of the wetland area is sunny. Also, in each wetland we recorded water depth (cm), hydroperiod duration (months) and substrate type, which was classified as 1-covered by vegetation, 2-covered by leaf litter or both (1 and 2). All wetlands were sampled in two occasions in May and November 2016. On each sampling event, ten hand net samples (net dimensions 36 cm x 9 cm x 25 cm; 2.5 mm pore size) were taken in the shoreline of each wetland (where larvae congregate during the spring season). Each sample was placed into a plastic try for separation of the caddisfly larvae from the rest of invertebrates. Caddisfly larvae were fixed in 70% ethyl alcohol and transported to the laboratory, where they were identified to species level under a stereomicroscope. Also, several individuals of *V. lutzi* last instar larvae were placed inside enclosures in Llao Llao 1 and Las Cartas (Fig. 1), to obtain the adult stage and associate it to the immatures. The enclosures (five enclosures in each wetland) were made with rectangular plastic baskets (41cm x 29 cm x 20 cm height) lined with a fine mesh to avoid the escape of the larvae but allowing water to flow through them maintaining similar conditions than outside the enclosure. Each enclosure was checked weekly for observation of caddisfly pupation (cases fixed to substrate)

Figure 1. Wetlands located in Llao Llao Municipal Park where *V. lutzi* was found. (a) Las Cartas (pond), (b) Llao Llao 1 (meadow), and (c): Llao Llao 2 (pool).

and subsequent capture of pharate adults and adults, which were preserved in 70% ethyl alcohol.

Identification and description of morphological characters

Adults were identified using usual entomological technics and proper bibliography. The genitalia was dissected and cleared in a hot solution of 10% NaOH for several minutes, neutralized with acetic acid, rinsed in distilled water and mounted in glycerin for observation.

The immatures were associated specifically to the adults using the metamorphotype method (Milne 1939) and analyzing the reared specimens. For viewing and drawing, a Leica® MZ8 stereomicroscope was used. The sclerites of the last instar larva and pupa left in the pupal case and entire larvae and pupae were examined. All the relevant structures were photographed under the microscope using an attached camera. Then the photographs were traced and rendered as line drawings using Adobe Illustrator®. The terminology used for the descriptions follows that of Angrisano (1983, 1986) and Wiggins (1996). Additionally, we examined specimens deposited in the collection of the Laboratorio de Entomología y Aracnología Aplicada (Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires) from Chubut province (Argentina).

Phenology and life history of *Verger lutzi*

The life cycle of *V. lutzi* was studied in detail for two wetlands where the species was found: Llao Llao 1 and 2. Both wetlands were visited monthly from March 2017, and then were visited weekly during November and December when pupation and emergence started. A dip-net sampling technique was used to collect the larvae (Florencio et al. 2012, Jara et al. 2013). All the caddisflies collected were poured in a tray and the number of *V. lutzi* was counted; a subsample of the larvae was preserved in 70% ethyl alcohol in order to measure the total length of each one under binocular microscope in the laboratory. For eggs, pupae and adults, only presence-absence was recorder and several adult specimens were preserved in alcohol for its examination. In addition, a data logger (i-buttom -45+45 °C) was placed in the shoreline of each wetland and set up to register the water temperature each hour. Other environmental variables were also recorded: rainfall (mm) (collected by a pluviometer installed in Llao Llao 1), water depth (cm) and conductivity (μS/cm), as water temperatures in intermittent or seasonal habitats fluctuate more than in permanent habitats and it is thought to be a key signal for insect larval development (Lund et al. 2016). Water depth was measured monthly and conductivity was taken during midday at different water depths where caddisfly larvae were captured.

Natural observation of resistance to dry conditions in pupal stage

In the past few years, we found several Trichoptera pupae among the wet leaf litter that accumulated at the bottom of the studied wetlands even after they had completely dried up. To determine if the pupae in these conditions were viable and if they can emerge as adults, pupal cases attached to the wet leaf litter (*N. dombeyi* and *M. exsucca*) were manually collected during January 2018 and transported to the laboratory. They were separated in groups of 3 or 5 and placed, along with the wet leaf litter, into 250 ml plastic containers with perforated lids. Twenty containers were placed outdoors under shade and natural photoperiod and checked daily for possible emergence of adults. The number of emerged adults was registered. Pupae that did not emerge as adults were dissected under binocular microscope.

Table I. **Wetland features (type, localization, area, depth, hydrology, light condition and surrounding forest species) and caddisflies species found in each wetland during the spring season. Forest species (1-8 from more to fewer individuals) 1-*Nothofagus dombeyii*, 2-*Astrocedrus chilensis*, 3-*Lomatia hirsuta*, 4-*Luma apiculata*, 5-*Salix* sp. (exotic), 6-*Maitenus boaria*, 7-*Sorbus* sp. (exotic), 8-*Acer* sp. (exotic). Light condition: 1-full sun, 2-partially shaded, 3-completely shaded. Substrate type: 1-covered by sedges, grasses and rushes, 2-covered by leaf litter.**

Wetland	Type	Location	Area	Depth	Hydroperiod	Light condition	Forest species	Substrate type	Caddisfly species
Las Cartas	pond	41° 4' 33"S	12600	1.2	10	2	1,2	1, 2	*Verger lutzi*, *V. vespersus*
		71° 31' 39"W							
Llao Llao 1	meadow	41° 2' 57"S	1600	0.38	8	2	1,2,3,4	1, 2	*V. Lutzi*, *V. vespersus*
		71° 34' 2"W							
Llao Llao 2	pool	41° 3' 5"S	35	0.6	7	3	1,2,4	2	*V. Lutzi*, *Austrocosmoecus* sp.
		71° 32' 36"W							
Llao Llao 3	pool	41° 3' 5"S		0.3	8	3	4	2	*Austrocosmoecus* sp.
		71° 32' 36"W							
LLao Llao 4	pool			0.4	8	2	3,4	1,2	*V. lutzi*, *V. vespersus*
Camping Musical	floodplain	41° 3' 46"S	---	0.6	12	1	4,6	1	*Verger* sp.
		71° 31' 15"W							
Fantasma	pond	41º 5' 35"S	12000	2	10	1	2,3,5,6,7,8	1	*V. vespersus*
		71º 27' 4"W							
Dos de Agosto	meadow	41° 5' 49"S	90	0.45	8	1	1,2,6	1	*V. vespersus*
		71° 27' 35"W							

Table II. List of plants present in each wetland inhabited by *Verger lutzi*.

