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Emergence patterns and adult flight season of Anisoptera at a managed wetland site in Hong Kong, southern China

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Anisoptera emergence in the seasonal tropics was monitored at a 35-ha managed wetland site in Hong Kong from February 2004 to November 2007. Exuviae records of 18 species from multiple emergence screens, exuviae traps and transect surveys were combined. The presence of adults during this period was also monitored. The study site comprised a mosaic of ponds separated by narrow bunds. Exuviae of larvae living amongst dense submerged vegetation, and adults of crepuscular species, were probably under-recorded. Anisoptera emergence was strongly seasonal in all four years, commencing in March, with EM50 – the point at which 50% of the annual population has emerged, expressed as number of days since the start of emergence – falling between April and June, for most species; but emergence also showed considerable inter-year variation, particularly after EM50. Emergence of three species continued into December in at least one year. Extended emergence periods were generally ascribed to multivoltinism associated with unregulated life cycles, presumably facultative in the case of tropical–temperate species. The migrant *Pantala flavescens* showed no clear seasonality in emergence patterns. Composite species emergence periods over the four years ranged from two to 11 months, with no clear difference between tropical and tropical–temperate species. No species were univoltine. Adult flying seasons usually commenced in March or April, and in eight species continued until at least November, although it is unlikely that any adults survived to the following spring. Five species were on the wing for six months or less. There was considerable phenological variation among species, with life histories commonly intermediate between those of equatorial and higher latitude species.

Keywords: Odonata; dragonflies; Anisoptera; Hong Kong; exuviae; emergence; voltinism; phenology; seasonality

Introduction

Hong Kong lies just within the tropics at 22° N on the coast of southern China and has a strongly seasonal climate, characterised by a warm wet summer monsoon lasting from May to September, alternating with a cool dry winter monsoon from November to February, with "transitional weather" inbetween (Dudgeon & Corlett, 2004). Average daily temperature in July is 28.8 °C, but in January it is 15.8 °C, and the temperature occasionally drops below 10 °C for periods of several days between December and March, during strong surges of the winter monsoon. Annual rainfall is very seasonal, with 77% of it falling during the summer monsoon, and

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only 6% in the winter monsoon. This marked seasonality is reflected in the phenology of Odonata in Hong Kong (Cheung, 2008; Dudgeon & Corlett, 2004; Reels, 2009, 2010; Wilson, 1995, 2004).

Certain species of lotic habitats in Hong Kong are univoltine or semivoltine (e.g. Corbet, 1999, p. 220; Dudgeon 1989a, 1989b) and have a narrow late spring/early summer emergence period coinciding with the onset of the wet season and rising temperatures, followed by a relatively short flight season. These species, generally not encountered on the wing after August, include *Mnais mneme* Ris (Calopterygidae), *Agriomorpha fusca* May (Megapodagrionidae), *Coeliccia cyanomelas* Ris (Platycnemididae), all species of Platystictidae, 15 species of Gomphidae and members of the genus *Macromia* (Macromiidae) (Wilson, 1995, 2004). Several other stream species, however, have a more extended flight season, lasting until October in the case of *Euphaea decorata* Selys (Euphaeidae), and even into December for *Neurobasis chinensis* (Linnaeus) (Calopterygidae) and *Heliocypha perforata* (Percheron) (Chlorocyphidae) (Wilson, 1995, 2004).

Such a lengthy flight season is the exception among species of lotic habitats in Hong Kong, but it is prevalent among species of lentic habitats. Many pond species in Hong Kong have a flying season reported to extend from March to December (Wilson, 2004), although 80–90% of total annual anisopteran emergence from ponds falls between March and May (Reels, 2009, 2010). Wilson (1995, 2004) noted that dragonfly emergence is typically negligible over the winter months; a fact corroborated by Reels (2009). So is the pattern of emergence of pond dragonfly species in Hong Kong closer to the uninterrupted development of equatorial species, or more typical of the "spring" and "summer" species of temperate latitudes? Does the pattern of emergence in Hong Kong of tropical-centred species differ from that of tropical–temperate species?

Systematic counting of exuviae throughout the emergence period is one of the best methods for monitoring Anisoptera populations (Moore & Corbet, 1990). Between January 2004 and November 2007, I collected data on annual dragonfly emergence patterns, by means of regular exuviae counts, at a large area of ponds in the north-west New Territories, Hong Kong. In combination with data from surveys of adults that I conducted, this work provided much information on the phenology of pond dragonflies in Hong Kong. This information is presented and discussed below.

Materials and methods

The data reported here were collected as part of a commercial environmental monitoring and management programme. Hence, the sampling strategy was necessarily dictated by budgetary and manpower constraints, rather than by an idealised experimental design, and sampling effort necessarily varied between and within years.

The study site was the Lok Ma Chau wetland compensation area, a 35 ha mosaic of more than 25 ponds ranging in size from <0.1 ha to 1.5 ha, separated by narrow earthen bunds. The site is located at 22°30′41″N 114°03′45″E in the north-west of Hong Kong, adjacent to the border with mainland China, and is *c*.2 m a.s.l. It is owned by the Mass Transit Railway Corporation (MTRC), and managed for ecological enhancement by Asia Ecological Consultants Ltd (AEC), to which the author was subcontracted during the study period. Pond marginal vegetation was dominated by *Panicum* grass, with emergent grasses, reeds and sedges in some ponds. A small number of ponds were planted with rooted submerged macrophytes, while lotuses were established in two ponds.

Apart from the period December 2005 to February 2006, exuviae surveys were conducted during every month from January 2004 to November 2007. Exuviae were monitored using a combination of transect surveys, emergence screens and exuviae traps. Sampling effort was generally reduced during the dry season (October to February). Prior to commencement of the present study, I conducted short transect surveys at the site from February to October 2003, during which an exuviae reference collection was assembled. A single trial emergence screen and exuviae trap were operated at the site from 4 January to 21 February 2004.

Transect surveys were initially (in 2004–2005) made along a fixed *c*.1 km long transect through the pond mosaic, extended to *c*.2 km in 2006–2007. The transect followed the margins of 10 ponds, extended to 20 ponds by 2006. All Anisoptera exuviae located within 1 m of the pond margins were collected. Surveys were conducted once or twice per month as follows: 17 surveys January–September in 2004; 16 surveys February–November in 2005; 16 surveys March–November in 2006 and 2007.

Emergence screens were modelled after Stoks (2001). Screens were 1 m wide and were placed upright in shallow water, orientated parallel to the shoreline, with the bottom of the screen flush with the pond bottom, and the top extending *c*.0.5 m above the water level. Deployment was as follows: 16 screens in two ponds February–October, 24 screens in three ponds November–December 2004; 20 screens in three ponds January–September 2005.

