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An emergence study of *Petalura gigantea* (Odonata: Petaluridae)

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Emergence studies in Odonata provide information on the behaviour, ecology and fundamental demographic parameters in population studies. This paper reports on a study of sex ratio at emergence, pattern and duration of the emergence season, and potential cohort splitting in *Petalura gigantea*. Sex ratio at emergence varied among years, habitat patches and swamp types. Across all collections, sex ratio varied significantly from a 1:1 ratio, with a bias towards females. The duration of the emergence season varied between sites and years, from at least 45 to at least 70 days, potentially commencing by late October and extending into early January and possibly beyond. Although some evidence suggested cohort splitting, it was not confirmed. Observations of spatially and temporally aggregated emergence clusters are consistent with observed oviposition patterns of individual females, suggesting cohort emergence. Observations of mortalities at emergence and of emergence location are provided; the latter should assist researchers and resource managers in identifying breeding sites in heterogeneous swamp vegetation.

Keywords: *Petalura gigantea*; Odonata: Petaluridae; emergence; emergence season; emergence pattern; sex ratio; exuviae; cohort splitting

Introduction

Larval and adult stages in Odonata offer opportunities for life history, ecological and demographic studies (Córdoba-Aguilar, 2008), although, unlike many aquatic species, the burrow-dwelling larvae of fossorial petalurids are not readily amenable to demographic studies. Exuviae and adults of fossorial petalurids, however, are amenable to such studies. Exuviae have been used successfully for many odonate community, population and emergence studies (e.g. Foster & Soluk, 2004; Moore, 1964; Ubukata, 1981), including for petalurids (e.g. Baird, 2012; Meyer & Clement, 1978; Svihla, 1960a; Taketo, 1960; Winstanley, 1981; Wolfe, 1953). In addition to measures of abundance at emergence, sex ratio at emergence is a fundamental demographic parameter for studies of odonate population dynamics, with exuviae typically used to provide this measure (Corbet, 1999; Cordero-Rivera & Stoks, 2008). The use of exuviae to measure sex ratio at emergence in Odonata has previously been reviewed (Corbet, 1999; Corbet & Hoess, 1998), and Moore and Corbet (1990) provided population monitoring guidelines. Sex ratio at emergence has been shown to vary among taxa, generally with slightly more males in Zygoptera and the reverse in Anisoptera. For an individual species, sex ratio at emergence may vary between years,

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and different habitats; previous researchers have therefore recommended that data from different years and sites not be combined for analysis (Corbet, 1999; Corbet & Hoess, 1998).

Information on the seasonal pattern of emergence, commencement and duration of the emergence season, and any variability among sites and years, is also fundamental to understanding the ecology and population dynamics of dragonfly species across their biogeographic range. Variability in commencement and duration of the emergence season in fossorial petalurids, in response to seasonal effects, and across altitudinal and latitudinal gradients, has previously been reported (e.g. Svihla, 1959, 1960a; Taketo, 1958, 1960; Wolfe, 1953). Where individual species are distributed across a wide climatic range the effects of different temperature regimes upon larval development may also be considerable. With the long larval stage of at least five years documented or extrapolated in the fossorial petalurids: *P. gigantea* Leach (J. W. H. Trueman, personal communication, 23 November 2006; Baird, 2012), *Tanypteryx hageni* (Selys) (S. Valley, personal communication, 22 November 2009; Baird, 2012) and *Uropetala* Selys spp. (Wolfe, 1953), the duration of the larval stage may vary by a number of years, even within a particular cohort. Rowe (1987) suggested that it is likely that the larval stage in *Uropetala* spp. may vary by as much as several years for a particular cohort, dependent on environmental conditions and food availability. Due to cohort splitting, some odonates with long larval stages may also extend or reduce the average larval stage duration by at least a year, even within cohorts (e.g. Aoki, 1999; Corbet, 1999). For species with long-lived larvae and spatially structured populations, such as *P. gigantea*, any cohort splitting may add considerable complexity to their metapopulation dynamics (Baird, 2012).

The presence of perched exuviae also provides confirmation of the presence of viable breeding habitat. Tillyard (1909) provided some early observations on the location of exuviae of *P. gigantea* in a swamp in Leura, Blue Mountains, New South Wales (NSW). He reported that exuviae "are found clinging to the tufts of sedge or to the trunks of teatree [a shrub], often being two to three feet above ground", and that larvae may "crawl three or four yards out of the mud before climbing a suitable twig". At the time of that publication, a fossorial larval habit had not been documented (see Tillyard, 1911), and in retrospect, the earlier suggestion that larvae may crawl several yards before climbing a suitable emergence support (Tillyard, 1909) may have been based upon an erroneous assumption in relation to the microhabitat requirements and lifestyle habit of larvae. More recent surveys primarily targeting imagines (Dearson, 1999; Theischinger, 2001; Trueman, 2000) have provided additional observations of breeding habitat, but did not include any systematic exuviae surveys or detailed microhabitat observations of confirmed emergence sites or burrow locations. Baird (2012) provided details of such microhabitat, based on observation of oviposition, burrow and exuviae locations across a range of habitats.

Petalura gigantea has been reported as inhabiting permanent seepages, bogs and swamps of the NSW coast and ranges, from near the Victoria border to near the Queensland border, and between near sea level and 1240 m altitude (Baird, 2012; Benson & Baird, 2012; Davies, 1998; Hawking & Theischinger, 2004; Theischinger, 2001; Theischinger & Endersby, 2009; Theischinger & Hawking, 2006; Trueman, 2000). The species is listed as Endangered in NSW (NSW Scientific Committee, 1998). All recorded breeding habitats of the species may be considered peat swamps or mires (bogs and fens; see Whinam & Hope, 2005 for a discussion of the Australian context) and included within the *Coastal Heath Swamps* or *Montane Bogs and Fens* Freshwater Wetland vegetation classes of Keith (2004). Both vegetation classes occur in the Blue Mountains and provide breeding habitat for *P. gigantea* (Baird, 2012).

The vegetation in these mires is characterised by considerable spatio-temporal heterogeneity in composition and structure, often at small spatial scales, and hydrology and fire are important drivers of this complexity (Keith, Rodoreda, Holman, & Lemmon, 2006). Vegetation includes sedgeland, fernland, heath and taller shrublands or scrub, typically forming complex mosaics in response to environmental gradients (Benson & Baird, 2012; Holland, Benson, & McRae, 1992; Keith & Myerscough, 1993; Keith et al., 2006). Breeding microhabitats used by *P. gigantea* are

generally dominated by sedgeland vegetation with a variable shrub and fern component, but may also include *Sphagnum* spp. as a conspicuous component. The vegetation complexity is a challenge to those attempting to identify suitable breeding microhabitat for these dragonflies, other than at a coarse spatial or wetland typological scale. It may frequently mask more subtle spatio-temporal heterogeneity in groundwater hydrology and associated substrate characteristics, which provide more meaningful indicators of potential larval habitat for *P. gigantea* (Baird, 2012).

