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Detection probabilities and sampling rates for Anisoptera exuviae along river banks: influences of bank vegetation type, prior precipitation, and exuviae size

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Exuviae collections have considerable value in population studies of Odonata, but methods for standardizing collections or estimating densities and detection probabilities have been little studied. I measured sampling rates for Anisoptera exuviae and used a maximum likelihood, four-pass, depletion population estimator to standardize collections and to estimate exuvial densities and detection probabilities along 10 riverbank stations in Wisconsin. First-pass sampling rates averaged slower than the overall average for experienced collectors (0.53 m min^{-1} compared to 0.90 m min^{-1}) because more exuviae were present on the first pass, increasing picking and handling time. Neither bank vegetation type (grassy versus forested) nor amount of prior precipitation affected sampling rate. Exuviae detection probabilities for a single pass ranged from 0.49 to 0.75, and averaged 0.64. The mean cumulative probability of detection increased to 0.87 after two passes, 0.95 after three passes, and 0.98 after four passes. A strong negative relationship existed between detectability and the amount of prior precipitation. Bank vegetation type did not affect detection probability. Smaller exuviae had an 8% lower probability of detection than larger exuviae. If four sampling passes are cost-prohibitive for some exuviae studies, making just two passes may provide an adequate estimate of sampling efficiency. The assumption that exhaustive collecting efforts will find all or most of the exuviae along vegetated natural banks is unfounded.

Keywords: Odonata; dragonfly; Anisoptera; exuviae; detection probability

Introduction

Anisoptera exuviae are valuable evidence of species' presence because they reveal a breeding site with certainty and demonstrate that the species was present at all stages of the life cycle (Aliberti Lubertazzi & Ginsberg, 2009; Oertli, 2008; Raebel, Merckx, Riordan, MacDonald, & Thompson, 2010). However, their value extends much beyond occurrence detection to include estimating larval population sizes, species distributions, and sex ratios, identifying diel and seasonal emergence patterns, and other ecological applications (Corbet, 1999, chapter 7.4; Foster & Soluk, 2004; Gibbs, Bradeen, & Boland, 2004; Horvath, 2012; Raebel et al., 2010). This broad range of usefulness led Corbet (1999, p. 244) to state that "it is impossible to exaggerate the value of exuviae collection for population studies." He also noted (p. 13) that for autecological

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studies to determine the status and continuity of breeding surveys, exuvial surveys were one of two quantitative methods that were disproportionately valuable.

Because collections of exuviae have value for a variety of applications, the ability to express the number of exuviae collected as a proportion of the number actually present is useful. However, no quantifiable techniques have to my knowledge been used to directly estimate population sizes or detection probabilities of exuviae at single sites. Species detection probabilities have been estimated for odonates using the likelihood-based modeling framework of MacKenzie et al. (2002), but this approach requires species occurrence data for adults and exuviae sampled repeatedly and concurrently across multiple sites (D'Amico, Darblade, Avignon, Blanc-Manel, & Ormerod, 2004; Raebel et al., 2010; also summarized by Bried, D'Amico, & Samways, 2012). Further, researchers have often assumed that exhaustive collecting efforts (i.e. moving slowly, parting vegetation with the hands to improve sight angles, examining potential emergence supports thoroughly, and collecting all found exuviae) will recover all or nearly all the exuviae that are present (Corbet, 1999, p. 248; Wissinger, 1988). For example, Benke and Benke (1975) stated that their daily collections of exuviae were "considered to be closely equivalent to total numbers emerging from a given length of shoreline." While this assumption could be accurate in some circumstances, it is likely unfounded in others. Corbet (1999, p. 244) noted that collecting all exuviae left behind by dragonflies emerging from a habitat, or a standard proportion of them, offers a powerful tool for quantifying a variety of emergence-related phenomena. Because collecting all exuviae that are present could be a difficult and perhaps unattainable goal at structurally complex emergence sites, having the ability to standardize collections is potentially useful (Oertli, 2008). To this end, a population estimation tool could provide reliable estimates of the total numbers of exuviae present and their associated detection probabilities in defined areas at given times, so that collections in multiple areas can be more readily compared.