Exuviae traps were modelled after Cook and Horn (1968). The traps were open at the bottom and at one side, with the top 60 cm × 60 cm and the sides 30 cm high. The traps were placed at the shoreline with the open side submerged so that dragonflies emerging within the traps were unable to fly out. Deployment was as follows: 16 traps in two ponds February–October, 24 traps in three ponds November–December 2004; 20 traps in three ponds January–September 2005; 28 traps in four ponds March–September, eight traps in one pond September–December 2006; eight traps in one pond January–February, 52 traps in seven ponds March–September 2007.

All available larval habitats at the pond margins were represented in the positioning of the emergence apparatus, with approximately equal representation for the north-, south- east- and west-facing aspects of each pond in which they were used. Reels (2009) determined that mean persistence of anisopteran exuviae in the field during the early wet season was 3.4 days. Therefore, exuviae on or in each screen and trap were collected, identified and counted every three or four days (occasionally, longer periods between collections were unavoidable). Exuviae were subsequently identified as described by Reels (2009, 2010).

Exuviae data from transects, screens and traps were pooled for each quarter-month period to produce composite cumulative emergence curves (Figure 1) for each species of which at least 10 exuviae were collected in a given year. Monthly dates for each quarter-month period were defined as: 1–8 (“early”), 9–16 (“2nd quarter”), 17–24 (“3rd quarter”), 25–30/31 (“late”); except for February when the following dates applied: 1–7, 8–14, 15–21, 22–28/29. Estimated EM50 (Corbet, 1999, p. 245) was calculated from the mid-point of the quarter month when emergence was first recorded to the mid-point of the quarter in which 50% of total annual emergence was reached, ± eight days. The collecting regime undoubtedly resulted in failure to record some exuviae, so Figure 1 should be regarded as an approximation subject to sampling error, especially when, as frequently occurred, the number of exuviae of a particular species collected in a given year was very low.

Dragonfly adults were surveyed along the same transect and with the same frequency as used for exuviae surveys (but not surveyed in December–January), between 0930 h and 1430 h, with all dragonflies to a distance of 5 m on the pond side of the transect identified and counted. These surveys were occasionally conducted on the same date as exuviae transect surveys, in which case the adult survey was conducted first, and then the transect repeated for exuviae.

For species with adults that are not migrants or crepuscular, and for which at least 10 exuviae were collected in a given year, combined bar and line charts were produced (Figure 2), showing pooled exuviae numbers and adult abundance in one selected year (usually the year in which exuviae of that species were most abundant), using quarter-month periods as described above, to further elucidate the voltinism of those species.

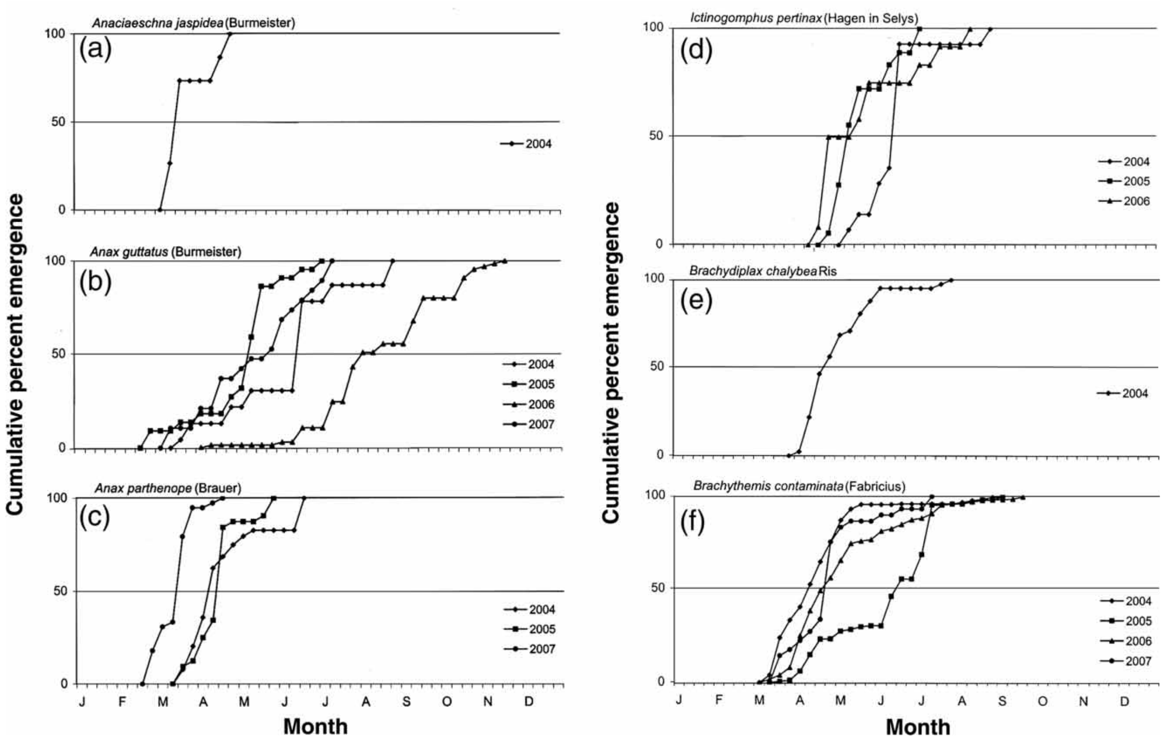

Figure 1. Continued.