Identifying habitat used by a species requires observation of at least one life stage. In the case of species such as *P. gigantea*, with cryptic fossorial larvae, in practice this means observation of either exuviae or adults. However, the presence of adult odonates not engaged in breeding activities does not confirm the presence of suitable breeding habitat (Corbet, 1999), and *P. gigantea* adults may not be present or detected during individual surveys in a particular swamp, even when it provides confirmed breeding habitat (Baird, 2012). Observation of ovipositing behaviour, also, may not be synonymous with deposition of eggs, or successful larval development to adulthood (Corbet, 1999), and consequently may not be a reliable indicator of suitable breeding habitat. Observation of the presence of exuviae, or emerging or teneral individuals, provides the only verification of successful life cycle completion and of the presence of suitable breeding habitat (Raebel, Merckx, Riordan, Macdonald, & Thompson, 2010). Barrett (1996) similarly noted that the most reliable indicator of the presence of suitable larval habitat in *P. hesperia* was the presence of exuviae, while at the same time emphasising the difficulty of locating them. One caution in relation to surveys for exuviae is that persistence of exuviae may vary over time, between species and substrates, and in response to climate variables. Sampling frequency in emergence monitoring studies should therefore be informed by an understanding of the persistence of exuviae in target species (Aliberti Lubertazzi & Ginsberg, 2009).

Observation of persistent exuviae of *P. gigantea* perched in swamp vegetation and identifiable to sex up to seven months after the completion of an emergence season (during a period of less than average rainfall) confirmed that exuviae are generally persistent at least across the duration of an emergence season and thus are suitable for use in emergence studies in the species (Baird, 2012). Baird (2012) also confirmed, however, that climate variables (particularly rain and wind) and contact with the substrate (e.g. biologically active soil layer or *Sphagnum*) affected persistence of *P. gigantea* exuviae and required consideration. In the absence of observed adult dragonflies engaged in breeding activities, the ability to better identify breeding microhabitat through the presence of exuviae will assist researchers and enhance the ability of resource managers to better manage threats to the species and its threatened mire habitats. Exuviae surveys may also provide the opportunity to document mortality at emergence and elucidate factors responsible, such as climate effects and predation. Such information may contribute to a better understanding of reproductive success and the limits to the potential biogeographic range or bioclimatic envelope of a species.

This paper reports on an emergence study of *P. gigantea*. Its aims are: to identify sex ratio at emergence, and any variability among years and swamp patches; to document the commencement, pattern and duration of the emergence season; to identify evidence of larval cohort splitting; to document emergence location; and to document mortalities at emergence and elucidate their causes.

Methods

Study location

This project was undertaken in the Blue Mountains, NSW, Australia (150°20′ E, 33°40′S; Figure 1) between late 2003 and early 2010. Study sites (*n* = 7) were located in three of the six swamp
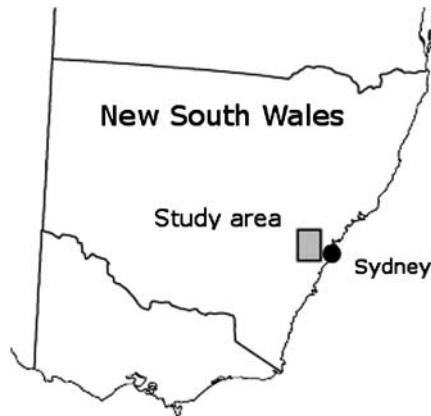
Figure 1.   Location map of the Blue Mountains study area. (base map © 2005 Commonwealth of Australia).

types where *P. gigantea* has been recorded in the Blue Mountains (Baird, 2012): Blue Mountains Sedge Swamps (PMH01, PMH08), Boyd Plateau Bogs (PKB02, PKB05, PKB07, PKB11) and Coxs River Swamps (PBB01) (for vegetation descriptions, see Benson & Keith, 1990; Keith & Benson, 1988).

Exuviae survey technique

Systematic exuviae surveys were conducted by searching all ground layer, sedgeland and shrub vegetation in identified potential *P. gigantea* breeding habitat. These surveys occurred independently of weather and time of day. Once sex and emergence location were recorded, exuviae were removed to avoid recounts. In a small swamp with limited potential breeding habitat, all potential habitats were systematically surveyed. This was achieved using a meandering walking survey that covered all vegetation within the potential habitat. This often occurred along a single seepage line and included any associated patches of suitable breeding habitat. In larger swamps, where only an identified area of breeding habitat was surveyed, a walking survey was undertaken systematically across the full width of the swamp or of the identified survey area. This occurred along parallel, 1.5 m wide belt transects. Based on the detectability of exuviae within the vegetation and on all sides of sedgeland vegetation tussocks and shrubs, this width provided for efficient surveying, with confidence that most exuviae were detected. To maximise the numbers of exuviae recorded, these surveys involved close examination of all vegetation, including *Sphagnum*, sedgeland vegetation, and live and dead shrubs. In some bog habitats (e.g. Boyd Plateau Bogs), it also involved examination of "marsupial lawns" (vegetation routinely grazed to near ground level by large marsupials) of sedgeland or herbland species such as *Empodisma minus* (Restionaceae).

Sex ratio at emergence

In exuviae of *Petalura* spp., in particular, males can be distinguished from females by the presence of two distinct protuberances on the distal end of the abdomen, associated with their superior anal appendages, and by the tapered distal end of the abdomen in females. These characters allow for rapid field identification of sex of exuviae.

Eleven systematic exuviae collections were made to provide data on sex ratio at emergence. These collections covered eight sites, representing three different swamp types and four different years of collection. These surveys were generally conducted late in the emergence season (mid-December to early January) when the majority of individuals had emerged. A chi-squared goodness of fit test was used to determine whether the sex ratio at emergence deviated significantly from a 1:1 ratio.

Characteristics of the emergence season

In addition to regular imagine surveys across the 2008–2009 flying season, one Coxs River Swamp in Ben Bullen State Forest, site PBB01, was surveyed systematically for exuviae at 7–10-day intervals. These surveys commenced at first evidence of emergence in mid-November and continued until no new exuviae were collected on two consecutive surveys. These surveys identified sex ratio at emergence, the duration of the emergence season, the pattern of emergence, and the temporal relationship between the emergence season and changing relative abundance of imagines within the swamp habitat. Survey results that revealed a consistent pattern of emergence were used to validate the utility of the exuviae survey technique in this environment.

