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## COMMENT/DEBATE

# A critique of the dragonfly delusion hypothesis: why sampling exuviae does not avoid bias

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**Abstract.** 1. A recent study comparing adult and exuvial odonate richness concluded that adult surveys overestimate the number of species reproducing successfully. The authors called this phenomenon the “dragonfly delusion” and recommended that only exuviae be used for biomonitoring and habitat quality assessment. However, they drew this conclusion from limited surveys and detection-naïve analysis and failed to acknowledge that exuvial richness is typically biased low.

2. Here, we quantify the exuvial bias using two related metrics: (i) species detectability from concurrent adult and exuvial surveys and (ii) estimated exuvial species richness at a site based on imperfect detectability and the regional pool (cumulative total across study sites) of exuvial species observed.

3. Using concurrent adult and exuvial data from lakes in south-west France, we found that detectability was generally lower in 1-h exuvial searches than in 20-min adult searches and that exuvial surveys may lead to strong negative bias in richness estimation. This suggests the alleged delusion of adult surveys was exaggerated.

4. Controlling for species detection probability is crucial in making unbiased inferences on how many odonate species occupy a site and, by extension, comparing adult and exuvial species richness. Exuviae sampling avoids *positive* bias, not bias in general, and requires either relatively intensive search effort, statistical accounting of false species absences, or acceptance of negatively biased richness.

**Key words.** Detection probability, monitoring, Odonata, sampling issues, survey bias, survey methods.

## Introduction

Raebel *et al.* (2010) compared adult, exuvial, and larval odonate richness across 29 farm ponds in the United Kingdom. In almost every pond, they observed more adult than exuvial species, concluding that adult surveys overestimate the number of species reproducing successfully. They called this phenomenon the “dragonfly delusion” and recommended using the exuvium for biomonitoring and habitat quality indication.

The exuvium is the shed cuticle left behind after ecdysis. In odonates, the last ecdysis (producing ultimate stadia exuviae) represents an important energy transfer and ontogenetic niche shift from aquatic to terrestrial existence (Corbet, 1999). Unlike the highly mobile adult stage, the presence of exuviae at a focal site confirms that the individual developed at that site. This has

clear implications for the study of reproductive success and species' distributions and provides a strong ecological basis for using exuviae in habitat quality assessment and monitoring resident species diversity.

We do not disagree with the core arguments of Raebel *et al.* (2010), but we do question whether there was a fair comparison of adult and exuvial richness. The reason is that Raebel *et al.* (2010) did not account for the probability of a species being seen when present. They relied exclusively on raw observations and implicitly assumed that adult and exuvial detection probabilities were equal. Detection probabilities are almost never constant among species, sites, and surveys (Dorazio *et al.*, 2006; MacKenzie *et al.*, 2006), and it seems unlikely that distinct life history stages would have equal detection probabilities. Failure to account for this may lead to an “apples and oranges” scenario when comparing adult and exuvial species richness.

Raebel *et al.* (2010) claimed definitively that exuvial surveys avoid the bias of adult surveys, yet their underlying analysis was biased to an unknown degree. Negatively biased exuvial richness

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may have exaggerated the delusion. In this critique, we discuss the likely exuvial bias, propose an analysis to quantify it, and provide an example of the analysis we propose.

### The exuvial bias

Raebel *et al.* (2010) emphasised that adult surveys lead to high-biased inferences of true richness, but failed to acknowledge that exuvial richness is typically biased low. Exuvial richness may be biased low or in favour of select species groups because of rarity, inclement weather, dense vegetation, inadequate search effort, and inter-specific differences in persistence (Aliberti Lubertazzi & Ginsberg, 2009; Samways & Niba, 2010). Exhaustive searches for exuviae, such as daily or every few days (e.g. Benke & Benke, 1975; Wissinger, 1988; Foster & Soluk, 2004), are required to minimise under counting of individuals. In a sample of Rhode Island wetlands, Aliberti Lubertazzi and Ginsberg (2009) documented > 50% loss of exuviae between triweekly visits, the same survey frequency used by Raebel *et al.* (2010). Obviously, the more individual exuviae missed, the greater the likelihood of false species absences and negatively biased richness. Negative bias owing to rarity is of particular concern because the species missed may have conservation value.

### Proposed analysis

We suggest quantifying the exuvial bias using two related metrics: (i) species detection probabilities from concurrent adult and exuvial surveys and (ii) estimated exuvial species richness at a site based on imperfect detectability and the regional pool (cumulative total across study sites) of exuvial species observed. The first metric involves analysis by species (where  $n$  is number of sites), and the second involves analysis by site (where  $n$  is number of species). The first metric requires species occurrence data for adults and exuviae sampled concurrently over multiple sites and repeated surveys (as in D'Amico *et al.*, 2004; Raebel *et al.*, 2010). Each species' detection probability is estimated from the adult and exuvial detection histories using the likelihood-based modelling framework of MacKenzie *et al.* (2002). This flexible approach permits missing observations along with measured auxiliary information thought to influence the probabilities of occupancy (e.g. hydroperiod, site area) and detection (e.g. weather, time of year).