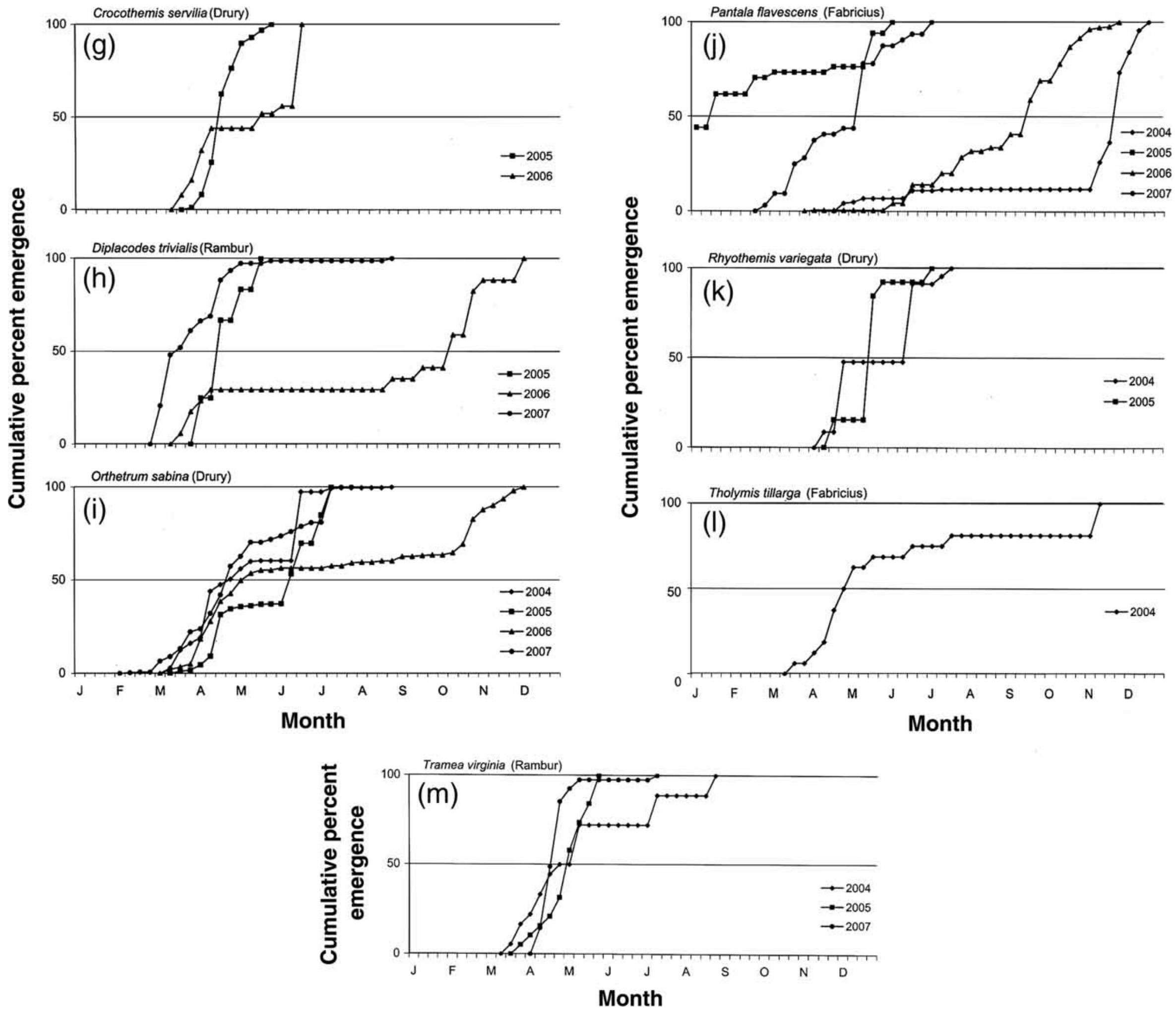

Figure 1. Cumulative numbers of exuviae of 13 species of Anisoptera at Lok Ma Chau wetland mosaic, Hong Kong, in 2004–2007.

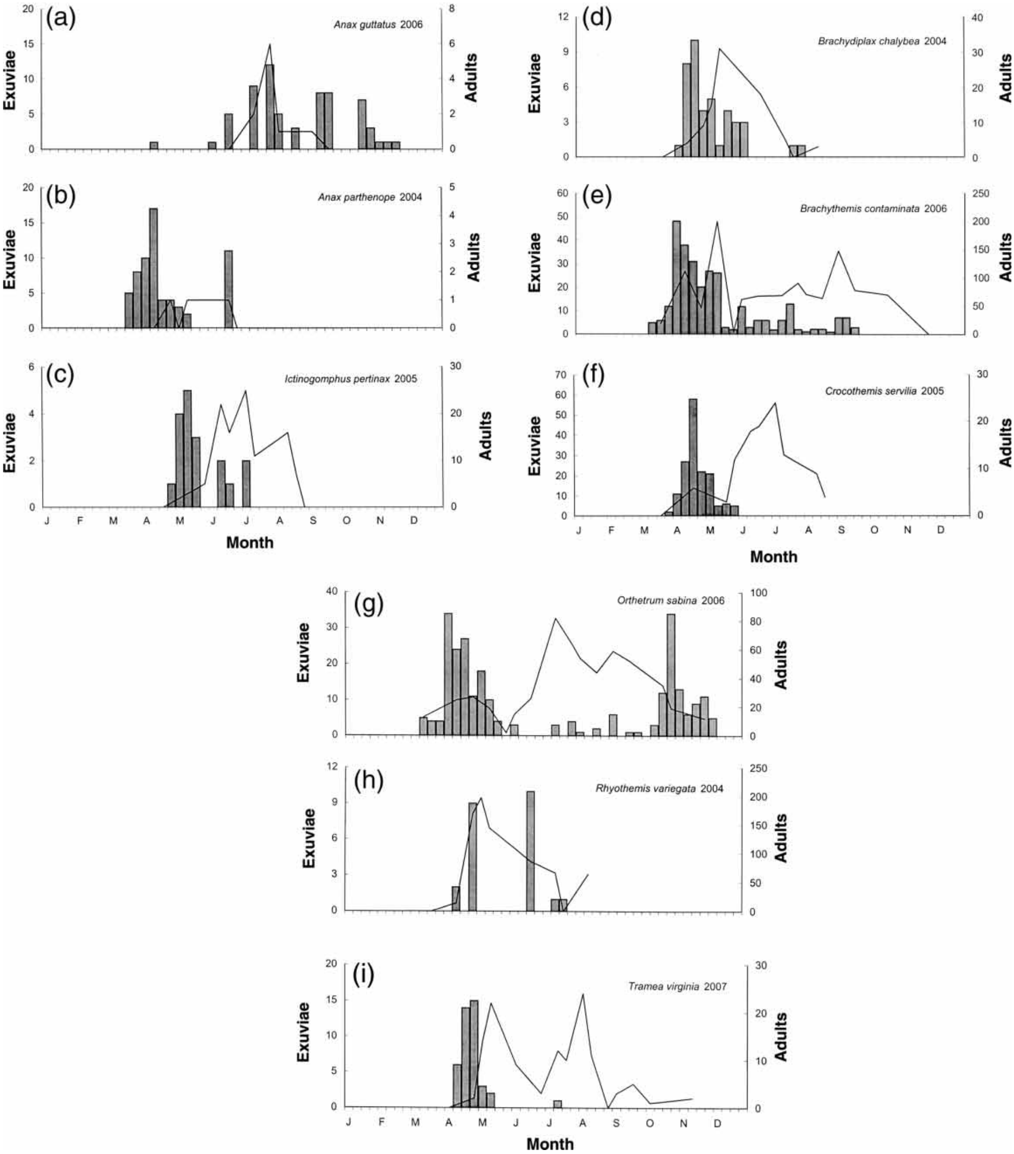

Figure 2. Abundance of exuviae (histograms) and adults (broken lines) of selected species at Lok Ma Chau wetland mosaic in 2004–2007.