Las Cartas	Llao Llao 1	Llao Llao 2
Potamogetom linguatus	*Schoenoplectus californicus*	*Carex niederleiniana*
Chara sp.	*Carex niederleiniana*	*Ranunculus repens*
Carex niederleiniana	*Juncus involucratus*	*Hydrocotile chamaemorus*
Carex aematorrincha	*Polypogon australis*	*Galium cfr. Palustre*
Juncus sp.	*Galium cfr. palustre*	*Lotus* sp.
Juncus involucratus	*Juncus balticus*	
Schoenoplectus californicus	*Alopecurus pratensis*	
	Juncus balticus	
	Polypogon australis	
	Agrostis cf. leptotricha	

Data Analysis

Larval size structure was compared between wetland for each month using t-test. Only the data of Jun, July, September, October and November were used (in May only one wetland had larvae).

RESULTS

Systematics

Verger lutzi (Navás, 1918)

Verger lutzi (Navás) 1918b: 499 [in *Nostrafilla*], Schmid 1955: 54 [to *Magellomyia*, incertae sedis], Cohen 2004: 79, Brand 2009: 225, Holzenthal & Calor 2017: 357.
—*pirioni* (Navás), 1929: 332 [in *Psilopsyche*], Schmid 1949: 403 [*Australomyia*], Schmid 1955: 53 [to *Magellomyia*], Flint 1974: 89 [checklist], Flint et al. 1999a: 80 [to synonymy].
—*latchani* (Navás), 1935: 374 [in *Psilopsyche*], Flint et al. 1999a: 79 [to synonymy].
(Figs. 2-5)

Larva. Length 17-18 mm (n=4). Sclerotized parts of the body reddish-brown, covered by erect, strong setae.

Head. Oval in dorsal view, coloration reddish-brown, with characteristic pattern of yellow and fuscous maculae, muscle scars darkly marginated; in lateral view 1.2x longer than high, dorsal and ventral margins straight, stemmata surrounded by a pale area; chaetotaxy typical for the genus, setae 9 and 15 very long (2/3 and 1x the length of the head respectively) (Figs. 2a-d). Frontoclypear apotome spatula-like, mesolateral notches very pronounced, anterior margin straight, dark, with a yellowish, hourglass shaped macula mesally (Figs. 2a, b), fronto-clypeal ratio= 0.5 (as defined by Angrisano 1983), in lateral view frontal area almost flat (Fig. 2d). Labrum rectangular, lateral margins straight, anterior edge rounded with a mesal cleft, chaetotaxy typical for genus (Fig. 2e). Mandibles symmetrical, each with an internal tuft of setae and 4 apical teeth (Fig. 2f). Anterior ventral apotome triangular, 2/3x the length of ventral ecdisyal line, anterior margin straight and produced laterally, posterior end produced in a thin rod almost reaching the posterior end of the ventral ecdisyal line (Figs. 2c, g).

Thorax. Pronotum completely sclerotized, divided mesally by longitudinal ecdisyal line into two hemitergites, each extending laterally to the coxae, with a transverse depression in the anterior third. Coloration in alcohol stramineous, with reddish-brown muscle scars. Anterior margin straight, darker, with a mesal cleft, antero-lateral edges rounded; posterior end blackish, separated by a transversal depression and a carina, in dorsal view with a mesal cleft (Figs. 3a, b). Chaetotaxy as showed in figure 3a, anterior margin with about 20 long, thick setae, mesal pair longer, and 20 medium sized setae between them, the rest of the sclerite covered by medium sized setae, except for very long and erect ones in different positions: 1 meso-dorsal pair, posterior to the transverse depression, 1 antero-lateral pair and 1 meso-lateral pair, above the pleural suture. Prosternum with a postero-mesal trapezoidal sclerite and 3 very small oval sclerites at each side, prosternal horn evenly arched.

Mesonotum sclerotized, rectangular, concave anteriorly, straight posteriorly, postero-lateral corners rounded, divided mesally by a thin ecdisyal line; with a transverse U-shaped depression running from one antero-lateral corner to the other; coloration in alcohol stramineous, with reddish-brown muscle scars, posterior margin darker (Figs. 3a, b). Sclerite covered by small to medium sized setae, except for a number of very long and erect setae: 1 meso-dorsal pair, 1 antero-mesal pair and a group of 3-4 latero-mesal setae on each side (Fig. 3a). Mesosternum with a group of 6 antero-mesal, small setae, posterior margin of the segment with a row of 4-5 small, rounded sclerites on each side of the medial line.

Metanotum with 6 sclerotized plates, antero-mesal pair (Sa1) small, oval, transverse, with 2-3 long and 1 small setae, postero-lateral pair (Sa2) subtriangular, with 2-3 very long and 2-3 small setae, lateral pair (Sa3) rectangular, long (reaching the posterior margin of the segment), produced mesally in the anterior third, curved ventrally, tapering to the ends, that are rounded, with 7-9 long and 3-4 small setae on the anterior half (Fig. 3b). Metasternum with 2 antero-mesal rows of setae, anterior one with 5 short setae, posterior one with 4.

Forelegs shorter and wider than mid- and hindlegs, midlegs longer than the others (Figs. 3b-e).