Based on early season indications of large emergence events in a number of sites during the 2007–2008 flying season, five Blue Mountains Sedge Swamp sites in the Mt Hay Range in Blue Mountains National Park (PMH01, PMH03, PMH08, PMH11, PMH13) were also surveyed systematically for imagines at 7–10-day intervals across the flying season as part of a larger landscape-scale study (see Baird, 2012). Opportunistic observations of tenerals were also recorded during these surveys. In an attempt to identify the commencement of the emergence season, the earliest surveys for these five sites were conducted at the beginning of November. This date was based on observations from the previous survey years. Observation of first sightings of tenerals or imagines and latest sightings of tenerals from these five sites permitted conservative estimates of the commencement of the emergence season and coarse-scale estimates of the duration of the emergence season. It thus allowed for some comparison among sites and years when compared with results of regular systematic exuviae surveys in PBB01 in the following year. However, these surveys in the Mt Hay Range sites consisted of meandering walking transects targeting imagines, and not systematic exuviae surveys such as undertaken in PBB01.

Additional earliest observations of tenerals or mature imagines at the beginning of the emergence season, and latest observation of tenerals, in additional swamp sites which were surveyed as part of a larger landscape-scale study of population dynamics (Baird, 2012) are also reported.

For the purposes of this study, tenerals were defined as individuals observed during or immediately post-emergence, with or without full coloration, which had not taken their maiden flight. This included individuals either still directly associated with their exuviae, or if not, with their wings held closed above their bodies in the typical post-emergence and pre-flight posture.

Larval cohort splitting

In one Coxs River Swamp, site PBB01 (2008–2009) and one small Boyd Plateau Bog, site PKB05 (2006–2007), all identified exuviae locations were marked with coloured flagging tape (marked with survey date and sex of exuviae) for later comparison of their locations with emergence sites marked in the following year, to identify any spatial correlations between emerging individuals in two consecutive years that could potentially provide evidence of larval cohort splitting. Observations of ovipositing by individual females throughout this landscape-scale study confirmed that females typically engage in high-density, spatially aggregated ovipositing behaviour while crawling along the swamp soil surface amongst vegetation (typically across $<0.5\,\mathrm{m}^2$ areas) or

wherever they can gain access to the substrate amongst denser vegetation tussocks. They then briefly take a low flight to repeat the behaviour a short distance away (generally no more than several metres and frequently much less). Observations of similarly spatially aggregated exuviae are consistent with the observed spatial arrangement and density of oviposition behaviour. This study to identify evidence of cohort splitting is based on the presumption that exuviae forming part of a spatially aggregated cluster of exuviae in close proximity, and separated by some distance from other exuviae (in an area with contiguous potential breeding habitat), most probably represent individuals from the same larval cohort associated with ovipositing by a single female. For the purposes of this study, the presence of such spatially clustered exuviae, with emergences distributed across more than one emergence season, was considered to constitute strong evidence of cohort splitting.

Mortality at emergence

For all systematic exuviae surveys, all remains of dead or dying individuals which had failed to successfully complete emergence or take their maiden flight were recorded. Any evidence indicating the cause of mortality was recorded, including climate variables (temperature, precipitation) on and immediately preceding the day of observation in the case of recently deceased individuals. Other than obvious tenerals, only remains that were closely associated with identified exuviae (<50 cm distant) were included, to minimise possible inclusion of adult mortalities that were only incidentally located near identified exuviae.

Emergence location

Exuviae perch height, perch plant species, slope and horizontal distance to burrows were recorded during systematic exuviae surveys. Observation of hundreds of additional perched exuviae and associated burrow locations across a range of different peat swamp types during imagine abundance monitoring surveys (Baird, 2012) also provided information in relation to emergence location, perch height and plant species used as emergence perches.

Results

Sex ratio at emergence

Eleven systematic exuviae collections were used to provide measures of sex ratio at emergence. Swamp sites, data collection date, number of exuviae collected (by sex) and sex ratio (%♂) are shown in Table 1. The sex ratio at emergence varied among sites ($n = 7$) within the same year (2007–2008, 34–53%♂), and among years for the two sites with more than one year's data (PBB01 [$n = 2$], 41–48%♂; PKB05 [$n = 3$], 40–48%♂). Sample size used to determine sex ratio varied considerably between collections ($n = 11$–254). There was a significant difference in the sex ratio of males to females ($\chi^2_{10} = 19.34$, $\alpha = 0.05$). The sex ratio is biased towards females.

Seasonal emergence pattern and duration of the emergence season

Results of surveys of exuviae carried out across the 2008–2009 emergence season in one Coxs River Swamp (PBB01) are presented in Table 2. The temporal pattern of cumulative abundance of recorded exuviae (by sex) in this swamp site is illustrated in Figure 2. For this emergence event the temporal emergence pattern for males and females was similar. Commencement of emergence for

Table 1.   Results of *Petalura gigantea* exuviae (ex) collections from swamp sites, with collection date, total of male (♂) and female (♀) exuviae, and percentage males.

Site[1]	Swamp type[2]	Survey date	♂ex	♀ex	♂ + ♀ ex	% ♂ ex
PMH01	01	4 December 2007	41	38	79	53
PMH08	01	4 November 2007[3]	9	12	21	43
PMW01	01	24 December 2007	8	10	18	44
PKB02	03	29 December 2007	29	57	86	34
PKB05	03	18 December 2006	7	9	16	44
PKB05	03	28 December 2007	121	133	254	48
PKB05	03	10 January 2010	8	12	20	40
PKB07	03	30 December 2007	4	7	11	36
PKB11	03	29 December 2007	12	21	33	36
PBB01	06	10 January 2009[4,5]	54	58	112	48
PBB01	06	30 December 2009	7	10	17	41

[1]Site location details (see Baird, 2012, Appendix 1).
[2]Swamp types (from Baird, 2012): Blue Mountains Sedge Swamps (type 01), Boyd Plateau Bogs (type 03), Coxs River Swamps (type 06).
[3]Data from only one site, PMH08, were collected early in the emergence season.
[4]Data for PBB01 are cumulative data from regular surveys for the 2008–2009 flying season (see Table 2).
[5]One additional male and female teneral were observed on the first day of surveying on 16 November 2008 in PBB01 without exuviae located (see Table 2) and are not represented numerically in the total.

Table 2.   Results of *Petalura gigantea* exuviae (ex) collections and recorded tenerals (T) for one Coxs River Swamp (PBB01) for the 2008–2009 emergence season, including cumulative count (C) of exuviae across the season, by sex.

Survey date	Day[1]	♂ ex	♀ ex	C ♂ ex	C ♀ ex	♂ T	♀ T
16 November 2008	16	1	1	1	1	2	2
22 November 2008	22	3	3	4	4	—	—
24 November 2008	24	4	3	8	7	4	2
26 November 2008	26	3	7	11	14	2	3
1 December 2008	31	12	11	23	25	5	6
2 December 2008[2]	32	1	1	24	26	0	0
5 December 2008	35	3	6	27	32	1	3
10 December 2008	40	13	14	40	46	6	1
17 December 2008	47	4	3	44	49	0	0
25 December 2008	55	8	7	52	56	0	0
31 December 2008	61	0	2	52	58	0	1
2 January 2009	63	1	0	53	58	1	0
10 January 2009	71	1	0	54	58	0	0
11 January 2009	72	0	0	54	58	0	0
16 January 2009[3]	77	0	0	54	58	0	0

[1]Day numbering sequence commences on 1 November as day 1.
[2]Sightings on 2 December 2008 were opportunistic and not included in Figure 2.
[3]The final date of exuviae surveying was 16 January 2009.

both sexes occurred by mid-November, although EM50 (50% of emergence) and EM100 (100% of emergence) for females occurred slightly before males.