Results

A total of 18 species of Anisoptera was recorded as exuviae. Tables 1, 2, 3 and 4 show respectively: annual abundance of exuviae, overall annual emergence pattern, estimated EM50 values and dates for each species of which at least 10 exuviae were collected in a given year, and overall annual abundance of adults.

In 2004, emergence of *Anaciaeschna jaspidea* (Burmeister) (Figure 1a) commenced in the 2nd quarter of March and continued until late April, with a month-long break from the 3rd quarter of March to the 3rd quarter of April. EM50 was 8 ± 8 days (Table 3). Only 15 exuviae were recorded. No exuviae were found in 2005–2007. Adults were seldom encountered (Table 4).

Table 1. Annual abundance of Anisoptera exuviae at Lok Ma Chau, 2004–2007: amalgamated data from emergence screens, exuviae traps and transect surveys.

Species	2004	2005	2006	2007	Total
Anaciaeschna jaspidea (Burmeister, 1839)	15				15
Anax guttatus (Burmeister, 1839)	23	22	65	19	129
Anax parthenope (Brauer, 1865)	64	32	1	39	136
Ictinogomphus pertinax (Hagen in Selys, 1854)	14	18	12	5	49
Sinictinogomphus clavatus (Fabricius, 1775)	3	3	1	1	8
Epophthalmia elegans (Brauer, 1865)	5	2	7	4	18
Acisoma panorpoides (Rambur, 1842)	1				1
Brachydiplax chalybea (Ris, 1911)	41	2	1	2	46
Brachythemis contaminata (Fabricius, 1793)	1209	757	291	62	2319
Crocothemis servilia (Drury, 1770)	7	157	25	5	194
Diplacodes trivialis (Rambur, 1842)	2	10	17	77	106
Hydrobasileus croceus (Brauer, 1867)	6				6
Orthetrum sabina (Drury, 1770)	273	664	255	541	1733
Pantala flavescens (Fabricius, 1798)	656	34	214	32	936
Rhyothemis variegata (Drury, 1773)	23	13	2	9	47
Tholymis tillarga (Fabricius, 1798)	16				16
Tramea virginia (Rambur, 1842)	18	19	1	41	79
Zyxomma petiolatum (Rambur, 1842)	6				6

Table 2. Emergence period of Anisoptera species at Lok Ma Chau pond mosaic (months in which exuviae were recorded, February 2004 to November 2007).

Species (total no. exuviae)	J	F	M	A	M	J	J	A	S	O	N	D
A. jaspidea ($n = 15$)			■	■								
A. guttatus ($n = 129$)		■	■	■	■	■	■	■	■	■	■	
A. parthenope ($n = 136$)		■	■	■	■	■						
I. pertinax ($n = 49$)				■	■	■	■	■				
S. clavatus ($n = 8$)				■	■	■		■				
E. elegans ($n = 18$)				■	■	■	■	■			■	
A. panorpoides ($n = 1$)				■								
B. chalybea ($n = 46$)				■	■	■	■	■				
B. contaminata ($n = 2319$)			■	■	■	■	■	■	■			
C. servilia ($n = 194$)			■	■	■	■						
D. trivialis ($n = 106$)			■	■	■			■	■	■	■	■
H. croceus ($n = 6$)				■	■							
O. sabina ($n = 1733$)		■	■	■	■	■	■	■	■	■	■	■
P. flavescens ($n = 936$)	■	■	■	■	■	■	■	■	■	■	■	■
R. variegata ($n = 47$)				■	■	■	■					
T. tillarga ($n = 16$)			■	■	■	■	■				■	
T. virginia ($n = 79$)			■	■	■		■	■				
Z. petiolatum ($n = 6$)			■	■	■							

In 2004, emergence of *Anax guttatus* (Burmeister) (Figure 1b) commenced in the 3rd quarter of March and continued intermittently until late August. The emergence period was even more extended in 2006, commencing in the 2nd quarter of April with a single exuvia, but then interrupted until early June, before continuing intermittently until the 3rd quarter of November (Figure 2a). In 2005 and 2007, however, the emergence period began and ended earlier, and was of shorter duration. In 2005 emergence was from late February to early July; in 2007 it was the 2nd quarter of March to the 2nd quarter of July. Mean EM50 was 89.8 ± 8 days (Table 3). Mean annual abundance of exuviae was $32.3 \pm$ s.e. 11.0. Adults were generally scarce but were observed from April to September, and were at their most abundant, on average, in July and September (Figure 2a; Table 4).

Table 3. Estimated EM50 expressed in number of days from beginning of emergence for each Anisoptera species of which at least ten exuviae were collected in a given year at Lok Ma Chau, 2004–2007; estimated date at which EM50 reached in parentheses.

	Estimated EM50 value and date (±8 days)				
Species	2004	2005	2006	2007	Mean
A. jaspidea	8 (20 March)				
A. guttatus	92 (20 June)	76.5 (12 May)	114 (4 August)	76.5 (27 May)	89.8
A. parthenope	23 (12 April)	31 (20 April)		23.5 (20 March)	25.8
I. pertinax	39 (20 June)	15 (12 May)	7 (27 April)		20.3
B. chalybea	23 (27 April)				
B. contaminata	31 (12 April)	92 (20 June)	46 (27 April)	38 (27 April)	51.8
C. servilia		23.5 (20 April)	61 (20 May)		42.3
D. trivialis		16 (20 April)	206 (12 October)	16 (20 March)	73.5
O. sabina	46 (27 April)	84 (12 June)	61 (12 May)	75.5 (27 April)	66.6
P. flavescens	213 (27 November)	16 (20 January)	169 (20 September)	75.5 (12 May)	118.4
R. variegata	69 (20 June)	30 (20 May)			49.5
T. tillarga	38 (27 April)				
T. virginia	53 (12 May)	37.5 (04 May)		15 (27 April)	35.2

In 2004 and 2005 emergence of *Anax parthenope* (Brauer) (Figures 1c, 2b) began in the 3rd quarter of March. Emergence was interrupted for one month after reaching ca EM80 in 2004, before ending in the 3rd quarter of June (Figure 2b). A similar, although shorter, interruption occurred at ca EM85 in 2005, with emergence ending in late May. In 2007, emergence started and ended earlier, in late February and the 3rd quarter of April, respectively. Mean EM50 was 25.8 $\pm$ 8 days (Table 3). Mean annual abundance of exuviae in 2004–2005 and 2007 was 45 $\pm$ 9.7. Only one exuvia was collected in 2006. Adults were scarce in all four years, but were recorded from April to November, and most abundant on average in April and November (Figure 2b; Table 4).

