

Larval habitat and behaviour of *Phenes raptor* (Odonata: Petaluridae): a review of current knowledge, with new observations

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Phenes raptor is one of only two petalurid dragonflies with a documented non-fossorial larval lifestyle. There have been few reported observations of larvae and their habitat, and the behaviour and ecology of this unique South American species remain largely unknown. This paper provides a review of previously published and unpublished information, and new observations on the habitat and behaviour of larvae and imagines. Larval habitat ranges from fens or seepages to moist terrestrial forest floor litter habitats. Better understanding the ecology and behaviour of the species will require observation of mating locations, additional observations of larvae in habitat and of oviposition and emergence sites across the species' broad geographic and bioclimatic range.

Keywords: Odonata; dragonfly; *Phenes raptor*; Petaluridae; larval habitat; behaviour

Introduction

Phenes raptor Rambur (Odonata: Petaluridae) is one of 11 currently recognised species in five genera in this dragonfly family (Fleck, 2011; Hawking & Theischinger, 2004); it is a large species and the only South American petalurid. The species includes two subspecies, *P. r. raptor* and *P. r. centralis* (Jurzitza, 1989a). It is recorded from Chile and Argentina (Garrison et al., 2006), extending south in Chile from the central region around Santiago (*P. r. centralis*) to Puerto Ramírez in northern Patagonia (*P. r. raptor*) (e.g. Garrison & Muzón, 1995; Heppner, 1996; Joseph, 1929; Jurzitza, 1989a, 1989b; Svihla, 1960); and with isolated records from Patagonian Argentina, on the eastern side of the Andes, in Neuquén (*P. r. raptor*) (Muzón, 1995) and Chubut Provinces (Pessacq, in prep.). The imago recorded from Chubut Province was damaged and could not be identified to subspecies (P. Pessacq, personal communication, March 20, 2012), but was presumably *P. r. raptor*. Records for the species also include Rio Chaitén on the coast of Isla Grande de Chiloé by Peña (1962, cited by Jurzitza, 1989b). The distribution map for the species provided by Garrison et al. (2006) does not include Chiloé within the identified distribution.

The record of a male imago from Chubut Province, Argentina, on the shore of Lago Puelo and at the mouth of the Rio Turbio is a new southern range extension for Argentina, although slightly north of the most southerly Puerto Ramírez locality in Chile. It is associated with a large

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river valley that connects Chile and Argentina, potentially providing low altitude connectivity through the Andes (via Paso Rio Puelo) for dispersing *Phenes* imagines. Pablo Pessacq (personal communication, March 20, 2012) has commented that there are additional unusual records from Puerto Patriada, 14 km west of the *Phenes* locality, of what he referred to as “intrusions of the Valdivian forest fauna” from Chile; including Odonata, Ephemeroptera and Plecoptera (see Pessacq & Miserendino, 2008). Similarly, the more northerly *Phenes* records from the area around San Martín de los Andes in Neuquén Province, Argentina (Muzón, 1995) are broadly associated with the Rio Hua Hum valley, which also dissects the Andes, providing potential low altitude connectivity between Chile and Argentina for dispersing *Phenes* imagines.

Within the Petaluridae, most species utilise a ground-dwelling, larval burrowing (fossorial) habit that is unique in the Odonata (Corbet, 1999). Fossorial petalurids excavate permanent burrows, with a burrowing habit documented in *Petalura gigantea* Leach, *P. hesperia* Watson, *Tanypteryx hageni* (Selys), *T. pryeri* (Selys), *Uropetala carovei* (White) and *U. chiltonii* Tillyard. These typically extend below the water table in boggy areas, although considerable variation in burrow depth and complexity is reported among species (Baird, 2012; Benson & Baird, 2012; Rowe, 1987; Svihla, 1959; Taketo, 1958, 1971; Tillyard, 1911; Watson, 1965; Winstanley, 1981, 1982; Wolfe, 1953). Early stadia larvae of *T. pryeri* (Taketo, 1958) and *T. hageni* (Svihla, 1984) have also been observed in moist sites amongst mosses and decaying leaves prior to burrow development. The larval habits of the Australian *P. ingentissima* Tillyard (North Queensland) are unknown, although exuviae have been found above small tunnels in rainforest stream banks (Winstanley, 1982). This habitat was similar to the muddy rainforest stream-bank ovipositing sites reported for this species by Davies (1998), who also reported that it was associated with boggy montane seepage sites. Exuviae of *P. pulcherrima* Tillyard and apparent ovipositing have been observed in swampy patches adjoining creek banks (Theischinger & Endersby, 2009). The larval habits of this second North Queensland species are unknown, although it may be presumed that they are similar to its congener, *P. ingentissima*. Based on their distribution and swamp habitat type, it may also be presumed that *P. litorea* Theischinger has a similar burrowing habit as its congener, *P. gigantea*.