Many factors could affect detection probabilities of Anisoptera exuviae on natural banks, including the experience of the collector, animal activity in the immediate area, size of the exuviae, types of vegetation on the bank, slope of the bank including the presence or absence of bank undercutting, extent to which areas of the bank are sheltered from the elements, and whether and to what extent the area had received precipitation since emergence. Experienced collectors would presumably detect a greater proportion of the exuviae present than would inexperienced collectors. Animal activity ranging from small arthropods like ants, beetles, and spiders, to large mammals like deer, bear, and cattle, can jostle exuviae, knocking them off their emergence supports or causing abrasion and fragmentation which can shorten the time frame during which they are detectable. Small exuviae would presumably be more difficult to detect than larger exuviae simply because of the limitations of human vision to detect small objects. Structurally complex emergence sites, such as areas with thick and diverse patches of riparian vegetation, would presumably present more challenges for detecting exuviae than structurally simple areas like open beaches, mowed lawns, and rock retaining walls. Exposure to strong winds will knock some exuviae off their emergence supports and wind-caused movements of nearby vegetation may cause abrasion and fragmentation which could shorten exuvial persistence (Aliberti Lubertazzi & Ginsberg, 2009). Additionally, precipitation after emergence may dislodge exuviae from emergence supports both indirectly by causing rivers to rise, which washes away those that are near the water's edge, and directly by knocking them off their emergence supports where they may land on the ground or in the water. When wetted on the ground the chitinous exoskeletons often darken and become flexible. Thus, after rains exuviae may be colored similarly to the substrate onto which they also become flattened, and they may quickly become fragmented. All of these changes can have a presumably negative effect on their detectability.

I used a depletion population estimator to standardize exuviae collections, estimate exuvial densities, and determine detection probabilities along a variety of river reaches in northern

Table 1. Sampling dates, river reaches, and latitude/longitude coordinates of 10 bank stations in Wisconsin, USA, from which Anisoptera exuviae were collected.

Trial no.	Date	River reach	Latitude/longitude coordinates
1	12 June 2007	Bois Brule River (Ranger Campground), Douglas Co.	N46 32′ 25″ W91 35′ 37″
2	19 June 2007	Eau Claire River (Beaver Creek), Eau Claire Co.	N44 48′ 35″ W91 16′ 22″
3	21 June 2007	Manitowish River (SH 51), Vilas Co.	N46 08′ 14″ W89 54′ 40″
4	9 June 2008	Tabor Lake Channel, Burnett Co.	N46 01′ 19″ W92 17′ 22″
5	9 June 2008	St. Croix River (Riverside), Burnett Co.	N46 04′ 29″ W92 14′ 55″
6	25 August 2008	Bois Brule River (High Landing), Douglas Co.	N46 36′ 15″ W91 35′ 01″
7	10 June 2009	Middle River (Grassy West Bank), Douglas Co.	N46 34′ 20″ W91 53′ 01″
8	10 June 2009	Middle River (Forested East Bank), Douglas Co.	N46 34′ 20″ W91 53′ 01″
9	1 June 2010	Bois Brule River (Co-op Park), Douglas Co.	N46 36′ 43″ W91 34′ 59″
10	3 June 2010	Chippewa River (Bruce), Rusk Co.	N45 27′ 00″ W91 15′ 36″

Wisconsin. I also evaluated the influences of bank vegetation type and prior precipitation on detection probabilities and sampling rates, and the effect of exuviae size on detection probability.

Materials and methods

Ten bank stations on seven rivers were selected for sampling Anisoptera exuviae based on bank type and accessibility (Table 1). Grassy banks or forested banks with some undercutting and associated washed root zones were selected when present because these types of banks had appeared to be more productive and time-efficient for collecting exuviae during prior sampling than brushy banks. One station (Trial 4) was unusual in having a different form of substrate to be searched, which was almost entirely restricted to cattail (*Typha* spp.) stems. Therefore, this station was excluded from analyses involving grassy and forested banks. Sampling stations were 15.24 m long, except that the Trial 5 station was reduced to 7.62 m and the Trial 10 station to 5.50 m because they held high densities of exuviae. All stations were flagged at each end. Bank slope, the presence of bank undercutting and basic type of bank vegetation (grassy/open or forested/canopied) were visually assessed at each sampling station (Table 2), but no measurements were made. The early- to mid-June dates of sampling at nine of the trial stations (Table 1) were selected because they coincided with the anticipated end dates of the emergence periods for most of the gomphid species in the rivers sampled. However, in no cases were the start and end dates of emergence known with certainty for any species. The late August sampling date for Trial 6 was selected to include a species of *Stylurus*, a genus of late-emerging, or summer, species.