Forelegs. Coxa with 1 dorso-proximal and 1ventro-distal long setae; dorso-distal margin with 3 long and 2 short setae in the external side; external surface of the segment completely covered by minute spicules; the rest of the chaetotaxy as shown in figure 3c. Ventral margin of throchanter covered by small spines, anteriorly with 2 thick spines; with 3 long setae ventrally, 1 anterior, 1 mesal and 1 posterior and a tuft of thin, medium sized setae antero-mesally; posterior, external surface covered by minute spicules; the rest of the chaetotaxy as shown in figure 3c. Antero-dorsal corner of femur with 1 long seta, posteriorly with 1 medium sized seta; ventral margin with very small spines in the first third of the segment and medium sized ones in the other two-thirds, additionally with 2 long spines mesally; postero-external surface covered by minute spicules ventrally; the rest of the chaetotaxy as shown in figure 3c. Tibia widened distally, with 2 antero-ventral large spines; dorso-distal corner with 2 medium sized setae. Tarsus with 1 apico-ventral and 1 apico-dorsal setae; ventral margin with 2 small spines distally and a series of rounded protuberances running from the apex to the middle of the segment. Claw curved ventrad, bearing a basal oblique spine (Fig. 3c).

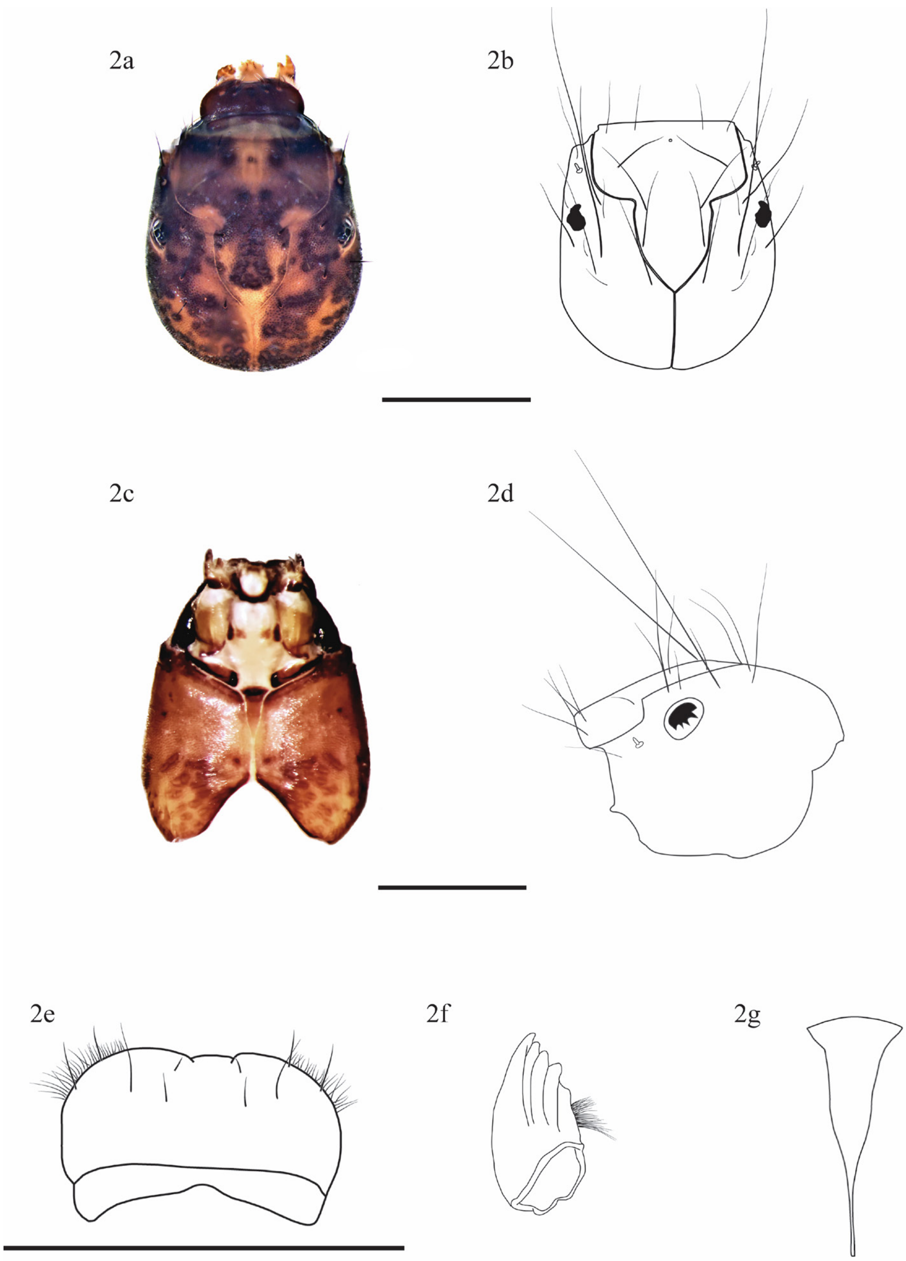

Figure 2. ***Verger lutzi*** **larva. (a) Head, dorsal. (b) Chaetotaxy of the head, dorsal. (c) Head, ventral. (d) Head, lateral. (e) Labrum, dorsal. (f) Left mandible, dorso-internal view. (g) Posterior ventral apotome. Bars: 1 mm (upper bar similar for figures a, b, c, d lower bar for figures e, f, g).**

Midlegs. Coxa with 1ventro-distal long setae; ventral margin with 3 long setae and 4 medium sized setae, dorso-distal margin with 3 long and 4 medium sized setae in the external side, internally with 2; dorso-proximally with 3 long and 5 medium sized setae; external surface of the segment completely covered by minute spicules; the rest of the chaetotaxy as shown in figure 3d. Throchanter with 3 long, ventral setae and 1 apico-ventral spine; ventral margin covered by small spines; ventro-external surface of the segment bearing minute spicules; the rest of the chaetotaxy as shown in figure 3d. Ventral margin of femur bearing 4 long spines and a series of small ones, additionally with 2 long setae; apico-dorsal corner of the segment with 1 very long seta; ventro-external surface of the segment bearing minute spicules; the rest of the chaetotaxy as shown in figure 3d. Tibia with 2 apico-dorsal long setae, posterior to them with 1 long and 1 medium sized setae; with 1 apico-ventral spine, the rest of the ventral margin covered by small ones; ventro-external surface of the segment covered by minute spicules. Tarsus bearing 1 very long seta near the apex and 1 long posteriorly; ventrally covered by small spines and with 1 subapical seta. Claw long, lightly curved ventrally, bearing 1 basal spine (Fig. 3d).