In contrast, the North American (eastern USA and Canada; Paulson, 2011) *Tachopteryx thoreyi* (Hagen) and *Phenes raptor* have a non-burrowing terrestrial larval habit (Corbet, 1999). Larvae of both species have been found amongst leaves and other litter in wet hillside seepage areas or fens, with no sign of burrows. *Tachopteryx* may be associated with forest seeps (Barlow, 1991; Dunkle, 1981, 1989) and with more open seepage areas in forest or graminoid fens (Ferro & Belshe, 1999; Walker & Smentowski, 2003; Williamson, 1932). Larvae of multiple age classes have also been found in close proximity amongst wet leaf litter and within the first few centimetres of boggy waterlogged soil along fen margins in Missouri (M. Ferro, personal communication, July 1, 2011). A previous observation by Williamson (1932) of a *Tachopteryx* larva near a vertical tunnel in muddy substrate in Missouri appears anomalous and was presumably either coincidental or the result of shallow tunnelling by the larva in the muddy substrate.

Svihla (1960) reported that D. S. Bullock had dredged *P. raptor* larvae from mud in shallow “bays” of slow-flowing streams in proximity to hillside seepage areas, a larval habitat which he was not able to confirm. Svihla (1960) subsequently collected an immature *P. raptor* larva foraging on wet ground in a nearby *Juncus*-dominated hill-slope seepage area above a stream. Svihla (1960) also reported that D. S. Bullock had found an exuvia attached “to the bark of a tree several feet above ground thus indicating that the nymphs may travel some distance after emergence before transforming”. Svihla (1960) suggested that *P. raptor* larval habitat might be similar to that of *T. hageni*, *T. pryeri* and *U. carovei*, “i.e., permanent, spring-fed swampy areas located on hillsides”. *Phenes raptor* larvae have subsequently been observed beneath “rotting tree stumps in dry wooded areas” on two occasions (Jurzitza, 1989b), and amongst moist, loose organic debris associated with a decaying log on damp earth in a relatively sunny, anthropogenic rainforest

clearing near Puerto Ramírez, Chile (Garrison & Muzón, 1995). In the latter case, larvae of three or four stadia were observed (J. Muzón, personal communication, February 25, 2012), suggesting a capacity for the species to complete larval development in a permanently moist forest-floor environment that would not be considered a fen or seepage area. Larvae were heavily encrusted with organic matter. In addition to possible cohort splitting, the presence of multiple stadia also suggests the possibility of more than one cohort within the litter habitat at the Puerto Ramírez site. Immediately prior to locating the larvae, a *Phenes* imago was caught nearby. According to R. Garrison (R. Andress, personal communication, September 30, 2007), an additional *Phenes* larva was also found amongst rocks with several *Phyllopetalia Selys* (Odonata: Austropetaliidae) larvae in a shallow riffle area nearby. The riffle had a slight current and maximum water depth of 2.5–5 cm in most places. Garrison also noted the presence of a seep not far from where larvae were found in the terrestrial litter habitat.

With a geographic distribution that encompasses a considerable geographic and bioclimatic range in Chile and Argentina, larval ecology is a subject of interest. This is particularly the case in the context of the long larval stage of at least five years documented or extrapolated in several fossorial petalurids; namely *Petalura gigantea* (J.W.H. Trueman, personal communication, November 23, 2006; Baird, 2012), *Tanypteryx hageni* (S. Valley, personal communication, November 22, 2009; Baird, 2012) and *Uropetala* spp. (Wolfe, 1953); and the likelihood that *Phenes* larvae also take a number of years to reach maturity.

Permanently humid tropical and temperate terrestrial environments such as moist forest-floor litter habitats have previously been recorded as larval habitat for a small number of odonate species (e.g. Watson, 1982; Watson & Theischinger, 1980; Winstanley, 1983), although it has also been suggested that such non-aquatic habitat use may be restricted to late stadia larvae of some species (Corbet, 1999). In view of the relatively high rainfall (> 3000 mm/yr) in the southern part of the species range, larvae of *P. raptor* (ssp. *raptor*) may also be commonly associated with permanently moist terrestrial microhabitats that may not be considered fens or seepage areas. The observation of *P. raptor* larvae in moist decomposing organic matter on the rainforest floor at Puerto Ramírez (Garrison & Muzón, 1995) and of oviposition in soil within a dark rainforest understorey (J. Muzón, personal communication, February 25, 2012) is consistent with this. The observations on two occasions of larvae beneath “rotting tree stumps in dry wooded areas” (Jurzitza, 1989b) appears somewhat anomalous, unless the rotting tree stumps were associated with small, and at the time of observation, either inconspicuous or temporarily drying seepages in the otherwise dry wooded areas; or the presence of such a seepage was not noted. Unless larvae are adapted to aestivation during dry periods (a characteristic of some odonates; Corbet, 1999), then presumably there would be a requirement for at least some permanently moist microhabitat to ensure that both eggs and early stadia larvae, in particular, do not desiccate, regardless of variation in broader habitat types where the species occurs. Desiccation resistance of larvae is unknown.