Collectors searched exhaustively for exuviae by visually scanning all emergence surfaces (vegetative and ground) from the water's edge to distance of about 1.25 m up the bank while wading slowly in the river along the shoreline. Sampling exuviae in this way (or from a small boat or canoe if water depths prohibit wading) is generally preferred to walking on the bank while collecting because sight angles are improved and sight distances are lessened, and exuviae are less often knocked off their emergence supports where they may be stepped on or otherwise lost from view. Sampling was done after, not prior to or during emergence, so that pharate adults staging near shore would not be stepped on or dislodged while wading. Although pharate adults of some species will travel horizontally away from water much further than 1 m before selecting an emergence support, and horizontal distances from water on exposed substrates like open sand beaches and areas of rip-rap may often exceed this (e.g. Martin, 2010; Wagner, Simmonds, & Thomas, 1995), the great majority of exuviae on vegetated banks will be found along a fairly narrow strip no more than 1 m in width along the water's edge (Corbet, 1999, p. 256). Occasional "spot checks" further than 1.25 m from the water line did not reveal any exuviae at any of the sites, indicating little or no movement of pharate adults beyond that distance. If river flows had

Table 2. Exuvial densities (all species pooled), detection probability categories (> 0.70 = high, 0.70–0.60 = mid, < 0.60 = low), prior precipitation, and bank and vegetation type at 10 stations on rivers in Wisconsin, USA, from which Anisoptera exuviae were collected.

Trial no.	Number of exuviae per linear m of bank length	Detection probability category	Precipitation (cm) during 3 days prior	Bank and vegetation type
1	1.0	high	0	Forested, low undercut with wrz
2	1.9	mid	1.3	Forested, vertical undercut with wrz
3	5.3	low	1.6	Grassy, open, gradual slope
4	4.7	mid	1.3	Cattail stems, gradual slope
5	95.4	high	1.3	Grassy, partially open, variable slope
6	4.0	high	0	Grassy, partially open, steep slope
7	3.2	low	2.5	Grassy, open, variable slope
8	1.5	low	2.5	Forested, vertical, partial undercut
9	8.3	high	0	Forested, vertical undercut with wrz
10	34.4	mid	0.5	Forested, vertical undercut with wrz

Abbreviation: wrz = washed root zone.

receded substantially after emergence, then exuviae of early-emerging species may have been much further from the water's edge at the time of sampling than they were when they emerged, but there was no indication that this had occurred at any of the sites. The visual scanning process included gently parting taller vegetation with the hands to improve visibility on stems and on areas closer to and on the ground. The postures adopted by various species during emergence (e. g. the "hanging" versus "upright" types of Eda, 1963) will affect the positions of exuviae on their emergence supports, which in turn can influence how readily exuviae are seen from above or from the side. Therefore, every effort was made to examine emergence supports from multiple sight angles. The author performed the collections for nine trials; another experienced collector performed the collections for Trial 2.

Exuviae were collected during four passes along each bank station. A pass consisted of a single collecting trip along the entire length of a bank station in one direction. Each subsequent pass began immediately after completion of the prior pass and proceeded in the opposite direction. A similar level of search intensity was maintained on each pass, with all the same areas visually scanned in order to maintain equal sampling effort on each pass. All found exuviae were gently removed from their emergence supports or from the ground, placed in jars with date and location labels, and were identified in the lab using appropriate dichotomous keys and by comparing them with reared exuviae.