Hindlegs. Coxa with 1 proximo-dorsal and 1 ventro-distal long setae; ventral margin with 3 long setae and 2 medium sized setae, dorso-distal margin with 2 long, 6 medium sized and 2 small setae externally; external surface of the segment completely covered by minute spicules; the rest of the chaetotaxy as shown in figure 3e. Throchanter with 3 long, ventral setae 1 medium sized mesal seta and 1 apico-ventral spine; ventral margin covered by small spines; ventro-external surface of the segment bearing minute spicules; the rest of the chaetotaxy as shown in figure 3e. Ventral margin of femur bearing 4 long, 4 medium sized spines and a series of small ones, additionally with 1 long seta near the apex; apico-dorsal corner of the segment with 1 very long seta; dorsal margin bearing 2 long and 2 medium sized setae; laterally with 2 external, long setae; ventro-external surface of the segment bearing minute spicules; the rest of the chaetotaxy as shown in figure 3e. Tibia with 2 apico-dorsal long setae, posterior to them with 2 medium sized seta; ventrally with 1 apical spine, the rest of the ventral margin covered by small ones; ventro-external surface of the segment covered by minute spicules. Tarsus bearing 1 very long seta near the apex and 1 small anteriorly; ventrally covered by small spines. Claw lightly curved ventrally, bearing 1 basal spine (Fig. 3e).

Abdomen. First abdominal segment without gills. Dorsum with a group of 4 long and 2 medium sized setae on each side of the dorsal hump, anteriorly with a row of 6 medium sized setae and 1 very long pair, the rest of the notum with very small setae. Lateral humps with 2 very long and 4 medium sized setae dorsally, postero-ventrally with 1 long seta. Sternum with 2 groups of 5 postero-lateral long setae, posteriorly with 2 rows of setae, anterior row with 9 (1 pair very long) and posterior row with 14, anterior to them with 1 mesal pair of very long setae, the rest of the sternum with about 60 medium sized and very small setae. All setae, except for the small ones, arising from a very small circular sclerite.

Tracheal gills densely branched, present from segment II to VIII. Position of the gills and number of branches as shown in figure 4 (number of branches found on one specimen, there is a lot of variation between individuals, even in different sides of the same specimen).

Lateral fringe from segment III to VIII, formed by very thin setae, each setae about 1/5x the length of the segment.

Dorsum of segment II with 2 pairs of long setae anteriorly and 3 very long postero-mesally, additionally with 2 lateral pairs (one dorsal long, and one ventral short) and a ventral pair of long setae. Segment III with 1 dorsal and 1 ventral pair of long setae. Segments IV to VIII also bearing the dorsal pair, additionally segment VII with 2 dorsal pairs of short setae and segment VIII with a posterior row of 30 medium sized setae, 1 lateral pair of long setae and a very short postero-ventral pair.

Segments III to VII with oval, transversal, sclerotized rings; in segment III this ring is short (about 0.15x the wide of the segment), in the other segments is 2x wider.

Tergite IX strongly sclerotized, rectangular, anterior and posterior margins concave, covered by thick spines and black, rigid setae, the postero-mesal pair extremely long; anterior to the tergite with 2 rows of 6-8 medium sized, thick