Although some fossorial petalurids such as *Petalura gigantea* demonstrate adult male territoriality in mire breeding habitat (Baird, 2012), there have been no observations of male territoriality in association with potential larval habitat in *Phenes raptor*. However, there have been limited observations of confirmed larval habitat. Imagines are typically sighted foraging, flying and perching in a range of habitats, particularly sunny clearings in *Nothofagus* forest or woodland (e.g. Garrison & Muzón, 1995; Joseph, 1929), although they have also been reported from shady gorges with running water (Joseph, 1929) and mountainsides and gorges (Peña, 1987). Observations in Argentina were also associated with *Nothofagus* forest (Muzón, 1995). Imagines have also been recorded far away from water (Jurzitza, 1989b). Ray Andress (personal communication, September 5, 2011) reported that G. Jurzitza observed imagines at one site “at the edge of swampy land along a stream, in an open area with low vegetation (mainly introduced blackberries), situated at about 200 m elevation, in the high forest being sunny and wind protected”. Jurzitza also observed

the species in a clearing in dry forest at 700 m elevation about 20 m above a fast running, mountain river. This clearing was also grown over with introduced blackberries. He continued: “the appearance of *Phenes* at these two sites was intermittent, I met it at two sites but it was not always present there; one day I saw several, the next day with seemingly the same weather, none”. Jurzitza considered both sites perching and foraging habitat. Moore (1992) observed a male aeshnid attempting to mate with a half drowned female *P. raptor* struggling on the surface of a shallow man-made pond in semi-natural habitat bordering secondary *Nothofagus* woodland in the Los Lagos Region. In this instance, a variety of aquatic habitats including small seepages and a river were identified nearby.

A number of authors have commented on the capacity of *P. raptor* imagines for rapid and skilful “raptorial” flight to capture prey, including close to the ground, and sometimes above the canopy (Joseph, 1929; Svihla, 1960). Joseph (1929) observed that “they throw themselves on their prey with the speed and certainty of a bird of prey”, and reported them perched eating prey high in the tree canopy and low in Chilean bamboo, *Chusquea* sp. He also reported that when a *Phenes* flies into a forest clearing, smaller odonates present quickly ceased flying and perched in the foliage. Carle (1996) also reported that “on one occasion a feeding swarm of over one hundred *Aeschna* rapidly dispersed after being attacked by a few *Phenes* and a *Hypopetalia*”. According to R. Andress (personal communication, September 5, 2007), G. Jurzitza observed the species using low shrubs, terrestrial bromeliads and small terminal branches for perching, including hanging from twigs, and basking in sunny forest clearings during foraging activity. It has not been reported using tree trunks as perches, as has *Tachopteryx thoreyi*. Jurzitza (1989b) noted that recorded prey included butterflies, *Aeschna* spp., bumblebees, honeybees, and in one case, the Chilean stag beetle *Chiasognathus grantii*. Joseph (1929) also reported Diptera, Lepidoptera and Odonata as prey. Some fidelity to particular forest openings has also been noted, with individuals returning to the same open areas via the same route, often above the canopy, for foraging purposes (Svihla, 1960). These areas were not identified as potential larval habitat. Ray Andress (personal communication, June 14, 2011) has noted that behaviourally they appear more similar to aeshnids than percher-type petalurids, such as *Petalura gigantea*.

There are considerable gaps in our understanding of this large dragonfly. Emergence has not been observed, and it will be interesting to confirm emergence style, i.e. upright versus hanging back, in the context of observations of other petalurids (for review, see Baird & Ireland, 2006). Mating has also not been documented. The only reported observation of oviposition is of a female photographed ovipositing in the soil in a dark area inside a *Nothofagus* forest in Parque Nacional Puyehue in the Los Lagos Region (Chile) (J. Muzón, personal communication, February 25, 2012). In addition, a single female was disturbed “flying near the ground in the brush close to the mucky side of a small stream”, probably investigating ovipositing opportunities (Svihla, 1960). In view of previous observations of the larval habitat of the species, it is to be expected that oviposition in *P. raptor* is endosubstratic (see Matushkina & Klass, 2011), as with other petalurids. All observations of oviposition in petalurids have involved insertion of the ovipositor, and sometimes distal abdominal segments, into some form of moist organic-rich soil substrate, into fissures in the substrate, or amongst or under live or decomposing plant material overlaying the substrate, including graminoids, mosses, liverworts, roots and litter (for review, see Baird, 2012).