A four-pass, exact maximum-likelihood, depletion (= successive removal) population estimator (MicroFish 3.0; http://www.microfish.org; Van Deventer & Platts, 1989), which included the refinement of Carle and Strub (1978), was used to estimate the densities and detection probabilities (= capture probabilities) of Anisoptera exuviae on each bank. The probabilities of detection and capture are assumed to be equivalent for inanimate objects incapable of escape, although a small number of found exuviae may have been inadvertently dropped or blown from the hand by the wind before being secured in jars. The term "population" is used here in the statistical sense of an aggregation of individuals that are not necessarily animate, and the population was considered to be limited to the number of visibly detectable exuviae on a bank. Exuviae that may have been on the banks but were covered by leaves or were in any other way not visible at any sight angle were not considered to be part of the population. A depletion estimator operates on the principle that as a known number of individuals are removed from a defined area with each sample, the catches are affected in subsequent samples (Otis, Burnham, White, & Anderson, 1978; Zippin, 1956). The rate of decline as numbers of individuals are removed in successive samples is directly related to the probability of capture. A basic concept is that a constant sampling effort will remove a constant proportion of the individuals present at the time of sampling. Although the depletion estimator used was designed for estimating fish populations, the methodology is applicable to any population as long as the following assumptions are met: (1) the population is closed; (2) the probability of capture (= detection) is constant for all individuals and sampling periods; and (3) sampling effort is equal for all passes (Carle & Strub, 1978). Population closure is the most important assumption in depletion sampling (Otis et al., 1978). The first and third assumptions were met in this study as there were no additions (no emergence) or significant deletions of exuviae from the sample areas during sampling, and equal sampling effort, which is controlled by the collector, was maintained throughout all passes. The extent to which the second assumption was met cannot be substantiated and is probably unattainable in natural populations (Carle & Strub, 1978; Raleigh & Short, 1981). However, any effect of violation of this assumption on the population estimate is likely to be small and the estimator used is known to be robust against violations of this assumption (Carle & Strub, 1978).

The amount of time used as the collector moved along a bank station to complete a sampling pass (hereafter sampling rate) was recorded for all four passes during six of the 10 trials. The elapsed time during a pass consisted of time used for searching, to remove found exuviae from their emergence supports or pick them off the ground or from the water, and to place them in a collecting jar. Searching time included all time used to visually scan the surfaces of vegetation and substrate in the station that might hold exuviae as well as the time spent to part grasses and move other pieces of vegetation so that the various surfaces that potentially held exuviae could be seen.

Ten exuviae each of *Ophiogomphus howei* Bromley and *O. rupinsulensis* (Walsh) were measured to calculate mean body area estimates to compare detection probabilities between smaller exuviae (the former) and larger exuviae (the latter) as they would typically be seen in dorsal view. Body area was defined as equaling the total length of the exuvia times the maximum width of the abdomen.

Prior precipitation at each site was estimated post hoc by summing the precipitation totals recorded at the nearest weather-recording airport for the three days prior to the trial at a site (http://www.wunderground.com/history; accessed 9 September 2014). Distances of these airports from the trial sites ranged from 3 to 39 km and averaged 25 km. Because this study sought to contrast the environmental variables that might influence detection probabilities, the time frame for summing precipitation was chosen because it happened to include significant rainfall events that occurred at some of the trial stations.

I used *t*-tests to examine the effect of bank vegetation type on detection probabilities and to compare sizes of exuviae of *O. howei* and *O. rupinsulensis*. Coefficient of determination (r^2) was used to determine the strength of relationship between the amount of prior precipitation and both sampling rates and detection probabilities. Alpha was set at 0.05 in all cases.

Results

Taxonomic composition

A total of 1355 exuviae representing 27 species of Anisoptera in five families was collected from the 10 riverbank stations (Table 3). Exuviae of Gomphidae were numerically dominant at all stations, making up about 98% of the total collected. Among the gomphids (18 species), six species of *Ophiogomphus* Selys dominated at six of the 10 stations where they comprised 73% of the total number of exuviae collected. At the remaining four stations, exuviae of *Gomphus adelphus* Selys were dominant at two stations (on the same river), and *Dromogomphus spinosus* Selys and *Gomphus exilis* Selys were each dominant at one station.

Table 3. Numbers of Anisoptera exuviae collected during four sampling passes along 10 bank stations on rivers in Wisconsin, USA, with exuviae population estimates (95% CI) and detection probabilities (SE).