The temporal pattern of emergence for PBB01 indicates that after the first signs of emergence on day 16 (16 November), a relatively consistent rate of emergence was maintained for both sexes from near day 22 until day 40. After this date, the rate of emergence slowed, with emergence effectively completed by day 61 (31 December). Only two male exuviae were collected beyond this date. Based on coarse-scale data from nominally weekly surveys, females appear to have reached EM50 between day 32 and day 35. For the total recorded emergence population, EM50 also occurred between day 32 and day 35 (within the first week of December). Females may have reached EM100 1–10 days before males. A conservative estimate of this emergence event is that it commenced on day 16 when the first exuviae were recorded, with an emergence period of 45–55 days.
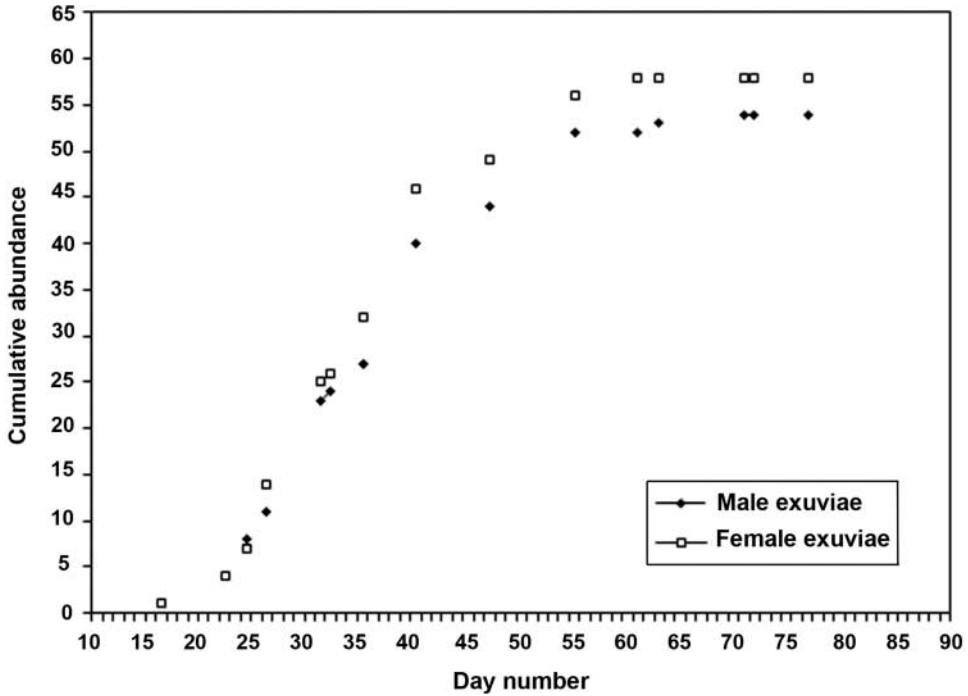
Figure 2.   Cumulative abundance of male (M) and female (F) *Petalura gigantea* exuviae (ex) recorded for one Coxs River Swamp (PBB01) for the 2008–2009 flying season (Day 10 = 10 November 2008, 77 = 16 January 2009; as per Table 2).

Results of the regular surveys for imagines during the 2007–2008 flying season in five Blue Mountains Sedge Swamp sites (PMH01, PMH03, PMH08, PMH11, PMH13), up until the last teneral was recorded, are shown in Table 3. For results of imagine surveys across the full duration of the flying season, see Baird (2012). Based on these coarse-scale observations at 7–10-day intervals, the commencement of the flying season varied among sites, from at least the beginning of November (PMH08) until late November (PMH11). The latest observation of a teneral in that year was on 26 December in PMH01.

The earliest date of observation of the species, during the larger landscape-scale study of which this emergence study formed part (Baird, 2012, Appendix 3), was of a post-teneral male imagine on 1 November 2003 near PMH01, confirming that emergence may commence before the end of October in some sites in some years. There was a large emergence event in that site in that year. The latest observation of a teneral made during annual imagine surveys of 111 swamp sites, across seven flying seasons, and conducted at different times across the duration of the peak of the flying season up until late January, was on 8 January.

Larval cohort splitting

In PBB01, 17 spatially isolated exuviae (7♂, 10♀) were found at the end of the 2009–2010 emergence season (30 December 2009). Two of these were within several centimetres of exuviae locations marked during the preceding flying season when there was a considerably larger emergence event (Table 1). Based on the broad spatial distribution of emergence locations at this site, the two emergences were consistent with a split cohort with emergence focused in the previous year. In the small Boyd Plateau Bog site, PKB05, where exuviae locations were also

Table 3. Results of surveys of relative abundance of male (♂) and female (♀) *Petalura gigantea* tenerals (T) and imagines (I) in five Blue Mountains Sedge Swamp sites for the first part of the 2007–2008 flying season up until the last date of observation of a teneral.

Site[1]	Survey date	Day[2]	♂ T	♀ T	♂ I	♀ I
PMH08*	4 November 2007	4	0	1	1	0
PMH01*	12 November 2007	12	7	7	21	3
PMH08	14 November 2007	14	8	8	26	2
PMH01	15 November 2007	15	9	15	18	2
PMH13*	16 November 2007	16	0	0	0	0
PMH11*	16 November 2007	16	0	0	0	0
PMH03*	16 November 2007	16	0	0	0	0
PMH08	21 November 2007	21	1	2	57	8
PMH01	26 November 2007	26	0	2	55	9
PMH08	28 November 2007	28	6	6	66	13
PMH13	28 November 2007	28	0	0	0	0
PMH11	28 November 2007	28	0	0	0	0
PMH03	28 November 2007	28	0	0	1	0
PMH01	3 December 2007	33	2	2	81	14
PMH08	6 December 2007	36	0	2	64	11
PMH03	7 December 2007	37	0	0	3	0
PMH11	7 December 2007	37	1	0	6	0
PMH13	7 December 2007	37	0	0	2	0
PMH01	14 December 2007	44	0	0	77	11
PMH08	15 December 2007	45	0	0	82	13
PMH11	15 December 2007	45	0	0	8	2
PMH13	15 December 2007	45	0	0	2	0
PMH03	19 December 2007	49	0	0	4	0
PMH01	26 December 2007	56[3]	0	1	67	2

[1]Site surveys marked as * were the initial surveys for each site.
[2]Day 1 is 1 November as in the previous section, to allow comparison between these sites and observations at PBB01.
[3]Day 56 (26 December) was the last day of observation of a teneral.

marked during the 2007–2008 season, the high-density emergence event in that site in 2008–2009 prevented any meaningful analysis of spatial correlation with emergence locations marked during the previous season. Based on these patterns of emergence, larval cohort splitting could not be confirmed.