The flying season may commence as early as October, continuing through into January, and may extend into February (Jurzitza, 1989b). Although imagines may be readily encountered opportunistically, identifying larval habitat and locating larvae is more challenging. The presence of exuviae likely provides the easiest means of identifying larval habitat where there has been some emergence that season; however, previous sightings of larvae were not reported to be associated with observations of exuviae and appear to have been largely the result of presumably well-informed opportunistic searches. The larvae were first described by Schmidt (1942) based on two damaged female exuviae. Needham and Bullock (1943) subsequently described the male exuvia,

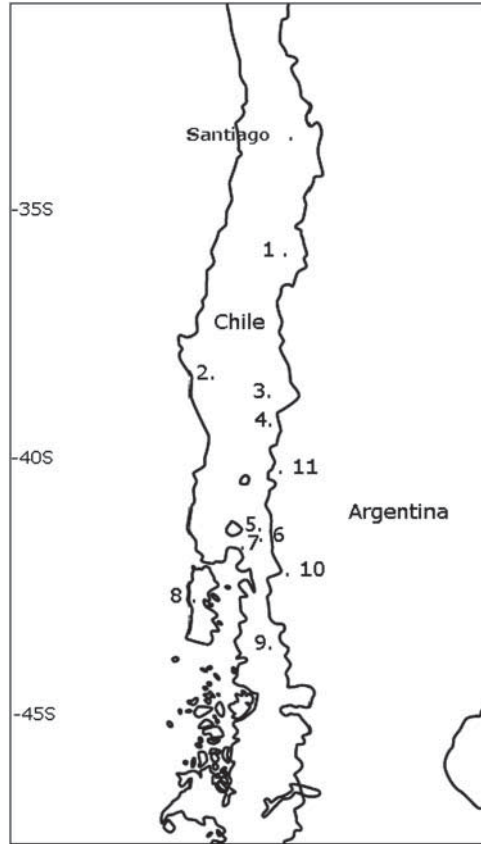


Figure 1. Map showing localities visited by the author in Chile during December 2011 ([1] Reserva Nacional Altos de Lircay, [2] Parque Nacional Nahuelbuta, [3] Parque Nacional Conguillo, [4] Parque Nacional Huerquehue, [5] Parque Nacional Vicente Pérez Rosales, [6] Rio Cochamó valley, [7] Parque Nacional Alerce Andino, [8] Parque Nacional Chiloé); the location of the most southerly *Phenes raptor* record from Chile (Puerto Ramírez [9]); and locations of records for Argentina (Chubut Province [10], Neuquén Province [11]).

Note: localities 1–8 were the only localities visited by the author. Localities 9–11 are previous records.

and a photo of a male exuvia was provided by Okumura (1960). Rosser Garrison documented observations of larvae in habitat at the site near Puerto Ramírez (Garrison & Muzón, 1995) with photographs, and these were examined for this paper. Few observations have been documented on the larval habitat of the species, and larval ecology requires elucidation. As part of ongoing petalurid research, and interest in their larval ecology, I undertook a trip to Chile in December 2011 with the objectives of further documenting the larval habitat of *P. raptor*, better understanding the biogeography of the species, and making observations on the behaviour of both larvae and imagines.

Methods

Based upon a literature review of observations and recorded localities of *Phenes raptor* in Chile, a range of habitats, primarily within conservation areas, were investigated during December 2011. Travelling south from Santiago, searches for larval habitat were undertaken in Reserva Nacional Altos de Lircay, Parque Nacional Nahuelbuta, Parque Nacional Conguillo, Parque

Nacional Huerquehue, Parque Nacional Vicente Pérez Rosales, the Rio Cochamó valley to the north of Parque Nacional Hornopirén, Parque Nacional Alerce Andino and Parque Nacional Chiloé (Figure 1).

Searches for larval habitat focused on locating any at least moderately sunny seepage habitats that were considered to be likely to provide relatively permanent, well oxygenated, groundwater seepage, shallow surface sheet flow or saturated substrate. Identification of potential larval habitat occurred while walking established hiking trails or driving to or through conservation reserves. Potential habitats were investigated selectively (due to time constraints) for the presence of exuviae by inspecting emergent vegetation, rocks and woody debris within the seepage habitat, and rocks, tree trunks, shrubs and graminoids in surrounding vegetation. Larval searches involved turning over any large woody debris, such as fallen tree limbs and pieces of bark, and investigating aggregations of decomposing leaf litter within selected seepage areas.