Exuviae of *Sinictinogomphus clavatus* (Fabricius) were scarce in all four years (Table 1). Three exuviae were collected between late April and the 2nd quarter of May in 2004; three between the 3rd quarter of May and the 2nd quarter of June in 2005; one in the 3rd quarter of August 2006; one in late April 2007. Adults were uncommon but recorded from April to September, with highest abundance in May (Table 4).

In 2004, emergence of *Ictinogomphus pertinax* (Hagen in Selys) (Figure 1d) did not start until the 2nd quarter of May, EM50 was reached during the 3rd quarter of June, when nearly 60% of all exuviae were collected, and emergence was subsequently interrupted for two months before finally ending in late August. In the two following years, emergence commenced progressively earlier, in late April in 2005 and the 3rd quarter of April in 2006. EM50 was reached rapidly in both years, within one or two weeks, and then continued intermittently, until early July in 2005 (Figure 2c) and the 2nd quarter of August in 2006. Mean EM50 was 20.3 $\pm$ 8 days (Table 3). Mean annual abundance of exuviae in 2004–2006 was 14.67 $\pm$ 1.76. Only five exuviae were collected in 2007. Adults were recorded April to October. They were scarce in April, increasing steadily in abundance until July, after which numbers declined (Figure 2c; Table 4).

Table 4. Mean (and overall total) monthly abundance of Anisoptera adults (males + females; species of which exuviae were recorded) in transect surveys at Lok Ma Chau, 2004–2007; n = number of surveys conducted.

Species	March $n = 5$	April $n = 8$	May $n = 8$	June $n = 8$	July $n = 8$	August $n = 8$	September $n = 4$	October $n = 4$	November $n = 3$
A. jaspidea		0.1 (1)	0.3 (2)			0.3 (2)			
A. guttatus		0.1 (1)	0.8 (6)	0.8 (6)	1.1 (9)	0.4 (3)	1.5 (6)		
A. parthenope		0.9 (7)	0.3 (2)	0.4 (3)		0.1 (1)	0.8 (3)	1.3 (5)	1 (3)
I. pertinax		0.1 (1)	3.1 (25)	12 (96)	15 (120)	10.3 (82)	8.5 (34)	2 (8)	
S. clavatus		0.1 (1)	1.0 (8)	0.1 (1)	0.1 (1)		0.3 (1)		
E. elegans		0.9 (7)	0.5 (4)	0.8 (6)	0.4 (3)	0.5 (4)	1.8 (7)	0.3 (1)	
A. panorpoides		0.5 (4)	1.5 (12)	0.1 (1)	1.1 (9)	1.1 (9)	2 (8)	0.5 (2)	
B. chalybea		2.5 (20)	14.5 (116)	6 (48)	2.6 (21)	2.1 (17)	7 (28)	2 (8)	0.7 (2)
B. contaminata	6.2 (31)	57.6 (461)	128.3 (1026)	102.9 (823)	100.1 (801)	57.7 (462)	92.8 (371)	45 (180)	4.7 (14)
C. servilia	0.8 (4)	6.1 (49)	7.8 (62)	13.1 (105)	14.2 (113)	13.6 (109)	18.5 (74)	7.8 (31)	7 (21)
D. trivialis	0.8 (4)	8.3 (66)	8 (64)	6.9 (55)	5.5 (44)	9.2 (74)	1.5 (6)	2.5 (10)	2.3 (7)
H. croceus			0.8 (6)	2.1 (17)	1.8 (14)	0.8 (6)			
O. sabina	3.6 (18)	28 (224)	34.8 (278)	53 (424)	73.1 (585)	54.6 (437)	45.3 (182)	17.8 (71)	9 (27)
P. flavescens		1.3 (10)	4.4 (35)	0.9 (7)	5.1 (41)	121.7 (970)	142.5 (570)	27.5 (110)	9 (27)
R. variegata		40.3 (322)	146.5 (1172)	106.4 (851)	70 (560)	54.8 (438)	82 (328)	6.5 (26)	
T. tillarga			0.1 (1)		0.4 (3)	0.4 (3)	0.3 (1)		
T. virginia		3.4 (27)	8.3 (66)	7 (56)	8.5 (68)	7.5 (60)	4.8 (19)	2.5 (10)	0.7 (2)

Exuviae of *Epophthalmia elegans* (Brauer) were scarce in all four years (Table 1). Five exuviae were collected between late April and 3rd quarter May in 2004; two between the 2nd quarter of July and the 2nd quarter of August in 2005; seven between early April and late November in 2006; four from the 2nd of quarter May to the 2nd quarter of July 2007. Adults were uncommon but recorded from April to October, with highest abundance in September (Table 4).

A single exuvia of *Acisoma panorpoides* Rambur was collected in 2nd quarter April 2004. No further exuviae records were made of this species. Adults were generally uncommon but were recorded from April to October, with highest abundance in May and September (Table 4).

In 2004, emergence of *Brachydiplax chalybea* Ris (Figures 1e, 2d) commenced in early April and continued until late July, with a lengthy interruption from early June to the 3rd quarter of July. EM50 was 23 ± 8 days. Forty-one exuviae were recorded. Exuviae were scarce in subsequent years (Table 1), with just two collected in 2005 (late July and the 2nd quarter of August), one in early August 2006, and two in 2007 (3rd quarter of April and 2nd quarter of June). Adults were moderately abundant and recorded from April to November, with peak abundance in May (Figure 2d; Table 4).

Emergence of *Brachythemis contaminata* (Fabricius) (Figures 1f; 2e) commenced in the 2nd or 3rd quarter of March and ended in September, apart from in 2007, when emergence ended in the 2nd quarter of July. Very few exuviae were recorded after the 2nd quarter of July. Mean EM50 was 51.8 ± 8 days (Table 3). Mean annual abundance of exuviae was 579.8 ± 254.8. Adults were generally abundant from April to October and were present from March to November (Figure 2e; Table 4).

In 2005, emergence of *Crocothemis servilia* (Drury) (Figures 1g, 2f) commenced in late March and continued without interruption until late May, with EM50 passed by 3rd quarter April. In 2006, the emergence period was a month longer, from the 3rd quarter of March to the 3rd quarter of June, with a lengthy interruption from mid April to mid May (Figure 2f). Mean EM50 was 42.3 ± 8 days (Table 3). Mean annual abundance of exuviae in 2005–2006 was 91 ± 81.8 ($n = 157$ in 2005; 25 in 2006). Only seven exuviae were recorded in 2004, and five in 2007. Adults were recorded from March to November, and most abundant on average in July and September (Figure 2f; Table 4).