		Numbers of exuviae collected					
Trial no.	Taxon	Pass 1	Pass 2	Pass 3	Pass 4	Exuviae population estimate	Detection probability for a pass
1	*Ophiogomphus colubrinus*	10	0	1	1	—	—
	Cordulegaster maculata	3	0	0	0	—	—
	Total	13	0	1	1	15 (15.0–15.6)	0.75 (0.11)
2	*Dromogomphus spinosus*	1	0	0	0	—	—
	Gomphus[1,2]	3	1	0	0	—	—
	Ophiogomphus[3,4]	8	7	0	0	—	—
	Neurocordulia yamaskanensis	1	1	0	0	—	—
	Total	16	11	0	0	28 (27.0-29.4)	0.67 (0.09)
3	*Dromogomphus spinosus*	33	10	4	4	—	—
	Gomphus[5,6,7,8]	4	2	0	0	—	—
	Hagenius brevistylus	1	0	0	0	—	—
	Ophiogomphus rupinsulensis	0	1	0	0	—	—
	Didymops transversa	1	1	0	1	—	—
	Epitheca[9,10,11]	7	6	1	2	—	—
	Total	46	20	5	7	81 (78.0–86.0)	0.55 (0.06)
4	*Basiaeschna janata*	0	1	0	1	—	—
	Gomphus exilis	46	15	2	4	—	—
	Epitheca spinigera	0	0	1	0	—	—
	Total	46	16	3	5	71 (70.0–73.8)	0.63 (0.06)
5	*Gomphus*[1,2,12,13]	60	10	2	3	—	—
	Ophiogomphus howei	359	55	22	24	462 (460.0–465.7)	0.72 (0.02)
	Ophiogomphus[3,14,15]	161	17	5	6	—	—
	Total	580	82	29	33	727 (724.0–730.8)	0.74 (0.02)
6	*Boyeria vinosa*	0	1	0	0	—	—
	Gomphus adelphus	1	0	0	0	—	—
	Ophiogomphus colubrinus	24	8	6	0	—	—
	Stylurus scudderi	17	4	0	0	—	—
	Total	42	13	6	0	61 (61.0–62.5)	0.71 (0.06)
7	*Gomphus*[7,12]	15	6	5	1	—	—
	Ophiogomphus[3,15,16]	11	2	3	2	—	—
	Cordulegaster maculata	0	0	0	1	—	—
	Total	26	8	8	4	49 (46.0–54.9)	0.49 (0.08)
8	*Gomphus*[7,12]	10	4	4	1	—	—
	Ophiogomphus[3,15,16]	1	2	0	0	—	—
	Total	11	6	4	1	23 (22.0–26.6)	0.51 (0.11)
9	*Ophiogomphus colubrinus*	89	23	6	2	—	—
	Cordulegaster maculata	4	1	0	1	—	—
	Total	93	24	6	3	126 (126.0–127.7)	0.74 (0.04)
10	*Basiaeschna janata*	1	0	0	0	—	—
	Dromogomphus spinosus	1	0	1	0	—	—
	Gomphus[1,2,8,12]	24	11	2	4	—	—
	Hagenius brevistylus	2	0	1	1	—	—
	Ophiogomphus howei	62	12	10	3	88 (87.0–90.6)	0.66 (0.05)
	Ophiogomphus rupinsulensis	33	8	6	1	48 (48.0–49.7)	0.68 (0.07)
	Macromia illinoiensis	3	0	0	0	—	—
	Total	126	31	20	9	189 (186.0–193.0)	0.63 (0.04)

[1]*G. quadricolor;* [2]*G. viridifrons;* [3]*O. rupinsulensis;* [4]*O. smithi;* [5]*G. fraternus;* [6]*G. lineatifrons;* [7]*G. lividus;* [8]*G. vastus;* [9]*E. cynosura;* [10]*E. princeps;* [11]*E. spinigera;* [12]*G. adelphus;* [13]*G. ventricosus;* [14]*O. anomalus;* [15]*O. colubrinus;* [16]*O. carolus.*

Sampling rate

The speed at which an experienced collector moved along a bank while sampling for exuviae averaged 0.90 m min^{-1} for all passes and ranged from 0.16 to 2.18 m min^{-1} (Table 4). First pass sampling rates ranged from 0.16 m min^{-1} in the station that held the most exuviae (Trial 5) to 1.02 m min^{-1} in the station that held the least (Trial 4; Table 4), and averaged 0.53 m min^{-1}.

Table 4. Sampling pass times (min), station lengths (m), and sampling pass rates (m min^{-1}) for six trials on river reaches in Wisconsin, USA, from which Anisoptera exuviae were collected.