Observation of imagines was based on searches in a range of habitats where some potential breeding habitat had been observed within the locality. These searches focused on seepage areas, relatively sunny clearings within forest or woodland, successional regrowth forest vegetation with a low canopy and clearings, or sunny clearings along walking or vehicle trails.

Results

Potential larval habitats identified were primarily small seepage areas within forest or woodland areas, or small seepage fed streamlets with associated boggy margins. Seepage habitats occurred across a range of slopes, although most were relatively gently sloping ($<10^\circ$). Most seepage areas investigated were relatively small ($<100\text{ m}^2$, often much less). These seepages could generally be considered fens. The only larger mire or peatland habitats investigated were Magellanic mires (ombrotrophic bogs) in Parque Nacional Chiloé (southern section, along the coast and ranges north of Cucao), near the northern limit of their distribution (for vegetation, see Godley & Moar, 1973), where limited searches were undertaken. One larva was recorded at one locality, Reserva Nacional Altos de Lircay; and two imagines were observed at each of two localities, Vilches Alto (adjoining Reserva Nacional Altos de Lircay) and Parque Nacional Alerce Andino.

Observations of larvae

On 5 December 2011, a small patch ($c.4\text{ m} \times 8\text{ m}$) of gently sloping ($c.4^\circ$), north-facing fen seepage habitat ($35^\circ35'56.30''\text{ S}$, $71^\circ02'30.18''\text{ W}$) in Reserva Nacional Altos de Lircay was searched for larvae and exuviae. This seepage was in a relatively sunny area adjacent to, upslope of, and on the southern side of a hiking and packhorse trail, sendero El Sillabur. The seepage patch (Figure 2) was located $c.250\text{ m}$ east of the entrance gate to the Antaluoirra camping area. The Reserve is located $c.70\text{ km}$ by road east from Talca, via San Clemente, Vilches and Vilches Alto. The Vilches Alto area has previous records for *Phenes*. The seepage area crosses the trail and on the opposite side of the track had numerous horse footprints and was quite degraded compared to the upstream section. The seepage area appears to be fed by permanent snowmelt seepage and occurs within a mature evergreen coihue, *Nothofagus dombeyi*, dominated patch of forest at $c.1300\text{ m asl}$. This forest occurs in moister and more protected areas within the deciduous roble-hualo (*N. obliqua*–*N. glauca*) forest type of the region, which is transitional to rocky alpine vegetation at higher elevation and drier sclerophyllous shrublands and stunted deciduous forest at lower elevation in that part of central Chile (see Veblen et al., 1995; Wilcox, 1996). The seepage line includes areas within undisturbed coihue forest, upslope and down-slope of the sunnier area where the larva was located adjacent to the trail, where past tree clearing had occurred for track



Figure 2. *Phenes raptor* larval habitat in seepage area in anthropogenic clearing in *Nothofagus* forest, Reserva Nacional Altos de Lircay, Chile, 5 December 2011. Seepage flows out from the undisturbed *Nothofagus* forest at left and flows to the right across the track. A *Phenes* larva was concealed beneath the larger of the two right-hand fallen branches on the seepage area.

construction. A small area of temperate evergreen Valdivian rainforest, at its northern limit, also occurs in a sheltered location nearby at slightly lower elevation. Average annual precipitation at this site is 2070 mm, with 1800–2000 mm of snow cover during the winter and up to five dry months in the summer (J. Fuentes, personal communication, December 6, 2011). The region is characterised by a distinctive Mediterranean-style climate.

Shortly before commencing a search of this seepage area, a very large dragonfly, probably *Phenes raptor*, was observed cruising along the trail two metres above ground level, but was not clearly identified. The similarly large *Allopetalia reticulosa* Selys (Odonata: Aeshnidae) is also recorded from nearby Vilches Alto. A thorough search for exuviae, within and adjoining the seepage patch, was unsuccessful. The *P. raptor* larva (3.7 cm long) (Figure 3) was found at 1500 h under a recently fallen section of tree branch (*c.* 25 cm diameter \times 2 m) with a rotting partly concave underside. The edges of the log were mostly embedded in the wet soil, thus providing a relatively dark environment within the limited space under part of the log. The log was lying in the seepage patch with other woody debris, pieces of bark, scattered emergent embedded rocks and decomposing *Nothofagus* leaves. The vegetation comprised very low open sedgeland of *Juncus* sp. and other hydrophilic herbs. Much of the seepage patch had relatively sparse litter or plant cover, and was characterised by very shallow seepage flow and microtopography with water-filled micro-depressions. The substrate comprised a shallow, soft, waterlogged, organic-rich soil layer (<10 cm deep) overlaying an impenetrable layer of small rock fragments in a mineral soil matrix. When first observed, the larva, although wet, was half out of the water in the confined space under the log, with the terminal abdominal segments and underside of the body submerged in a small shallow water-filled micro depression (1–2 cm deep). When first handled and turned upside down, the larva promptly flipped over. With subsequent handling, the larva exhibited thanatosis with its