Emergence of *Diplacodes trivialis* (Rambur) (Figure 1h) in 2005, during which only 10 exuviae were recorded, lasted from early April to 3rd quarter May, with EM50 passed by the 3rd quarter of April. The pattern of emergence was very different in the two subsequent years. In 2006, although emergence commenced in the 3rd quarter of March, there was a very lengthy interruption after ca EM30, of more than four months, from the 2nd quarter of April to the 3rd quarter of August. EM50 was not reached until the 2nd quarter of October, nearly seven months after emergence commenced, and emergence did not end until early December. In 2007, emergence commenced in early March, rapidly reached EM50 by the 3rd quarter of March, and was at *c*. EM95 by early May. A period of three months elapsed with no exuviae recorded, but a single exuvia was collected in late August. EM50 in both 2005 and 2007 was 16 ± 8 days; in 2006 it was 206 ± 8 days (Table 3). Mean annual abundance of exuviae in 2005–2007 was 34.7 ± 18.4. Only two exuviae were recorded in 2004. Adults were generally recorded from March to November (although not until June in 2004), and were generally most abundant from April to August (Table 4).

Exuviae of *Hydrobasileus croceus* (Brauer) were scarce in 2004, with just six collected between late April and the 2nd of quarter May (Table 1). No exuviae of this species were found in 2005–2007. Adults were uncommon and only recorded from May to August, with peak abundance in June (Table 4).

Emergence of *Orthetrum sabina* (Drury) (Figures 1i, 2g) commenced in the 2nd or 3rd quarter of March in 2004–2006, but a month earlier in 2007. Emergence ended in July in 2005 and 2007, but continued until late August in 2004, and in 2006 it was very prolonged, continuing until early December, after a month-long break in June–July (Figure 2g). Mean EM50 was 66.6 ± 8 days (Table 3). Mean annual abundance of exuviae was 433.3 ± 101.0. Adults were generally abundant from April to September and were present from March to November (Figure 2g; Table 4).

The emergence pattern of *Pantala flavescens* (Fabricius) (Figure 1j) varied considerably from year to year. In 2004, emergence of this migrant species was under way by late April, but had only reached EM10 by the 3rd quarter of June, after which there was no emergence until early November. Emergence continued until the 3rd quarter of December, and in fact it followed on into 2005, when EM50 was reached as early as the 3rd quarter of January (16 ± 8 days; Table 3), continuing intermittently until early June. In 2006, a single exuvia was collected in early April, but there was no subsequent emergence for two months. Emergence then proceeded gradually until late November. In 2007, emergence started in late February and ended in early June. Mean annual abundance of exuviae was 234 ± 147.0. Adults were present April to November, and occasionally very abundant, as in August–September 2006 and September 2007, but were not recorded until June in 2004, and were scarce or completely absent in June–July in most years.

In 2004, emergence of *Rhyothemis variegata* (Drury) (Figures 1k, 2h) commenced in the 2nd quarter of April and continued intermittently until the 3rd quarter of July, with EM50 passed by the 3rd quarter of June. In 2005, the emergence period was again intermittent, but shorter, from the 3rd quarter of April to early July. Mean EM50 was 49.5 ± 8 days (Table 3). Mean annual abundance of exuviae in 2004–2005 was 18 ± 6.2. Only two exuviae were recorded in 2006, and nine in 2007 (Table 1). Adults were generally abundant from April to September, particularly in May–June, and were present from April to October (Figure 2h; Table 4).

In 2004, emergence of *Tholymis tillarga* (Fabricius) (Figure 1l) commenced in the 3rd quarter of March and continued intermittently until the 2nd quarter of November, with a very lengthy interruption from the 3rd quarter of June to the 2nd quarter of November. EM50 was 38 ± 8 days (Table 3). Sixteen exuviae were recorded. No further exuviae were collected in 2005–2007 (Table 1). Adults were scarce but recorded from May to September (Table 4).

Emergence pattern of *Tramea virginia* (Rambur) (Figure 1m) was initially similar in 2004–2005 and 2007, commencing between the 3rd quarter of March and the 2nd quarter of April, and reaching EM50 between late April and early May. Emergence ended by late May in 2005, but in 2004 and 2007 it was interrupted for lengthy periods, ending in late August in 2004, and the 2nd quarter of July in 2007 (Figure 2i). Mean EM50 was 35.2 ± 8 days (Table 3). Mean annual abundance of exuviae in 2004–2005 and 2007 was 26 ± 7.5. Only one exuvia of this species was collected in 2006. Adults were not seen before April and were scarce by October, but were recorded as late as November in 2007 (Figure 2i, Table 4).

Exuviae of *Zyomma petiolatum* Rambur were scarce in 2004, with just six collected between the 3rd quarter of March and early May (Table 1). No exuviae of this species were found in 2005–2007. No adults were recorded throughout the study.

Discussion

Asynchrony of emergence

In the current study, the strongest evidence of synchronised emergence (EM50 <10 days) among resident species occurred for *Anaciaeschna jaspidea* in 2004, and *Ictinogomphus pertinax* in 2006 (Table 3). Weaker synchronisation (EM50 10–25 days) was exhibited by *Anax parthenope*in 2004 and 2007, *I. pertinax* in 2005, *Brachydiplax chalybea* in 2004, *Crocothemis servilia* in 2005 and *Tramea virginia* in 2007 (Table 3). Notably, however, all of the above species, with the exceptions of *A. jaspidea* and *B. chalybea* – for which there was only one year of good emergence data – also had unsynchronised emergence (EM50 >25 days) in at least one of the study years (Table 3). The migrant *Pantala flavescens*, and *Diplacodes trivialis* – which may also be migratory in Hong Kong (Wilson, 2004) – are both capable of completing larval development within 50 days in north-west India (Kumar, 1984a, 1984b), and had widely varying annual emergence patterns. No species showed the very tight synchronisation characteristic of univoltine "spring" species such as *Anax imperator* in Britain, with EM50 at 3 days (Corbet, 1962); most underwent one or more lull periods, lasting several weeks or months and presumably corresponding to larvae that overwintered in progressively earlier stadia, within the annual emergence pattern. *Brachythemis contaminata*, *C. servilia*, *D. trivialis* and *Orthetrum sabina* are all known to have unregulated life cycles in north-west India (Corbet, 1999; Kumar, 1976, 1984a, 1989), while *P. flavescens*, although multivoltine, has a regulated life cycle because newly emerged adults are obligate migrants (Corbet, 1999; Kumar, 1984b). *Anax guttatus* was clearly unregulated, with an average EM50 of 89.8 days (Table 3) – the longest for any species in the study other than *P. flavescens*.