	Minutes per sampling pass							
Trial no.	Pass 1	Pass 2	Pass 3	Pass 4	Station length (m)	Pass 1 sampling rate (m min^{-1})	Pass 4 sampling rate (m min^{-1})	Mean sampling rate (m min^{-1})
2	30	17	13	13	15.24	0.51	1.17	0.84
3	18	15	11	11	15.24	0.85	1.38	1.08
4	15	10	9	7	15.24	1.02	2.18	1.49
5	47	19	12	13	7.62	0.16	0.59	0.33
6	27	19	18	13	15.24	0.56	1.17	0.79
9	22	19	16	15	15.24	0.69	1.02	0.85

Fourth pass sampling rates, when fewest exuviae were present in the stations, ranged from 0.59 m min^{-1} (Trial 5) to 2.18 m min^{-1} (Trial 4), and averaged 1.16 m min^{-1}.

There was no clear difference in fourth-pass sampling rates, when fewest exuviae were present to be picked and processed, between grassy banks ($\bar{x} = 1.05$ m min^{-1}, $n = 3$) and forested banks ($\bar{x} = 1.10$ m min^{-1}, $n = 2$). The Trial 4 station, which was comprised of cattail stems, had a relatively fast fourth-pass sampling rate of 2.18 m min^{-1}. The fourth pass sampling rate at the five grassy and forested bank stations for which sampling rates were timed averaged 1.07 m min^{-1}. The coefficient of determination between sampling rate and amount of prior precipitation was weak ($r^2 = 0.067$, df $= 4$, $p = 0.619$).

Exuvial densities

Densities ranged from 1.0 exuvia per linear meter (exuvia m^{-1}) to 95.4 exuvia m^{-1} with the two largest rivers, the Chippewa (34.4 exuvia m^{-1}) and the St. Croix (95.4 exuvia m^{-1}), having much higher densities than the smaller rivers (range: 1.0–8.3 exuvia m^{-1}; Table 2). Densities were about twice as high on the open, grassy bank of the Middle River as on the canopied, forested bank on the same afternoon (Trials 7 and 8; Table 2).

Detection probabilities

Detection probabilities for a single pass (all species combined) ranged from 0.49 to 0.75 (Table 3), and averaged 0.64. Applying this average to additional passes gives estimates of 87% of exuviae collected after two passes, 95% collected after three passes, and 98% collected after four passes (Figure 1). Detection probabilities ranged from low (0.51) to high (0.75) along banks that were forested and canopied with nearly vertical sides or undercut washed-root zones, and the range of detection probabilities was similar (0.49–0.74) along banks that were grassy, variably sloping, and at least partially open (Table 2). Although the mean detection probability on grassy banks (0.62) was slightly lower than that on forested banks (0.66), the difference was not significant ($t = 0.516$, df $= 7$, $p = 0.622$). Further, detection probabilities were similar for trials 7 and 8 (Table 2), which were done on a grassy bank and a forested bank of the same river reach on the same afternoon with the same suite of Anisoptera species and precipitation history. The Trial 4 station had a form of emergence substrate that was unique in the dataset (predominantly cattail stems), but the detection probability there of 0.63 was mid-range (Table 2).

A strong negative relationship was found between detection probability and the amount of precipitation during the three days prior to sampling a site ($r^2 = 0.722$, df $= 8$, $p = 0.002$). Detection probabilities averaged 0.68 for the eight stations that had received 1.6 cm or less of precipitation during that time frame, but averaged only 0.50 for the two sites that had received 2.5 cm of precipitation, a 36% difference.

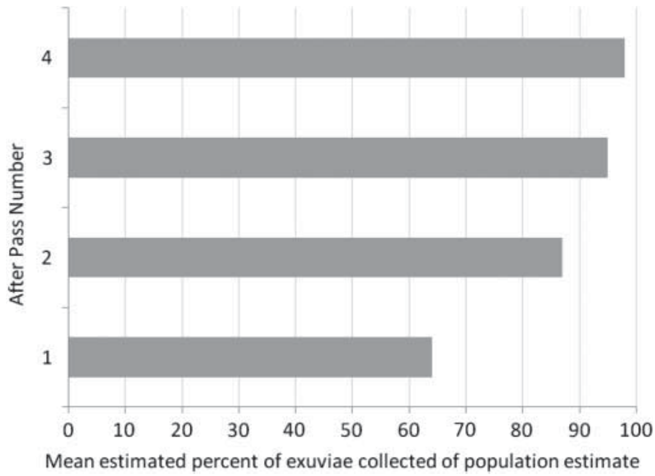

Figure 1. Mean estimated percentage of total population estimate of Anisoptera exuviae collected after each of four sampling passes along riverbanks in Wisconsin, USA.