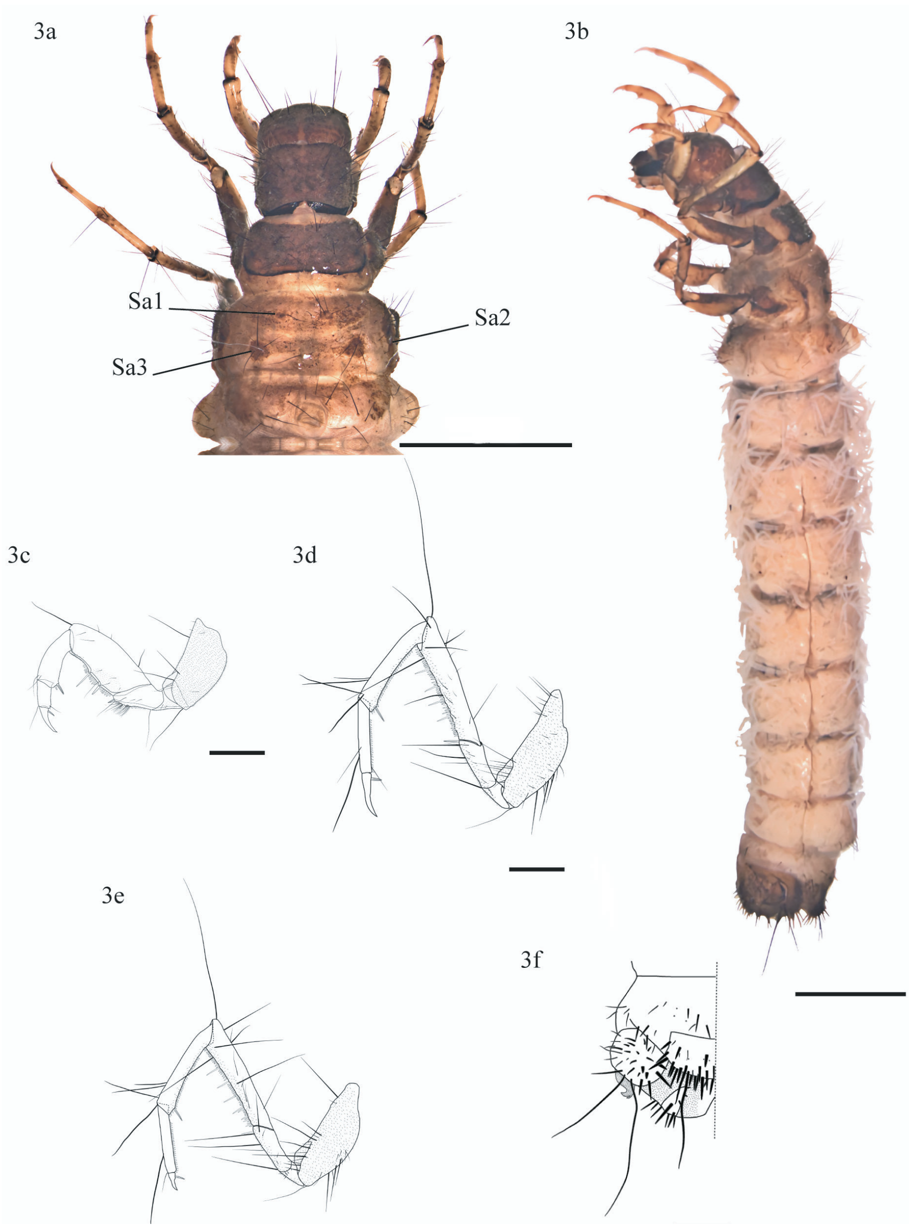

Figure 3. ***Verger lutzi*** **larva. (a) Head, thorax and first abdominal segments, dorsal. (b) Habitus, lateral view. (c) Left foreleg, external view. (d) Left midleg, external view. (e) Left hindleg, external view. (f) Abdominal segment IX and anal proleg, dorsal (left only). Sa1: setal area 1, Sa2: setal area 2, Sa3: setal area 3. Bars: 2 mm.**

setae, the rest of the notum with thin and small setae distributed as in figure 3f. Sternum with a mesal pair of medium sized setae and about 10 small setae. Lateral sclerite also bearing thick spines and black, rigid setae, 1 pair very long. Anal prolegs with 1 accessory tooth. Membrane between anal prolegs and anal invagination covered by minute spines, in this area there is an oval, elongated perianal sclerite bearing small, rigid spines (Fig. 3f), subperianal sclerite oval, straight anteriorly, posterior margin with 6 long setae.

Case. Tubular, lightly curved ventrally, constructed with small pieces of plant material arranged obliquely to its longitudinal axis; in some specimens with large fragments of leaves covering the posterior third of the case (Fig. 5a).

Pupa. The pupae of the known species of *Verger* are very similar. Here we describe the distinctive characters found in the pupa of *Verger lutzi*.

	I	II	III	IV	V	VI	VII	VIII	IX
Dorsal		15 18	15 14	12 10	9 8	8 7	8 6	6	
		6	6	3					
		9	4	2					
Ventral		14 17	15 16	13 13	9 10	9 8	7 7	6	

Figure 4. Position and number of branches (arabic numerals) of abdominal tracheal gills in the larva of the caddisfly *Verger lutzi*. I-IX: number of segment.

Habitus as showed in figure 5b.

Head. Labrum quadrangular, curved lateral and anteriorly, bearing 2 anterolateral groups of long, thick, black, erect setae with the apex curved (hook-like); anterior margin lightly produced mesally, with a pair of white, small setae; postero-mesally with 2 lateral groups of 3 setae (1 mesal long, black and 2 lateral smaller, white); mesal area of the labrum covered by small setae (Fig. 5c). Mandibles symmetrical, wide basally, apex acute, internal margin serrated, with 3 setae postero-ventrally (Fig. 5d).

Thorax. Pronotum with 2 pairs of setae, 1 anterior and the other posterior. Mesonotum bearing 1 pair of long, mesal setae. Metanotum with 1 pair of long, mesal setae and 1 small seta at each side of this central pair. Pterotecae reaching segment IV of the abdomen (Fig. 5b). Legs with swimming setae reduced: in forelegs absent, midlegs with tarsites I-IV bearing lateral rows of long setae, hindlegs with setae in the same position as in midlegs but short.

Abdomen. Segment I-VI bearing a pair of long, posterior setae, segment VII additionally with 2 pairs of latero-posterior short setae, segment VIII with 1 pair of long, anterior setae and posterior pairs, segment IX bearing 3 pairs of long setae posteriorly. Dorsal hook plates typical for the genus (Figs. 5b, e), present in segments I (only posteriorly) and III-VII (anteriorly except for segment V that bears a pair of oval, transverse posterior plates). Lateral fringe of setae from segment VI to VIII, bending ventrally where both sides meet. Apical processes as in figure 5b.

Material examined. ARGENTINA: Río Negro province: Llao Llao Municipal Park. Mallín Las Cartas, 30.xi.2016, 4 larvae, 2 pupae, 2 females, 4 pharate males. Mallín Llao Llao, 19.xi.2016 6 larvae, 2 females, 1 male. Poza Llao Llao, 2.xi.2017, 5 larvae. Chubut province: Aldea Escolar, A° Blanco, 7.ii.1993, Valverde col., 3 larvae.