Mortality at emergence

Confirmed or presumed mortalities during emergence or before the maiden flight, that were identified during systematic exuviae surveys (Table 1, $n = 11$), are included in Table 4. Sex of individuals is not included as some were not identifiable to sex. Generally, individuals had been preyed upon by small swamp ants, either pre- or post-death. Some individuals were observed being preyed upon by ants while still alive. A high proportion of recorded dead individuals consisted of those which had failed to fully withdraw from their exuviae and/or tenerals which had one or more deformed wings that had not expanded properly. In some cases, all wings were crumpled together and thus unable to open. Some tenerals located near exuviae consisted of remains only and it was not possible to identify probable cause of death.

Emergence location

Larvae appear to ascend the nearest stable vegetation they encounter after leaving their burrows, and all observed emergence perch locations were less than 25 cm horizontally, and usually much less, from the burrow opening. Prior to ecdysis, larvae perched either vertically, or were oriented

Table 4.   Identified mortalities at emergence in *Petalura gigantea* recorded during systematic exuviae surveys in the Blue Mountains, NSW.

Site code	Survey date	Total exuviae recorded	Mortalities at emergence	% mortality at emergence
PMH01	4 December 2007	79	0	0
PMH08	4 November 2007	21	0	0
PMW01	24 December 2007	18	0	0
PKB02	29 December 2007	86	7[2]	8.1
PKB05	18 December 2006	16	0	0
PKB05	28 December 2007	254	8[3]	3.1
PKB05	10 January 2010	20	2	10
PKB07	30 December 2007	11	1	9.1
PKB11	29 December 2007	33	1	3
PBB01[1]	10 January 2009	112	6	5.4
PBB01	30 December 2009	17	0	0

[1]Data for PBB01 are cumulative data from regular surveys across the 2008–2009 flying season (see Table 2).
[2]All seven dead adults/tenerals located within 50 cm of an exuvia.
[3]Remains of five additional adults/tenerals were recorded not associated closely with exuviae. Because of the difficulty of differentiating between the two after they have been dead for some time, it probably included some tenerals at least.

leaning slightly backwards due to the arrangement of the vegetation and the weight of the larvae, in either sedgeland or shrub vegetation. Most exuviae recorded were perched in graminoid sedgeland vegetation (Figure 3). Larvae were observed rearranging their hold on vegetation immediately prior to ecdysis to establish a secure emergence position. Because of the large size of larvae, a number of small shrub branches or twigs, or sedgeland stems, are usually grasped to provide the necessary stability. Some of the sedgeland species used as emergence perches are relatively robust, e.g. *Baloskion australe* (Restionaceae), *Baumea rubiginosa*, *Gymnoschoenus sphaero-cephalus*, *Lepidosperma limicola* (Cyperaceae) and *Juncus* spp. (Juncaceae), while others such as *Empodisma minus* (Restionaceae), *Carex gaudichaudiana* (Cyperaceae), *Tetrarrhena turfosa*

Figure 3.   *Petalura gigantea* ♂ exuvia perched in razor sedge *Lepidosperma limicola* in a Blue Mountains Sedge Swamp. Note the coloration due to dark muck-peat substrate (photo Ian Baird).

(Poaceae) and *Xyris ustula* (Xyridaceae) also provide suitable emergence perch sites. Shrubs used as perches include a wide range of swamp species, particularly those with effectively upright main stems, including *Leptospermum*, *Baeckea* and *Callistemon* spp. (Myrtaceae). Additional shrubs that have been observed as perch sites include, but are not limited to, *Epacris* spp. (Ericaceae), *Acacia ptychoclada*, *Pultenea divaricata* (Fabaceae), *Hakea microcarpa* (Proteaceae) and *Boronia deanei* ssp. *deanei* (Rutaceae). Most exuviae were observed perched 30–60 cm above the substrate, reflecting the general upper height limit of suitable stable perching sites in sedgeland vegetation, with the highest recorded during this study perched in a shrub 136 cm above the substrate. Perch height in shorter sedgeland vegetation was, however, sometimes lower than 30 cm above the substrate. Although the great majority of observed emergence sites were as described above, there were exceptions in a small number of cases. These situations occurred in bog patches (e.g. Boyd Plateau Bogs; Keith & Benson, 1988) with relatively low uniform vegetation, such as *Sphagnum* hummocks, or dense, low, herbaceous groundcover (e.g. *Empodisma minus*) maintained by grazing marsupials ("marsupial lawns"), but without nearby shrubs or sedgeland vegetation with upright stems. In these few cases, exuviae were observed perched either effectively horizontally or inclined (variably) upwards on any sloping groundcover vegetation or *Sphagnum* hummock.

Discussion

Sex ratio at emergence

Sex ratio at emergence was characterised by a preponderance of females. This observation is consistent with the reported trend in anisopterans generally (Corbet, 1999; Corbet & Hoess, 1998). While previous synopses (Corbet, 1999; Corbet & Hoess, 1998) of cited studies have demonstrated a general preponderance of males over females at emergence in zygopterans and the reverse in anisopterans, there are numerous records to the contrary in each sub-order. None of these reported studies included data on petalurids, although Winstanley (1981) noted that the proportion of males at emergence reported for petalurids was higher than generally observed in the Anisoptera.

It appears that *Petalura gigantea* has a greater preponderance of females at emergence than previously reported for petalurids. Taketo (1960) reported a 1:1 sex ratio ($n = 94$) in a field study of *T. pryeri* and 42.9% males ($n = 84$) from a reared population. Based on larger exuviae collections at five different localities ($n = 163$–637), Wolfe (1953) found that across the duration of the emergence season in *U. chiltonii*, the sex ratio approximated 1:1, but with a male bias early in the season. Winstanley (1981) also reported an approximate 1:1 sex ratio for each of the three sites with the largest exuviae collections in a study of *U. carovei*. In the case of *T. hageni*, Meyer and Clement (1978) collected 81 exuviae (48% ♂), and Svihla (1960a) collected 20 exuviae (55% ♂) at two different sites. With the exception of the reared population of *T. pryeri* (Taketo, 1960) and small exuviae collections reported for *Tachopteryx thoreyi* (Dunkle, 1981) and *Tanypteryx hageni* (Svihla, 1959), all of these studies demonstrated an approximate 1:1 sex ratio at emergence. A similar sex ratio (48–53% ♂) was also observed in three of the largest exuviae collections ($n = 79$–254) in this study of *P. gigantea*. However, across all collections there was an overall bias towards females at emergence.