Table 5. Detection probabilities for small exuviae (*Ophiogomphus howei*) and large exuviae (*O. rupinsulensis*) collected during trials on the St. Croix and Chippewa rivers in Wisconsin, USA (n).

Species	Mean body area in dorsal view (cm^2)	Detection probabilities		
		St. Croix	Chippewa	Mean
Small (*O. howei*)	1.23 (10)	0.72	0.66	0.71
Large (*O. rupinsulensis*)	2.10 (10)	0.80	0.68	0.77

Detection probabilities for larger exuviae (represented by *O. rupinsulensis* with a mean surface area of 2.10 cm^2) averaged 8% higher than for smaller exuviae (represented by *O. howei* with a mean surface area of 1.23 cm^2) at two sites for which sufficiently large samples of both species were found (Table 5). The difference in size between the two species was significant ($t = 19.49$, df $= 18$, $p < 0.0001$) with non-overlapping ranges. Vertical and horizontal distances from the water's edge were not measured for either of these species and both species were found in both hanging and upright positions.

Discussion

The depletion (= successive-removal) population estimation technique used in this study was a reliable tool for estimating densities and detection probabilities of Anisoptera exuviae within defined sampling areas at single points in time. The assumptions inherent with this estimator are unlikely to be seriously violated with inanimate objects. The most important assumption is that of population closure, so caution should be used if emergence is still occurring while areas are sampled. Because successive passes in this study were done immediately after the previous ones, there was little time for additions to (new emergences) or deletions due to any causes from the populations of exuviae. Substantial emergences of new individuals would have been noticed if they had occurred during any of the sampling events. Some violation of the assumption that the probability of detection will remain constant for all individuals and sampling periods was inevitable. It is obvious that detection probabilities are rarely constant among any groups of animals (Dorazio, Royle, Soderstrom, & Glimskar, 2006), and detection probabilities did differ slightly between larger and smaller exuviae in this study. However, any effects of violations of this assumption on population estimates are likely to be small unless the differences in detection probabilities are great (Seber & Whale, 1970). Although substantial differences in detection probabilities among species of exuviae were not apparent in this study, researchers should be alert for such differences, especially concerning very small exuviae and for those species (especially some gomphids [e.g. Martin, 2010; Wagner et al., 1995] and macromiids [e.g. Hill & Hill, 2008]) known to travel long horizontal distances after leaving the water. Bried et al. (2012) presented exuvial detection probabilities for six species of Anisoptera that showed differences among them, but these were estimated from a number of lakes in France under different circumstances and are not directly comparable.

Experienced exuviae collectors maintained a mean sampling rate of approximately 1 m min^{-1} along grassy and forested river banks alike when few exuviae were present, but the sampling rate was dramatically reduced when exuviae were abundant and the reduction was in approximate proportion to exuvial density. Although equal searching effort was maintained for all passes, the first pass took the most time in all trials because there were more exuviae present to be picked and placed in jars than on subsequent passes. The relatively slow fourth-pass sampling rate at the Trial 5 station was due to the high numbers of exuviae at that site and not to any effect of bank vegetation type. Because larger, wider rivers may have more area for nymph habitation than smaller, narrower rivers (assuming acceptable habitat quality across good portions of the breadth of a river), exuvial densities may be higher and therefore sampling rates may be lower on productive larger rivers. This was the case on the Chippewa and St. Croix rivers, both of which were known by the author (unpublished data) to have exceptional habitat quality for nymphs of a number of gomphid species. The weak correlation between sampling rate and prior precipitation suggests that the collectors were comfortable moving at a certain speed and did not adjust when exuviae were harder to find.

The results showed that detection probabilities were significantly lower after heavy rains. This result was likely due to changes in positioning of exuviae caused by rain, although the positions of found exuviae were not recorded. Rain tended to knock exuviae onto the ground, flattened them down, and contributed to their fragmentation, and when in such a condition they were evidently more difficult to detect than when they were still attached to their vegetated emergence supports. Because the amount of precipitation after emergence, not any specific number of days since emergence had occurred, had the greatest effect on detection probabilities for exuviae, scheduling exuviae collections prior to significant forecast rainfall events is advantageous.