Figure 3. *Phenes raptor* larva in seepage habitat, Reserva Nacional Altos de Lircay, Chile, 5 December 2011 (covering branch temporarily removed).

legs extended. The setae were partly encrusted with mud and organic debris. When replaced on the substrate at the edge of the clear water, it partly submerged itself in the shallow water-filled micro-depression.

The following morning, 6 December at 1043 h, the log was turned over to check the status and location of the previously observed larva. A search failed to locate the *Phenes* larva, but surprisingly, a second smaller larva (2.7 cm long), tentatively identified as a *Phyllopetalia* sp., was located in almost the same location as the larva observed the previous day. The second larva was observed out of the water in the space under the log next to a water-filled micro-depression, standing with its legs extended and its body held above the substrate. It was conjectured that this posture may have been defensive and a response to the log being rolled over, exposing the larva. When handled, the larva was active and did not immediately exhibit thanatosis, although it became subdued with repeat handling. Although P. Pessacq (personal communication, August 11, 2012) has indicated that in his experience, aquatic *Phyllopetalia* larvae always exhibit thanatosis when handled, strongly flexing their bodies ventrally with legs held close to the body, Carle (1996) noted that larvae of semi-terrestrial *Phyllopetalia* species flexed their bodies less dramatically in response to handling than the rheophylic species. When returned to the edge of the water-filled depression, the larva fully submerged itself. A short time later, it released a bubble from its rectal opening.

In saturated litter under the log and amongst other nearby wet woody debris lying on the seepage, several large (up to 2.5 cm long) predatory megalopteran larvae, tentatively identified as *Archichauliodes* sp. (Corydalidae), were also located. These large aquatic larvae could be expected to predate on smaller larvae of *Phenes* or other odonates, and vice versa. A trichopteran larva with an unadorned, tubular, silken case was also observed in close proximity to the *Phenes* larva in the small water-filled depression under the log. Small earthworms were observed within the decomposing surface of the underside of woody debris in the seepage area.

Underneath the log there were some traces of short, indistinct and more or less horizontal “tunnels” within the top 2 cm of waterlogged muck and litter, which may have been caused by foraging *Phenes* larvae, or other species such as the megalopteran larvae.

Later the same day, at 1815 h, the seepage site was again checked. The log was turned over and the smaller “*Phyllopetalia*” larva recorded earlier in the day was found to have moved 20 cm, but was still concealed under the log. The larva was wet and next to another small water-filled micro-depression and completely out of the water, although the rectal opening was in contact with saturated substrate. There was limited space between the underside of the log and the boggy soil surface at this location. When photographed with a flash the larva responded by contracting. The log was returned and 10 minutes later the larva was checked again; it was in the water-filled depression with only its head and upper thorax out of the water.

The late instar *Phenes* larva observed in the current study (3.7 cm length) was considerably smaller than the 4.8 cm length previously indicated for final instars by Needham and Bullock (1943). The wing sheaths of the larva observed in the current study were, however, proportionately longer than illustrated by Needham and Bullock (1943) for a final instar, and longer than those of a similarly sized (3.6 cm length) late instar larva illustrated by R. Andress (personal communication, July 1, 2007), based on material from the Puerto Ramirez locality (Garrison & Muzón, 1995).

Observations of imagines

Following the recommendations of a Ranger at the adjoining Reserva Nacional Altos de Lircay, a private conservation reserve 300 m east of the archaeological site “de las piedras”, near the environmental information centre at Vilches Alto, was searched for *Phenes* imagines. On 6 December, between 1230 and 1330 h, two imagines of *P. raptor* (presumably ssp. *centralis*) were observed separately. Both were observed flying rapidly, hawking within sunny clearings in regrowth *Nothofagus* forest at c. 1200 m asl. One was observed to briefly perch hanging on terminal branch foliage several metres above the ground. The weather was sunny and warm with no breeze. In the adjoining forest there were some boggy seepage areas, generally with low–moderate sunlight intensity. There were, however, limited locations within this broader area with surface seepage or permanently wet forest understoreys.