Corbet (1999) emphasised that the sex ratio of individual species at emergence could vary between years and habitats and within habitats. The results of this study of *P. gigantea* also reveal variation in sex ratio at emergence within and among sites and years. The spread of sex ratio values reported here confirms the caution (Corbet, 1999; Corbet & Hoess, 1998) that combining results from different habitats and from different years to determine sex ratio is inappropriate. The two sites with more than one year's data, for example, both recorded a similar range of

sex ratios at emergence (PBB01, 41–48% ♂; PKB05, 40–48% ♂). Similarly, seven sites with collections during the same season also recorded a considerable range (34–53% ♂). The cause of this variability between sites and years can be expected to be largely the result of the effect of environmental factors during larval development (Corbet, 1999). In the context of the possible effect of environmental factors upon sex ratio at emergence, it is noteworthy that the three sites with the lowest recorded sex ratios (34–36% ♂) were three Boyd Plateau Bog sites during the 2007–2008 summer. This supports the notion that environmental factors during larval development in these higher altitude bogs may influence the sex ratio outcome within a larval cohort. This trend was not, however, replicated in the Boyd Plateau Bog site, PKB05, that same year, where there was an approximate 1:1 sex ratio (48% ♂). The sample size in this site, however, was large ($n = 254$) compared to the other three sites ($n = 11$–86).

Although larger emergence datasets have been recommended for odonates (Corbet, 1999; Corbet & Hoess, 1998), larger collections are generally based on readily surveyed species of typical lotic or lentic habitats with relatively large, high density, seasonal emergence events. With the exception of the sample sizes reported for *U. chiltonii* (Wolfe, 1953), all previous reported exuviae collections for petalurids have been relatively small, reflecting their particular life history attributes, demographics and patchily distributed habitat. Providing larger *P. gigantea* exuviae collections from systematic surveys is similarly constrained by (often) low densities, patchily distributed emergence clusters within potential habitat, and often, dense vegetation (thus low detectability); and larger emergence events within individual patches are unpredictable. The extent of the exuviae sampling in this study, however, has overcome some of these issues and demonstrated variability in sex ratio at emergence for *P. gigantea*, among sites and years.

Seasonal emergence pattern and duration of emergence season

The results of the exuviae study and observations of tenerals at emergence revealed that in the Blue Mountains *P. gigantea* may have an emergence period that extends from at least the end of October to early–mid-January. The duration, however, varied among sites, from at least 45 to potentially more than 70 days. Observations in PBB01 confirmed that male and female emergence commenced by mid-November (for this site in this year), with the emergence pattern for both sexes following a similar trend. The consistent trend observed validated the utility of the exuviae survey methodology in this particular environment. There was a consistent rate of emergence throughout much of the emergence season, although EM50 and EM100 for females occurred slightly before that of males. The latest date of observation of a teneral at emergence in this study is 8 January. Where larger emergence events occur in any year, the duration of the emergence period may be longer than in the case of small emergence events, with a greater probability that some emergences will be outliers from the more usual distribution. Earliest sightings of imagines or fresh exuviae were at the beginning of November. Both of these observations were either in, or adjoining, swamps (PMH01, 2003–2004; PMH08, 2007–2008) where large imagine (and emergence) abundance was documented that season. These observations suggested possible maximum emergence periods of at least 70 days if the recorded early January emergences noted above were associated with sites where emergence had commenced by the end of October. The earliest date of emergence of *P. gigantea* in a previous study (Tillyard, 1909) was 21 November, with new exuviae collected until 12 December. Based on observations during the current study, these dates underestimate the duration of the emergence season for *P. gigantea* in the Blue Mountains, at least in some years.

The only other reports of emergence season duration for a *Petalura* sp. are for *P. hesperia*, which occurs at similar latitude as the Blue Mountains region. In one population of *P. hesperia* in Western Australia, Watson (1965) observed that emergence commenced during the second half of November, but adults mostly disappeared by January. The first specimen of this species, however,

was collected in October, and the paratype was collected on 10 November (Williams, 1993; Williams & Williams, 1995). Williams and Williams (1995) reported a flying season extending to February. The commencement of the emergence season (and duration of the flying season) in *P. hesperia* in the south-west of Western Australia thus appears similar to that of *P. gigantea* in the Blue Mountains.

All petalurids, including the non-fossorial species, have a spring–summer- or summer-centred emergence and flying season. Considerable variability in the date of commencement and duration of emergence seasons have been reported for these species, particularly across latitudinal and altitudinal gradients. Seasonal effects have also been documented. Emergence in *P. gigantea* may also be subject to such variability across its wide altitudinal and latitudinal range. Identifying the variability across these gradients for other petalurids may assist in better understanding similar potential effects in *P. gigantea*.

With a wide latitudinal and climate range, *T. thoreyi* may have spring (northern hemisphere) emergence commencement as early as late March at southern latitudes (e.g. Florida) (Dunkle, 1981; Westfall, 1953), with a flying season extending into late August in the north-east USA and Canada in some seasons (Donnelly, 2000). A late flying male was also recorded on 30 September in New Jersey (Barlow, 1991). Published observations for this species indicate that commencement of the emergence season is progressively later with increasing latitude.

Emergence in *T. pryeri* generally commences from early May (Taketo, 1958, 1960), although teneral imagines have been observed on 26 April (Asahina & Okumura, 1949), with the flying season usually in May and June at lower elevations in Central Japan (Taketo, 1960), but extending to the last week of July (Taketo, 1958). Taketo (1960) reported the duration of the emergence (EM100) from a marked area as 13 days in *T. pryeri*, but with a longer period observed for a reared population that took 14 days to reach EM50; considerably shorter than the emergence period observed in this study of *P. gigantea*.

Seasonal effects also occur in *T. hageni*. Svihla (1959) reported an emergence period of throughout July at one site (Tipsoo Lake, Washington, USA). Svihla (1960a) subsequently confirmed for this site that the emergence season could be highly variable, with commencement delayed until the end of July due to persistent snow cover, and completion near the end of August. In contrast, in a larval rearing study, Steve Valley (personal communication, 22 November 2009; Baird, 2012) reported all *T. hageni* larvae ($n = 11$) emerging within a 14-day period (after a five-year larval stage), similar to the field observations of *T. pryeri* by Taketo (1960). Meyer and Clement (1978) reported a minimum five-week emergence period for *T. hageni* from bogs in lower northern California (USA), with adults active from mid-May until early July (Clement & Meyer, 1980; Meyer & Clement, 1978). This period is only slightly shorter than the lower range (45 days) observed in *P. gigantea* in this study. These sites in the southern part of the species range are generally characterised by shorter periods of snow cover than montane sites in Washington or Oregon.