Physical characteristics of emergence sites did not appear to influence detection probabilities, which were similar on banks that were grassy, forested, undercut, or with a dense growth of cattail stems. This finding suggests that these types of emergence sites have similar levels of structural complexity and that an experienced collector readily adjusts to them. No trials were done along open beach shorelines or along retaining walls, cement berms, mowed lawns, areas of rip-rap or other simplified artificial structures, but higher detection probabilities would be expected in such areas. The comparison between detection probabilities of exuviae of *O. rupinsulensis* and *O. howei* showed that a decrease in body size decreases the probability of detection. Although relatively small, *O. howei* is not the smallest odonate in North America, and all else being equal detection probabilities are likely to be lower for species that are smaller than it.

The finding that experienced collectors, moving slowly and looking carefully (i.e. collecting exhaustively), found only about half to three-quarters of the exuviae present during a single pass along a vegetated, natural river bank was somewhat surprising. When collecting exhaustively, the impression is readily gained that one is collecting the great majority of exuviae that are present. However, these results show that researchers should be cautious about making this assumption. Even with exhaustive sampling, it is unlikely that more than three-quarters of the exuviae present will be detected on a single collecting trip along a natural, well-vegetated river bank. If precipitation has fallen after emergence or exuviae are very small, then detection probabilities may be substantially lower than 0.75. If researchers are aware of the tendency to overestimate the thoroughness of their collecting efforts and therefore decrease their sampling rate they are likely to improve their detection probabilities, but without estimating those probabilities directly, they will not know by how much.

Making multiple passes at exuviae collection sites will increase field costs, but when results must be quantifiable, the advantages offered by multiple passes will likely outweigh the costs. Exuviae sampling is relatively inexpensive compared to many other types of surveys because collectors do not require extensive training and relatively few collectors are typically needed, so the additional costs incurred with detection probability sampling may be acceptable. When detection probabilities are anticipated to be high ($> \sim 70\%$) three passes are likely sufficient to give estimates with acceptable confidence limits, and if detection probabilities are very high ($> \sim 90\%$) just two passes are likely adequate. If anticipated detection probabilities are unknown and field time is constrained, conducting just two passes will have the advantage of giving at least some indication of sampling efficiency, although confidence limits may be wide. Adding a second sampling pass to an exuviae collection plan will also increase the percentage of exuviae collected from river banks from an average of 64% to 87% at minimal cost (Figure 1).

The estimation technique used in this study can be used to standardize exuviae collections and to supply reliable population estimates and detection probabilities for visibly detectable exuviae along rivers. Although the focus of this study was to estimate detection probabilities of Anisoptera exuviae generally, not to estimate the probabilities of detecting the occurrences of rare species per se, the two are related because as more individual exuviae are known to be missed, the likelihood of arriving at false species absences will clearly increase. The estimator used does not account for exuviae lost between the time of emergence and the time of sampling, for exuviae that are outside the boundaries of the sampling area chosen, or for exuviae that are present in the sampling area but not visibly detectable. Therefore, it is incumbent upon researchers to sample sites as soon after emergence as feasible, and preferably before the arrival of inclement weather, when densities are to be estimated and species occurrences are to be detected.

These results are limited to detecting exuviae that are present in defined areas at single points in time. If total numbers of a species or community of odonates emerging at a site during a season are to be estimated, then collections must be made at regular intervals during the entire period of emergence (the shorter the intervals, the fewer the opportunities for losses of exuviae). It is important to realize that even well-planned exuviae collection efforts are likely to give underestimates of the actual amount of emergence at sites, at least to some extent. This is because sampling areas need to be defined in practical ways, and some pharate adults will move horizontal distances away from water beyond the boundaries of any reasonably defined area. I used a sampling area width of 1.25 m from the water's edge because most exuviae would be found within that area and when I did "spot checks' further from water I did not find any exuviae. However, it is likely that there were some exuviae at distances greater than 1.25 m. Because the maximum distances away from water that pharate adults can travel before they emerge are not known for all species under all conditions, it is not possible to define the extent of a sampling area that will subject all exuviae to the possibility of detection along any given stretch of river. Therefore, the frequency of exuviae collections and dimensions of sampling areas should be designed to achieve the goals of individual studies.

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