Environmental features of the larval habitat

Verger lutzi larvae were observed in three of the six wetlands sampled (Table I, Fig. 1), located in Llao Llao Municipal Park. Those wetlands were well preserved, and surrounded by vegetation, mainly *Nothofagus dombeyii, Luma apiculata* and *Myrceugenia exsucca*. The wetlands inhabited by *V. lutzi* were fully exposed to the sun or partially shaded by the forest (Table I). The bottom of these wetlands were covered by different species of sedges, grasses and rushes. Hydroperiod extended for several months (usually 8-10) and in some cases the wetlands turned in permanent (*e.g.* Las Cartas) (Table I). A characteristic of these water bodies was

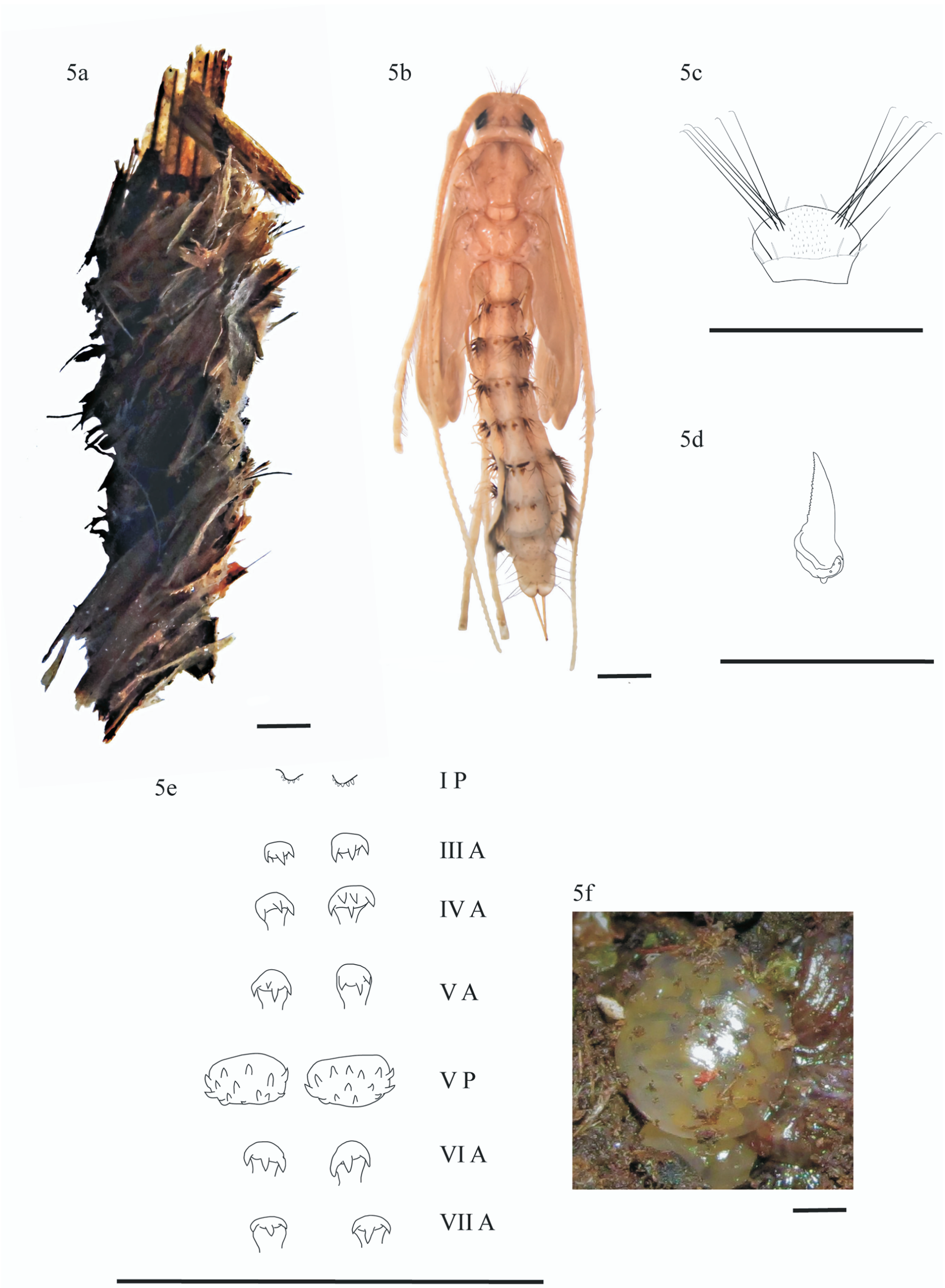

Figure 5. ***Verger lutzi*. (a) Case, lateral. (b) Farate adult, dorsal. (c) Pupal labrum, dorsal. (d) Pupal right mandible, dorsal. (e) Pupal dorsal plates. (f) Eggs. I-VII: number of segment. A: anterior. P: posterior. Bars: 2 mm.**

its seasonality, with low conductivity during autumn and winter (30-90 µS) that increased as they dried up during the spring season (up to 250 µS). Winter temperature pattern determined that these wetlands had frozen surface for periods of days or weeks. The pH was always close to neutral with a slight increase towards the end of the hydroperiod (6.5-7.8). The wetlands varied in size from very small, as pools, to large, semi-temporary wetlands (Las Cartas) (Table I). All three wetlands had aquatic vegetation as grasses and rushes, and no larvae were found in wetlands without aquatic vegetation (Table II).

Rainfall patterns in Llao Llao Municipal Park during 2016 showed an increase in precipitation during winter, especially in June and August (Supplementary Material - Figure S1). The air temperature in the area showed high temperatures during summer, low temperatures during autumn and winter and moderate temperatures during spring (Fig. S1). The wetlands inhabited by the larval stage of *Verger lutzi* were characterized by cold water temperature during fall and winter with low thermal amplitude, and moderate temperature with large daily fluctuation during spring (Fig. S2).