Wolfe (1953) reported noticeable differences in commencement of emergence in *U. chiltonii* due to mountainous and exposed southerly location. Emergence period for *U. chiltonii* lasted at least a month in the Cass Valley region (South Island, New Zealand [NZ]) with commencement in early December. Later commencement and a generally delayed emergence period occurred on more exposed south-west facing slopes, with the latest recorded emergence from such a site on 21 January. At sites in the Auckland and Coromandel Peninsular areas (North Island, NZ), emergence in *Uropetala* spp. began in the second week of November, with peak emergence in these most northerly sites generally two to three weeks ahead of southern localities (Wolfe, 1953). This early–mid-November commencement to the emergence season is similar to that observed in a number of sites in this study for *P. gigantea*. In his later study of *U. carovei* near Wellington (southern tip, North Island, NZ), Winstanley (1981) noted that emergence was protracted compared to other petalurids, with a minimum emergence period between 33 and 53 days for four of his six study sites,

and the maximum period ranging between 42 and 63 days for the same sites. As in the current study of *P. gigantea*, the differences between these maximum and minimum figures reflected frequency of exuviae surveys. These were not conducted daily and thus imposed some level of uncertainty about the actual dates of emergence between survey dates (Winstanley, 1981). The maximum range reported for *Uropetala carovei* is broadly similar to that observed in *P. gigantea* in this study. At his Wellington sites, Winstanley (1981) reported emergence commencing in early January with isolated emergence until early March. Averaged across all of his sites, EM50 occurred by day 16.

By comparison, *Phenes raptor*, the only other southern hemisphere species with data, has a reported spring emergence season commencing from early October (Jurzitza, 1989a, 1989b) and continuing into December (Svihla, 1960b), with a flying season extending at least through January (Joseph, 1929). The duration of the emergence season in that species is thus similar to that of *P. gigantea* documented in this study.

Data from the current study of *P. gigantea* demonstrate variability among sites in commencement and duration of the emergence season. As in *Uropetala* spp., similar variability for *P. gigantea* is also possible across the wide altitudinal and latitudinal range of the species. This may be most pronounced across the latitudinal range, although no data are available. Lower altitude coastal populations, even within the Sydney region at similar latitude, may also, for example, commence emergence earlier than the higher altitude montane bog sites of the upper Blue Mountains. However, the Blue Mountains is not characterised by the seasonal weather extremes, such as deep snow cover and cold, that occur within the range of each of the other petalurids discussed. Similar altitudinal effects on commencement of the emergence season within the Blue Mountains, compared to lower altitude sites at the same latitude in the Sydney region, are thus presumed to be limited.

Emergence timing and spatial clustering

The four emergences which have been documented in *P. gigantea*, during and prior to the current study (Baird, in press; Baird & Ireland, 2006), all commenced ecdysis shortly after sunrise, and most tenerals observed during the larger landscape-scale study could be presumed to have also commenced emergence during the first few hours after sunrise. Occasional teneral individuals, however, were observed up until early afternoon, in stages of transformation which indicated that ecdysis probably commenced late in the morning. In an unusual observation, a teneral female was observed in PMH01 (15 November 2007) with full coloration and wings still closed above its abdomen, perched above its exuvia at 05:35 (solar time), less than a metre from a female larva ascending sedge stems immediately prior to commencing ecdysis (see Baird, in press). This suggested that either emergence occurred during the night or that it occurred late the previous day and the individual did not take flight before nightfall. This observation of apparent near-synchronous emergence in individuals in close proximity was observed on many occasions throughout this study. Individuals have also been observed emerging on the same day or over several days, only centimetres apart in otherwise large habitat patches with relatively low emergence density. In many instances, these spatially aggregated emergence clusters (based on presence of exuviae or observed emergence) may have been separated by considerable distances from any other observed exuviae, or may have been the only emergences recorded from a particular swamp patch in that season.

Based on many observations of oviposition and emergence pattern and density, these fine-scale, spatially and temporally aggregated emergence clusters can reasonably be presumed to be part of a single cohort resulting from a single female ovipositing event. These have included observation of a minimum of 20 exuviae recorded from a $2\,\text{m}^2$ area and numerous observations of

at least three exuviae associated with individual sedgeland tussocks or inter-tussock hollows. These observations were frequently made in larger areas otherwise devoid of emergence, but with apparently suitable breeding habitat. In the context of the patchily distributed network of *P. gigantea* swamps, these observations suggested that breeding events in any site, particularly smaller and more isolated sites, may be dependent on the presence of only a single ovipositing female in any particular year. This has implications for understanding landscape-scale population dynamics and dispersal ecology in the species. This dynamic stands in contrast to observed high emergence abundance from some large, high quality swamp patches in some years, patches which may function as important source populations at a landscape scale (Baird, 2012). High densities or clusters of exuviae or burrows have also been reported for *T. hageni* (Svihla, 1975, 1979, 1981, 1984; Valley, 1993) and *Uropetala* spp. (Winstanley & Rowe, 1980; Wolfe, 1953). In one instance, the senior author observed a density of over 80 presumed *T. hageni* burrow openings within a 1 m^2 patch in a moss bed in a seepage fen in northern California that was a known locality for the species, but with no burrow openings observed in adjoining suitable habitat (Baird, 2012). These observations confirm that the phenomenon is not restricted to *P. gigantea*.

Larval cohort splitting

In the context of the long larval stage of *P. gigantea*, multiple annual larval cohorts may be expected to be present in a particular swamp patch at any time. In his *P. gigantea* burrow excavation in Medlow Bath (Blue Mountains, Australia), Tillyard (1911) reported the presence of larvae of more than one stadium within his burrow excavation area, including both early and late stadia. Larvae of multiple size classes of the non-fossorial *T. thoreyi* have also been observed within a 2 m^2 survey area in a fen margin in Missouri (USA; Mike Ferro, personal communication, 1 July 2011). In his comparison of larvae of *Uropetala* spp. collected at monthly intervals throughout the year, Wolfe (1953) reported that at any time of the year a full set of nymphal stages could be collected. He reported that eggs deposited in early January hatch within 21–25 days and could reach the third or fourth instar during winter months, that some eggs deposited in late February may not hatch until the following spring, and that first instar larvae and unhatched eggs could be found in mid-winter. He concluded that, dependent on locality and associated weather conditions, the duration of the larval period could vary by at least a year as a result of late hatchings from over-wintering eggs laid late in the summer season. The *Petalura gigantea* flying season may extend for at least four months (Baird, 2012), with a potential ovipositing period extending for at least three months. It is therefore probable that there will be hatchling cohorts from early season ovipositing events that will be developmentally advanced compared to larval cohorts hatched from late season ovipositing, as was observed in *Uropetala* spp. (Wolfe, 1953). This suggests that any annual emergence event in *P. gigantea*, in a particular swamp patch, may include individuals from more than one year's oviposition. This dynamic would function in addition to any potential cohort splitting (e.g. Aoki, 1999) which may be operating across the long larval stage due to differences in environmental conditions during larval development of particular cohorts (Corbet, 1999). Although cohort splitting was not confirmed, observations in one site provided some evidence that it occurs. Apart from *Uropetala* spp. (Wolfe, 1953), comparative observations for other partivoltine odonates with very long-lived larvae are, however, lacking.