On 24 December, in Parque Nacional Alerce Andino, south-east of Puerto Montt at the southern limit of the Los Lagos Region, at 1358 h, a *Phenes* imago (presumably ssp. *raptor*) was observed hawking 3–5 m above the ground in a sunny clearing in low *Nothofagus*-dominated, regrowth Valdivian rainforest adjacent to the walking trail, Sendero Laguna Chaiquenes. The *Phenes* imago perched briefly hanging from a leafy branch end. The weather was sunny and warm with a light breeze. The location was c. 4 km east of the Park entrance gate and guard post.

At 1447 h on the same day, and closer to the Park entrance gate, a male imago was observed flying at a height of 1–2 m along the same sunny trail surrounded by similar low regrowth rainforest. The imago briefly hovered in front of me and almost perched on me before perching two metres away in a low shrub in full sun. These sightings in Parque Nacional Alerce Andino were at c. 150 m asl (41°35'16.8" S, 72°34'51.30" W). Annual precipitation is 3300–4500 mm, with a January (austral summer) mean maximum temperature of 20 °C. There appears to be no previous reference to observations of the species in this national park.

Discussion

Based on documented sightings, *Phenes raptor* larval habitat occurs in association with a range of primarily forest ecosystems distributed across a considerable rainfall gradient, increasing from

north to south, and decreasing from west to east of the Andes in association with a rain shadow effect. The Central Region, in particular, is characterised by a distinct Mediterranean-style climate with long dry summers (Bannister et al., 2012). In this climate, potential larval habitat appears to be restricted to putatively permanently wet seepage habitats dependent primarily on precipitation (rainfall or snow) outside the summer flying season. These essentially groundwater dependent seepage habitats are typically distinct from surrounding forest or woodland in terms of their substrate characteristics, wetness and vegetation, e.g. recorded localities in and near Reserva Nacional Altos de Lircay and Parque Nacional Nahuelbuta; and sites visited in Parque Nacional Conguillo, Parque Nacional Huerquehue and Parque Nacional Vicente Pérez Rosales. In the case of Parque Nacional Vicente Pérez Rosales, although it occurs within the higher rainfall zone in the south of the los Lagos Region, the area visited near Petrohué during this study was dominated by eruptive volcanic material from Volcán Osorno, with limited locations identified with perennial seepage and impeded drainage that may provide the conditions for suitable larval habitat for *Phenes*. There were also limited locations with potential larval habitat identified during this study in Parque Nacional Conguillo due to the extensive areas covered by rock and ash from eruptive volcanic activity from Volcán Llaima. In one case, however, potential habitat had been created in this area following damming of a stream with volcanic material, causing flooding of the upstream valley to form Laguna Captrén, with subsequent development of a fen in association with a large delta of eroded material along the upstream lake margin. It is likely that disturbance associated with the high level of volcanic activity along the Andes is responsible for considerable spatio-temporal turnover in potential *Phenes* larval habitat in some areas.

It is possible that some seepage habitats in the Central Region are to some extent subject to summer drying regimes when groundwater fed seepages may provide insufficient water to maintain surface wetness across the full extent of these spatially restricted, patchy habitats. Unless larvae are capable of aestivating in drying habitats during extended summer dry periods in these more northerly habitats with a Mediterranean climate, then their persistence will be limited by availability of suitable microhabitat. Such microhabitat will presumably be characterised by at least some permanent groundwater seepage providing surface moisture, and the availability of soft moist organic substrates or woody debris where larvae can bury themselves or take refuge during temporarily drying conditions.

The larvae of *Phenes* and the likely *Phyllopetalia* observed in the seepage at Reserva Nacional Altos de Lircay were both located underneath a fallen branch lying on the surface. In this situation, most of the seepage area was characterised by a substrate with relatively open ground cover, which might provide limited concealment for larvae on the surface. Only part of the underside of the log provided a restricted crawl space for larvae; the remainder of the log was more or less in contact with the surface of the soft substrate, with the exception of localised micro-depressions. Although the larvae of *Phenes* may be relatively well camouflaged due to the adherence of plant and soil material, for them to move around the seepage while maintaining some degree of crypsis and minimising risk of predation, they would presumably need to do so during the night or by moving within the surface layer of the waterlogged soils and any accumulated litter. The traces of short horizontal “tunnels” in the shallow boggy substrate under the fallen branch suggested that larvae may push through soft waterlogged soils, in addition to litter, during foraging activities. The use of the term “tunnel” in this case does not, however, suggest anything resembling a burrow as developed by fossorial petalurids. Habitat use by *Phenes* larvae in this habitat, and in the seepage habitats reported by Svihla (1960), have apparent similarities to that of *Tachopteryx* in boggy soils in fen margins in Missouri observed by M. Ferro (personal communication, July 1, 2011).