Phenology and life history of *Verger lutzi*

Verger lutzi larvae had a univoltine life cycle in all studied wetlands, where they coexisted with three other limnephilids, *V. vespersus*, an undetermined *Verger* species and *Austrocosmoecus* sp. (Table I). Egg masses (Fig. 5f) were found during late summer, March-April, among detritus or leaf litter in the wetlands substrate (Fig. S2). Eggs hatched apparently after several weeks of flooded that occurred early in Llao Llao 1. First larvae were captured in May in Llao Llao 1 and in June in Llao Llao 2 (Fig. S2). Pupation was observed during November and emergence occurred during December (Fig. S2). The larval size structure ranged from 2.5 mm in recently hatched larvae to 21.4 mm in the last larval instar (Fig. S3). Comparisons by t-test indicated that larval total length differed between wetlands in June, July and October (June $t= 6.036$, $p<0.001$, $N=24$; July $t= 2.015$, $N = 30$; October $t = 2.906$, $p = 0.01$, $N = 30$).

Natural observation of resistance to dry conditions in pupal stage

The average daily air temperature during the period of observation was 14.6 ± 3 °C (range 9.8-22 °C; Fig. S4a). We found that the first adults emerged from the containers after five days since the pupae were placed in the containers and the last adult was observed at day 20 (Fig. S4b). After that no adult emerged and the remaining pupae were completely dry. In total twenty-five *V. lutzi* adults emerged during the experiment (Fig. S4b). Adult size was on average 11.59 ± 0.73 mm (range 10.22-12.77 mm).

DISCUSSION

Systematic considerations

The larva of *Verger lutzi* (Navás) is similar to that of *V. vespersus* (Navás). The characters that enable the differentiation of these two species are the coloration of the sclerotized parts of the body (especially the pattern of the cephalic capsule) along with the shape of the anterior ventral apotome, shape and distribution of metanotal setal areas, distribution of tracheal gills, number of accessory teeth in the anal prolegs and the pilosity of the body (Table III). Regarding the pilosity of the larvae of both species, *Verger lutzi* bears longer setae and is larger than *V. vespersus*.

These larvae, and the larvae of the other described species in the genus are compared in Table III (*Verger spinosus* was excluded because the characters used herein could not be obtained from the original description and illustrations). In addition to the characters named above, the length of setae 9 and 15 in the cephalic capsule, the fronto-clypeal ratio and the presence/absence of perianal sclerites are important for the identification of the known larvae of *Verger*.

The pupae of the genus *Verger* are very similar. Only the chaetotaxy of the body shows interspecific variation but there is no sufficient information in the original descriptions to give a list of diagnostic characters at the moment.

Habitat, phenology and life history

Trichoptera larvae inhabit a variety of aquatic environments. Although being more frequent in

Table III. **Diagnostic characters of the known larvae of the genus *Verger* (Navás). II-VIII: number of abdominal segment.AD: antero-dorsal, AV: antero-ventral, PD: postero-dorsal, PV: postero-ventral, AL: antero-lateral, PL: postero-lateral. N/A: not available. -: absent.**

	Verger lutzi	***Verger vespersus***	***Verger appendiculatus***	***Verger porteri***	***Verger bruchinus***	***Verger masafuera***
Anterior ventral apotome.	Triangular (2/3x the length of ventral ecdisyal line), posterior end elongated.	Lanceolate, almost reaching posterior end of head.	Pentagonal.	N/A	Triangular, short.	N/A
Head setae 9.	2/3x length of head.	2/3x length of head.	1/2x length of head.	7/2x length of head.	3/4x length of head.	3/2x length of head.
Head setae 15.	1x length of head.	1x length of head.	1/2x length of head.	7/2x length of head.	3/4x length of head.	5/2x length of head.
Anterior margin frontoclypear apotome.	Hourglass-shaped macula.	Hourglass-shaped macula.	Rectangular macula.	Round macula.	Vase-shaped macula.	N/A
Fronto-clypeal ratio.	0.5	0.45	0.5	0.5	0.45	0.5
Metanotal setal areas (sa) Sa 1 Sa 2 Sa 3	Oval, small. Subrectangular, long. Subtriangular.	Oval, small. Subrectangular, long. Subtriangular.	Oval, small (reaches midline). Subrectangular, short. Subtriangular.	Oval, large (reaches midline). Subrectangular, long. Divided. 2 subrectangular, large, 2 oval, small.	N/A N/A N/A	Oval, small Subrectangular. N/A
Position of gills. AD AV PD PV AL PL	II-VIII II-VIII II-VII II-VII II-IV II-IV	II-VIII II-VIII II-VII II-VII II-IV II-V	II-V II-IV II-IV II-VII - II	II-VIII II-VIII II-VII II-VII II-IV II-III	II-VIII II-VIII II-VII II-VII III III	II-VIII N/A II-VII N/A II-IV N/A
Perianal sclerites.	Present.	Present.	Absent.	Present.	Absent.	Present.
Number of anal proleg accessory teeth.	1	2	1	N/A	1+ 1 or 2 very small.	1
Mean body length.	18.5 mm	15 mm	13.5 mm	18 mm	12.5 mm	15 mm

cool, lotic habitats, they can also be found in permanent or temporary, lentic sites (Flint et al. 1999b). Five of the eight families that have been recorded in lentic habitats, including Limnephilidae, are portable-case makers. The ability of the members of these Trichoptera families to exploit these habitats relies on their capability to obtain oxygen and to resist desiccation (Wiggins 1996).

Verger lutzi, as well as co-occurring species inhabit lentic temporary habitats, with a univoltine life cycle without overlapping of generations. These larvae overwinter in temporary wetlands of various sizes free of fish predators, and develop fast during spring when temperature increases and aquatic insect predators colonize the wetlands (e.g. belostomatids; Jara 2019). At least in this study, *V. lutzi* larvae were present at higher densities in wetlands partially shaded or fully exposed to the sun, may be as a response to the growth of a diverse species of grass in the wetland stimulated by the sun (see Table II). Also the wetlands received the subsidy of organic matter from leaves of trees that probably were used as food resources by the larvae and for the construction of their cases. Studies on the feeding ecology of the Patagonian species of *Verger* are required to better understand its trophic role. Typically, the wetlands had neutral or more alkaline pH and conductivity increased with the habitat desiccation similar to water temperature. These variables probably have an effect in the development of the larvae as occurs in another groups of aquatic insects (Sweeney 1984).