Mortality at emergence

Observations of recorded mortality at or immediately following emergence indicate that most such individuals either fail to successfully complete emergence or are unable to fly due to

some wing deformity. These deformities are typically the result of a failure of a wing(s) to properly expand following emergence. Some tenerals without obvious signs of deformity are presumed to have either died as a result of ant predation or exposure to a long period of cold and/or wet weather during and/or following emergence. Individuals were recorded emerging during wet weather. In some cases, these individuals may have spent up to a week perched low in swamp vegetation during unfavourable weather before having an opportunity to take their maiden flight and forage with the return of suitable weather conditions. Larvae appear to leave their burrows and undergo ecdysis when they are ready, regardless of weather conditions. Observations of increased mortality at emergence during periods of cold weather at some higher altitude Boyd Plateau Bog sites used by the species (up to 1240 m asl) suggested a temperature constraint. The maximum elevation of identified potential habitat for the species on the Boyd Plateau (and across the Blue Mountains region) was 1270 m asl. These mortalities may, however, have also been linked to extended periods of wet weather. Higher altitude sites used by the species, which are characterised by periods of cold wet weather during the summer flight season, may be near the bioclimatic limit for the species, although the ability of the species to persist under colder temperatures is unknown. While *P. gigantea* is known from montane mires of the Gibraltar Range and elsewhere on the far Northern Tablelands of NSW, with potential habitat up to 1250 m asl, it has not been recorded from higher altitude sub-alpine or montane mire sites further south in the south-eastern highlands, at Barrington Tops, or in the Werrikimbie or Cathedral Rocks areas, with mires with apparently suitable habitat up to 1370 m asl (Baird, 2012).

In most cases, the commencement of emergence, near sunrise, typically allows individuals to be prepared for their maiden flight, or, at the least, to be able to flutter a short distance (before their muscles have strengthened), by the time of commencement of diurnal activity by the ubiquitous swamp ants. These small predatory ants, which build litter-mound nests above the saturated peaty soils, do not generally appear to forage actively before mid-morning. By this time, most emerging *P. gigantea* are presumed to be sufficiently advanced in their transformation to minimise risk of predation. Any emerging individuals that have not completed ecdysis, or fully expanded their wings and bodies at the least, are highly vulnerable to predation by such ants. The early morning timing, when ambient temperatures may still be relatively low, also presumably minimises risk of predation by swamp herpetofauna, such as the Blue Mountains water skink *Eulamprus leuraensis* (Scincidae). Anecdotal evidence and personal observation indicates that this species preys upon adult *P. gigantea*, and assuming sufficient warmth, they and other reptiles may also be potential predators of emerging or teneral individuals. During hundreds of swamp surveys in the Blue Mountains (Baird, 2012), including various sites with high abundance of *P. gigantea* adults, no birds or other fauna were observed to prey upon the species.

Emergence location

Although emergence heights observed were up to 136 cm above ground, emergence probably occurs higher in shrub perches on occasions. In addition to noting that all *P. gigantea* exuviae he had observed were perched between 30 and 60 cm above the ground (consistent with most observations in this study), Gunther Theischinger (personal communication, 9 January 2013) also observed an exuvia of *P. litorea* perched *c*.150 cm above the ground in a shrub in a coastal swamp in northern NSW. Watson (1965) also provided a photograph of a *P. hesperia* exuvia perched vertically in sedgeland vegetation, similar to the position and location frequently observed in the current study of *P. gigantea*. Extrapolation from a landscape-scale population study (Baird, 2012) and a partial larval rearing study (J.W.H. Trueman, personal communication, 23 November 2006; Baird, 2012) suggest a larval stage of at least six years, and possibly 10 or more, in *P. gigantea*.

With such a long larval stage, oviposition sites in more open sedgeland vegetation with low regenerating shrubs (obligate seeders or resprouters) in the first few years following fire may become dominated by closed heath or taller shrubland with a sedgeland understorey by the time larvae undergo emergence (Baird, 2012). In these cases, larvae may climb higher to reach a suitable emergence location. Mire habitats of *P. gigantea* are generally (but variably) fire-prone environments, and along with hydrology, fire regime has been identified as an important driver of vegetation dynamics (e.g., Keith et al., 2006). Remarkably, Watson (1958) reported that exuviae of *P. hesperia* had been found up to 15 feet above ground on tree trunks in dense swamp vegetation in Western Australia. The vegetation structure of habitats of *P. hesperia*, however, may be quite different to that of *P. gigantea*. In the case of *P. gigantea*, although swamp habitats may include tall shrub thickets (scrub), they rarely have small trees associated with breeding habitat, and such high emergence sites are thus unlikely to be available. However, dense, taller, shrubland or scrub vegetation is less likely to be surveyed than sedgeland due to access difficulties, and detectability of exuviae would also be reduced. This may contribute to a bias in favour of observation of exuviae perched in sedgeland vegetation. Although sedgeland with a varying proportion of shrubs has been confirmed as the typical habitat of *P. gigantea*, tall, dense, shrubland patches may sometimes include breeding habitat in some situations and should be considered in planning surveys for exuviae. In the context of the long-lived larval stage of the species, choices should be informed by some understanding of the fire history and fire ecology of the habitat, and that in such habitat, oviposition may have occurred in the early years post-fire, before dense and taller shrubland vegetation had regrown.

During this study, the few observations of exuviae perched other than vertically were all in instances where they were perched either near horizontally or on sloping surfaces of low grazed herbland or sedgeland vegetation ("marsupial lawns") or *Sphagnum* hummocks, indicating flexibility in terms of emergence site selection when ascending vegetation supports in close proximity were unavailable. No actual emergence was observed in such situations. Emergence shortly after a fire event, such as a late spring or early summer fire, frequently results in perch selection being limited to burnt shrub stems or the burnt bases of old sedgeland tussocks.

Conclusion

This study identified sex ratio at emergence, and the commencement, pattern and duration of the emergence season in *Petalura gigantea* in the Blue Mountains. It has also confirmed variability among sites and years, consistent with observations for other petalurids. These demographic parameters are fundamental to understanding the complex, landscape-scale population dynamics of this patchily distributed, mire-dwelling species. Although there was some evidence suggesting larval cohort splitting, it was not confirmed. This study has also validated the utility of the systematic exuviae survey technique in this environment. The observations of the location of exuviae reported here, and of the timing of the emergence season, should assist researchers and land managers in more effectively identifying breeding habitat for the species, based on the presence of exuviae, and support the conservation of the species and its mire habitats.

Acknowledgements

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