Inferences on voltinism – tropical–temperate species

It is perhaps notable that *A. guttatus*, an Oriental species, took up to seven months to complete annual emergence (Figure 1b) and was multivoltine, emerging in any month from February to November (Figure 2a, Table 2), whereas the congeneric *A. parthenope*, which is distributed across the Palaearctic, had a much more stable, temporally restricted emergence pattern, confined to three months from February to June (Table 2), and may have been bivoltine (Figure 1c). In 2004, for example, when 64 *A. parthenope* exuviae were collected, there were two discrete periods of emergence: the main one lasting from mid-March to mid-May (77% of the total emergence), and a shorter period during the second half of June (Figure 2b). As noted above, this pattern was repeated in 2005, with an apparent interruption during the first half of May; however, the 2005 emergence pattern may have been confounded by exceptionally heavy rainfall during May of that year, which would have increased the rate at which exuviae were lost from emergence supports before they could be recorded, as well as possibly suppressing normal emergence activity: rainfall in May 2005 exceeded 500 mm (>60% above the average for the month) and fewer than 88 hours of sunlight were recorded – the third lowest total since records began in 1884 (Hong Kong Observatory, 2010).

Among other species with Palaearctic as well as tropical ranges, there was even less evidence for bivoltinism. *C. servila* in 2006 showed a discrete emergence period from mid-March to mid-April, followed by a second rather diffuse emergence period from mid-May to a peak in the 3rd quarter of June (Figure 1g), but the small dataset from that year – only 25 exuviae – makes interpretation unsafe. In 2005 on the other hand, 157 exuviae were collected, and the emergence period was apparently uninterrupted throughout its relatively short duration from late March to late May (Figure 2f) – a pattern and duration that might suggest the species is univoltine in Hong Kong, were it not for the evidence of multivoltinism in 2006.

Emergence of *T. virginia* in 2007 fell into two discrete periods (Figures 1m, 2i), again possibly indicating bivoltinism, but the second of these periods, in the second quarter of July two months after the end of the first period, involved only a single exuvia record, so interpretation is unsafe. The species was at any rate apparently multivoltine in 2004 (Figure 1m).

Exuviae of *O. sabina* were recorded in every month apart from January (Table 2), and the species was evidently multivoltine in all four years (Figure 1i), although invariably there were two peak emergence periods in each year, the first falling in April and the second in June/July, apart from in 2006, when the overall emergence was very extended, and the second peak fell in October (Figure 2g).

There was insufficient emergence data for *Sinictinogomphus clavatus* or *Epophthalmia elegans* to draw any inference on their voltinism, but exuviae of these two species were recorded as late as August and November, respectively (Table 2).

Inferences on voltinism – tropical species

Emergence patterns possibly suggestive of bivoltinism were displayed by the tropical-centred *A. jaspidea* and *B. chalybea* (Figures 1a, 1e), although for both of these species there was usable emergence data for one year only. Fifteen exuviae of *A. jaspidea* were collected in 2004, in two discrete periods separated by one month; 11 exuviae in March and four in April. In the case of *B. chalybea*, 41 exuviae were collected in 2004, 95% of which were recorded during an apparently uninterrupted emergence period lasting from early April to early June, with the remaining 5% emerging in the second half of July (Figure 2d). However, given the paucity of emergence data for these two species in the present study, it is unsafe to postulate bivoltinism.

In addition to *A. guttatus*, apparent multivoltinism was displayed by all other tropical species for which there was usable emergence data. Annual emergence of *I. pertinax* was repeatedly interrupted in all three years 2004–2006 (Figure 1d). In 2005, for example, there were apparently three discrete emergence periods: late April to late May, mid-June and early July (Figure 2c). *B. contaminata* emergence commenced in March each year and continued to September (July in 2007) (Figure 1f), apparently uninterruptedly in 2006 (Figure 2e), albeit in successive waves, with clear peaks and troughs. In the case of *Rhyothemis variegata*, annual emergence was punctuated by repeated interruptions in 2004 and 2005 (Figure 1k). In 2004, there were emergence peaks in late April and the third quarter of June, in addition to two other apparently discrete emergence periods (Figure 2h), although few exuviae were collected, relative to the abundance of adults, and it seems clear that emergence of this species was under-recorded.

There was insufficient emergence data for *Acisoma panorpoides*, *Hydrobasileus croceus*, *Tholymis tillarga* or *Zyxomma petiolatum* to draw any inference on their voltinism, but exuviae of *T. tillarga* were recorded from March to as late as November, while exuviae of the other three species were confined to the March–May period.

Annual variation in emergence patterns

It is evident from Figure 1 that the emergence pattern of most species was subject to considerable annual variation. This was most clearly exhibited by *D. trivialis* and the migrant *P. flavescens*. *D. trivialis* had closely synchronised emergence in both 2005 and 2007, but very extended emergence in 2006, marked by a 4.5 month interruption (Figure 1h). Since adults were quite abundant in April 2006, and the species is capable of rapid larval development, this interruption is difficult to explain. Adult *P. flavescens* were not recorded at the study area until June in 2004, but were abundant in August, many having arrived with late summer typhoons. This presumably explains the sudden mass emergence in November of that year, following a prolonged interruption in emergence from June to early November (Figure 1j). Similarly, adults were not seen until April in 2006, with emergence accelerating in June of that year and continuing until November, after another large typhoon-borne influx of adults in August and September.

Annual variations in emergence patterns were also pronounced in several resident species; notably *A. guttatus*, *A. parthenope*, *C. servilia*, *O. sabina* and *T. virginia*. The scope of the present study did not allow for an investigation into the causes of these inter-year variations.

However, temperature probably pays a key short-term role in determining the seasonal placement of emergence (Corbet, 1999). This may be a particularly pertinent consideration for tropical species in subtropical Hong Kong, that are living close to the limits of their ideal developmental conditions. Annual variations in seasonal temperature might explain some of the annual variations in emergence periods and EM50 observed in the current study, and it is unfortunate that this parameter was not measured. Severe rainfall events such as occurred through May 2005 are also likely to affect emergence, as tenerals are presumably highly vulnerable to heavy rainfall.