Caddisfly species living in temporary ponds exhibit a number of strategies that allow their survival (Williams 1997). These adaptations are commonly divided into three types: physiological tolerance, life history modification, and migration. *Verger lutzi* presents only one generation each year, with adults emerging in late spring that live through summer to oviposit in summer - early autumn in wetland basins. The same pattern was registered for other limnephilids by Wiggins et al. (1980). Also, eggs were observed covered by sediments and leaf litter, sometimes together with amphibian eggs of the terrestrial-breeding frog *Batrachyla* spp. (Jara, pers. obs.).

The duration of the life cycle, from egg hatching until emergence as adults is adapted to the hydrological conditions of each pond. Our field data observation indicated that the egg hatching can be delayed for several weeks until pond flooding. In this sense, species that inhabit temporary aquatic environments show life history characteristics (fast larval growth and development, desiccation-tolerant eggs) that allow them to reproduce and develop in both permanent and temporary habitats (Wissinger et al. 2003). Therefore, we hypothesized that *V. lutzi*, along with the other caddisfly species found in the studied wetlands, have desiccation-tolerant eggs, as well as other limnephilid species (Holzenthal et al. 2015). For example, in 2016 ponds filled later in August and after two weeks we observed small *V. lutzi* larvae. In 2017, ponds filled in early May and small *V. lutzi* larvae were observed in late May, early June. As well as hatching time (Ruiz-Garcia & Ferreras-Romero 2007), pupation and metamorphosis can be accelerated or delayed following different environmental signals (Schneider & Frost 1996, Williams 1996, 1997). Pupation started in late November and all the larvae disappeared from the wetlands during December. The typical increase of water temperature during spring and the large thermal variation that occurred during the day probably played a key role in the pupation initiation and adult emergence of this species. In this sense, the increase of water temperature caused some aquatic insects to mature more quickly and at smaller sizes (Sweeney & Vannote 1978, Hogg & Williams 1996). It is possible that in cold adapted species, as *V. lutzi*, developmental rate is thermally sensitive, which would allow tracking of the seasonal changes in temperature due to natural desiccation of the habitat. Thus, these environmental features impose to species a common trade-off in temporary environments, short development time vs emergence at large adult size (Chown & Nicolson 2004). Frequently, caddisfly larvae inhabiting intermittent water bodies survive dry periods as large aestivating larvae or pupae in leaf litter (Zale et al. 1989). However, most of the observations have been conducted in lotic environments, herein we present one of the first reports in lentic temporary environments of Patagonia. As evidenced in the present contribution, the pupal stage of *V. lutzi* shows resistance to desiccation. After fourteen days, we observed the pupae survived under the wet leaf litter and emerged as adults during semi-experimental conditions. This resistance can be an adaptation for survival in a crucial stage in their life history, emergence into the adult. In this sense, during extremely short hydroperiods some individuals in the population can still reach the adult stage. Various environmental cues have been postulated to explain developmental and behavioral responses in aquatic organisms: increased temperature (e.g., Harper & Peckarsky 2006), decreased water volume or depth (e.g., Juliano & Stoffregen 1994), variations in food availability and also combinations of them (Johansson et al. 2001, De Block & Stoks 2004a, b, Jannot et al. 2008).

Austrocosmoecus sp. was found in fully shaded wetlands with few or no grasses but a great abundance of leaf litter in the bottom that larvae use to construct their cases. The role of caddisfly larvae in aquatic ecosystems have been discussed in several works (Shin et al. 2013, Morse et al. 2019). They feed on detritus, plant detritus, living macrophytes or living macroinvertebrates. They can belong to different functional groups as shredders, scrapers, filter-feeders or predators (Brand & Miserendino 2011). In aquatic ecosystems of Patagonia, caddisfly larvae play a key role in organic matter fragmentation in both, lentic (temporary ponds, Diaz Villanueva & Trochine 2005) and lotic ecosystems (streams and rivers, Brand & Miserendino 2014), where the leaf litter covers the entire bottom in forested wetlands as the ones studied here. In some situations, the trophic role of caddisflies can change according with the ontogeny of the species. Recently, Lund et al. (2016) found that some Limnephilidae species in temporary ponds cannibalized small congeneric larvae as response to stress conditions (protein intake) produced by drying wetland process. We observed aggressive behavior of larger congeneric larvae of *V. lutzi* upon smaller ones, and in some cases we observed attacks of this species upon small anuran tadpoles (*Pleurodema thaul,* Leptodactylidae) and some were partially consumed. Therefore, further investigation on caddisfly larvae are needed to understand the real trophic role and their implications in the food web of temporary ponds, especially because the food sources in each pond appears to be different.

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SUPPLEMENTARY MATERIAL

Figure S1. Cumulative precipitation in mm and average maximum air temperature (°C) during 2017 in the study area.
Figure S2. Phenology of the caddisfly *Verger lutzi* in two wetlands (a: Llao Llao 1, b: Llao Llao 2) in relation with water temperature. 1: mating and eggs laying, 2: embryos development, 3: larval development, 4: pupation, 5: adult emergence.
Figure S3. Larval size-size structure of *Verger lutzi* in the sampled wetlands. (a) Llao Llao 1 and (b) Llao Llao 2. August was the month where the wetlands surface was completely frozen. * indicates significant differences between wetlands (t-test p > 0.05).
Figure S4. Emergence of adults of *Verger lutzi* from pupae kept in dry conditions. (a): daily air temperature (mean ± SD) and (b): Cumulative adult emergence during the experimental period.

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