The co-occurrence of *Phenes* and *Phyllopetalia* larvae in the same seepage is also of some interest. While larvae of other *Phyllopetalia* spp. are aquatic (see Carle, 1996; Von Ellenrieder, 2005), Carle (1996) referred to larvae of *Phy. excrescens* (Carle) and *Phy. altarensis* (Carle)

as semi-terrestrial. Carle (1996) observed female *Phy. excrescens* ovipositing in seeps high on canyon walls and a female *Phy. altarensis* ovipositing in soft herbaceous plants at the head of a steep-sloped seep; somewhat similar slope seepage habitats to those used by *Phenes* across at least part of its range. Carle (1996) noted that in the Central Region of Chile around Santiago, *Phy. altarensis* larval habitat is restricted to a narrow altitudinal band at about 1900 m elevation, “between tundra-like and semi-arid regions where snow melt is sufficient to maintain isolated springs and spring seeps”. These seeps have similarities to the altitudinally-restricted seepages encountered in and near Reserva Nacional Altos de Lircay, where a *Phenes* larva was recorded in association with a “*Phyllopetalia*” larva in this study. These seeps also occupy a spatially and altitudinally restricted bioclimatic envelope, albeit at somewhat lower elevation to those further north near Santiago.

With increasing latitude south through the Los Lagos Region, characterised by increasing rainfall, decreasing average temperature, increasing duration and depth of snow cover, and an increasing predominance of temperate Valdivian rainforest (see Bannister et al., 2012), the boundary between patchily distributed seepage habitat and permanently moist forest soils becomes increasingly obscured, e.g. sites visited during this study along the Rio Cochamó valley, and in Parque Nacional Alerce Andino and Parque Nacional Chiloé. Targeted larval and exuviae searches of the more clearly differentiated seepage habitats in the more northerly part of the species range in Chile with a Mediterranean climate are thus likely to be easier than attempting to search in forest types that do not have such clearly differentiated potential larval habitat.

Habitat use by *Phenes* on Chiloé (Peña, 1962) is also a subject of interest. Chiloé is separated from the mainland by a narrow strait, Canal de Chacao, and has a similar climate to the Puerto Ramírez locality in northern Patagonian Chile to the east, with very high rainfall and expanses of remnant Valdivian rainforest. Within the recorded latitudinal range of *Phenes*, Chiloé also has the most northerly occurrence of small mire areas (with the exception of some small mire areas on the mainland immediately north of Chiloé), which may also provide habitat for *Phenes*, particularly where there are adjacent rainforest ecosystems. These mires represent the most northerly occurrence of Magellanic mires or ombrotrophic bogs, ecosystems that are more widely distributed in southern Patagonia and Tierra del Fuego (e.g. Kleinebecker et al., 2007, 2010; Krisai, 2005). However, there are currently no records for the species in such mire habitat. Some of these mire areas on Chiloé are probably the result, at least in part, of historical anthropogenic clearing (also see Godley & Moar, 1973).

The observations reported here indicate that *P. raptor* is capable of utilising different larval habitats, ranging from shallow aquatic and semi-aquatic seepage habitats, particularly in lower rainfall Mediterranean climates, to moist temperate rainforest-floor litter habitats in higher rainfall areas with lower average temperatures. This differentiation in habitat types also appears to broadly mirror the geographical range of each of the two subspecies; with *P. r. centralis* characteristically associated with patchily distributed seepage habitats in the more northerly Mediterranean climate zone, and *P. r. raptor* also associated with habitats within, or in association with, more permanently moist temperate rainforest ecosystems, in addition to seepages. With the widespread occurrence of such moist forest floor habitats in the southern part of the species’ range in the Los Lagos Region, Chiloé and Patagonia, the environmental variables that may limit larval establishment and successful development through to emergence are of interest. With average temperatures decreasing with increasing latitude and altitude, the species’ range will also be constrained by any negative temperature effects upon imagines. Jurzitza (1989a) noted some apparent overlap in the distribution of the two subspecies, based on the presence of a specimen of *P. r. raptor* in an earlier collection from the Vilches Alto area, well within the distribution of *P. r. centralis*.

Observations of mating may confirm whether mate-meeting is opportunistic or associated with potential larval habitat, and if so, to what extent males demonstrate territoriality in relation to such habitat. Further observations of larvae in habitat and of oviposition and emergence sites in

different locations across the species' latitudinal and bioclimatic range will also contribute to a greater understanding of the behaviour, ecology and biogeography of this unique South American dragonfly. This may also contribute, in time, to understanding the evolutionary divergence in larval lifestyles between the fossorial and non-fossorial petalurids, in conjunction with phylogenetic and historical biogeographic (palaeoecological) research.

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