The various management practices at the Lok Ma Chau wetland mosaic undoubtedly had local impacts on odonate emergence over the four-year study period. These practices were too numerous and varied to monitor their impacts, although one major impact seems obvious. Several species, including *A. jaspidea*, *A. panorpoides*, *H. croceus* and *Z. petiolatum* were recorded as exuviae in 2004 only, during the course of the study. All exuviae of these species were recorded in a single, long-established, fish-free shallow weedy pond ("Pond 3" in Reels, 2010), which was deliberately flooded in the latter half of 2004, and subsequently fish-stocked. Thereafter, no more exuviae of these species were found, across the study area. Most exuviae of *B. chalybea* and *T. tillarga* recorded in the study were also from this pond in 2004; *B. chalybea* exuviae abundance was much lower after 2004, and *T. tillarga* was not recorded after 2004.

Adult phenology

Abundance of exuviae did not always reflect abundance of adults. Notable examples are *A. panorpoides*, regularly recorded as an adult but with only a single exuvia collected over four years, and *R. variegata*, of which relatively few exuviae were found, despite the fact that adults were very abundant through the wet season (Tables 1 and 2; Figure 2h). It is likely that the exuviae sampling strategy resulted in under-representation of these species; perhaps their larvae were emerging on emergent macrophytes some distance in from the pond margin. Two other species with weed-dwelling larvae – *Neurothemis tullia* (Drury) and *Urothemis signata* (Rambur) – occurred regularly in the study area as adults but were never recorded as exuviae. On the other hand, timing of adult surveys undoubtedly resulted in under-recording of crepuscular species such as *A. jaspidea*, *T. tillarga* and *Z. petiolatum*, all of which were recorded more frequently as exuviae than as adults.

The adult flight season generally commenced in March or April (Table 4), with *H. croceus* and the crepuscular *T. tillarga* not seen until May. It is unfortunate that adult surveys were not conducted in December–February: of the 18 species recorded as exuviae, eight were still being recorded as adults in November (Table 4). The survey schedule was based upon the fact that Anisoptera adults are scarce in December–February, as subsequently verified by Cheung (2008), who recorded Odonata adults at Luk Keng, a large Hong Kong freshwater marsh, every two weeks from February 2005 to April 2006. Cheung recorded no odonates in December–January, and apparently fewer than five individuals – possibly zygopterans – in February. These were probably recently emerged individuals, as no odonate species in Hong Kong is known to diapause over the cool dry season, with the possible exception of *Lestes nodalis* Selys (Wilson, 1995), and it seems unlikely that any could survive it as active adults. Nevertheless, Wilson (2004) reported several Hong Kong species, including *B. contaminata* and *O. sabina*, as having a flight season extending into December, corroborated by my own unpublished observations. Given that 80–90% of annual emergence of most pond anisopterans takes place between March and May (Reels, 2009, 2010), it appears likely that such dragonflies are capable of surviving as adults for several months, with stragglers surviving into December and even January. It is noteworthy that pond odonates in Dehra Dun, north-west India, have an adult life-span of eight to nine months, over a similar period and under climatic conditions apparently similar to those in Hong Kong (Kumar, 1972, 1976). However, a number of species at Lok Ma Chau had a considerably shorter flying season; notably *A. guttatus* and *Sinictinogomphus clavatus* (April to September) and *H. croceus* (May to August), while six other species were not seen as adults after October.

Occurrence of adults also showed wide inter-year variability. For example, *A. guttatus* was only recorded in June and July in 2004, and only in April, May and September in 2007. *A. parthenope* was only recorded in April to June in 2004 (Figure 2b), and only in November in 2007. The flying season of the more commonly observed *I. pertinax* extended to October in 2006 and 2007, but only to August in 2005 (Figure 2c), with peak annual abundance progressively shifting from June–July in 2004 to August–September in 2007.

Among resident, non-crepuscular libellulids, *B. chalybea* had a significantly shorter flight season in 2005 (May–September) than in 2007 (April–November), and had a single abundance peak in spring 2004 (Figure 2d; but note that adult surveys ended in August in that year) and 2005, but a second abundance peak, in September, in 2006 and 2007. The flight season of *T. virginia* progressively extended in 2005 to 2007, from April–September to April–November, with a single abundance peak in 2004–2006, but two peak abundance periods in 2007 (Figure 2i).

More stable annual flight seasons were observed in *B. contaminata*, *C. servilia*, *O. sabina* and *R. variegata* – the four most abundant and commonly recorded non-migrant species, suggesting the possibility that the annual variation among the less frequently observed species described above may be at least partly attributable to insufficiently thorough field surveys.

Exuviae abundance did not always foreshadow adult abundance. For example, in 2004, *A. guttatus* adults were not seen after early September, even though emergence continued until the middle of November (Figure 2a), and the September peak in adult abundance of *T. virginia* in 2007 was not preceded by any corresponding emergence event (Figure 2i), perhaps indicating adult immigration in this case. In most cases, however, there appears to be a clear time-lag relationship between abundance of exuviae and of adults (Figures 2c–2h).

Conclusions

The overall emergence periods derived from four years pooled data in Table 2 vary considerably between species and appear to bear no relationship to tropical/tropical–temperate species provenance, as might be expected of the generally widespread, opportunistic eurytopic species represented. Exuviae of resident tropical species were recorded in from two months (*A. jaspidea* and *H. croceus*) to 10 months (*A. guttatus*), while those of tropical–temperate species were found in four months (*C. servilia*) to 11 months (*O. sabina*). Exuviae of *P. flavescens* were recorded in all months, while those of *D. trivialis* were recorded from March to December, although never during June–July.

The two most abundant species emerging at Lok Ma Chau, the tropical *B. contaminata* and the tropical–temperate *O. sabina*, had annual emergence periods lasting up to six or nine months, respectively, but generally showed very similar emergence patterns, including an extended lull during May 2005 (Figures 1f and 1i), which may have been weather-induced (see comments above).

Such temporally dispersed emergence suggests that most if not all species had, to varying degrees, unregulated (*sensu* Corbet, 1999) multivoltine (including bivoltine) life cycles, with continuous larval development, overwintering in up to several stadia. In the case of tropical–temperate species, multivoltinism was presumably facultative. Data on larval duration for all of these species in Hong Kong, that would provide definitive information on voltinism, are unfortunately lacking.

In conclusion, 80% or more of annual emergence of most pond Anisoptera species in Hong Kong occurs in March to May. However there remains considerable variation in phenology and life history strategies between species, with emergence patterns generally closer to the uninterrupted life histories of equatorial areas than the strongly regulated life histories of species at higher latitudes. The degree of flexibility in emergence patterns varies greatly from species to species. Although the results in general lend confidence to the usefulness of exuviae surveys in elucidating lentic anisopteran phenologies, the absence of exuviae of several species frequently recorded as adults points to some limitations of the method, at least within the habitat studied. Also, while applicable to the study area in 2004–2007, these observations may have only limited generality in the regional context: many different environmental factors can contribute to variation in voltinism and emergence patterns (Corbet, 1999).

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