For the second metric, the standard occupancy-detection modelling (MacKenzie *et al.*, 2002) is conceptually modified to extrapolate how many species were present as exuviae and therefore how many successfully reproduced. Instead of estimating the proportional occupancy of a *species* from the site  $\times$  survey matrix, the modified analysis estimates the proportional occupancy of a *site* from its species  $\times$  survey matrix (see MacKenzie *et al.*, 2006: 250–253). Here, we let the cumulative exuvial species across the sample represent the regional species pool or the maximum resident species richness expected at any given site. Undetected species from the regional pool serve as statistical dummy variables for estimating the number of exuvial species present but overlooked. Species heterogeneity factors such as breeding

status (e.g. resident vs. vagrant) or primary phenology (e.g. spring vs. summer) could be incorporated in the same manner as site-level covariates in the standard occupancy-detection modelling.

One important assumption with this modelling framework is that for a given species, sites must stay occupied or unoccupied during the study period (MacKenzie *et al.*, 2002, 2006), regardless of individual mortality and movement. To help meet this closure assumption for odonates, the sampling period could be truncated to each species' local emergence/flight period (van Strien *et al.*, 2010). The artificial missing observations would get treated as neutral in the modelling. Because the estimation problem requires repeated detection/non-detection data, truncation is possible only when three or more surveys are conducted. If the sampling period is shorter than the local flight period, no truncation is necessary. If local phenology is poorly known (true in many locations), then it may be best to avoid truncation. For multibrooded odonate species, the analyst might consider the between-season occupancy model developed by MacKenzie *et al.* (2003).

### Worked example

We used data from D'Amico *et al.* (2004) to demonstrate the proposed analysis. The same experienced observer surveyed adults and exuviae biweekly from May through August (eight visits) at five limed lakes and five untreated lakes in south-west France. Adult surveys took place on sunny days and lasted 20 min during 11.00–15.00 hours, and exuviae were collected during 1-h searches in early afternoon. Both stages were searched in the same fixed location (20  $\times$  2 m littoral plot) each survey.

We ran two models in the analysis by species: a null model assuming imperfect (< 1) but constant occupancy and detection probability, and a model relating lake type (limed vs. untreated) to occupancy. This analysis was repeated for all species with sufficient detections ( $\geq 10\%$  of cells in the site  $\times$  survey matrix) in both the adult and exuvial surveys. Confidence intervals were constructed from the detection probability standard error using  $t = 2.262$  for  $n - 1$  degrees of freedom. In the analysis by site (lake), we ran the null model and a model allowing survey-specific detection probability (see MacKenzie *et al.*, 2002). Surveys in the same month were combined, halving the number of surveys (from 8 to 4). This was carried out to improve the species to variable ratio in the survey-specific model and mitigate overparameterization. Although other covariate information was available, we chose to keep models simple because of small sample size and because our goal was to estimate survey bias, not to test ecological hypotheses. For all modelling, we used PRESENCE v3.1 (Patuxent Wildlife Research Center, United States Geological Survey, Laurel, MD, USA) and followed the same approach for model selection, model averaging, and over-dispersion as described in Bried *et al.* (2011b).

Despite exuvial searches lasting three times longer than adult searches, the analysis by species revealed a trend of lower detection probability for exuviae (Table 1). The difference was especially clear for *Ceriagrion tenellum* and *Ischnura elegans* because confidence intervals did not overlap. Statistical power was

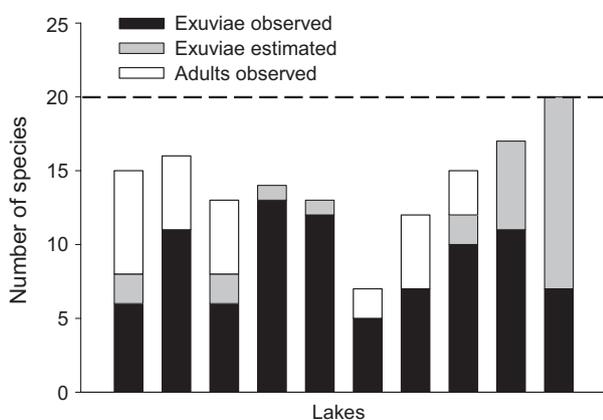
**Table 1.** Estimated species detection probability ( $p$ ) and confidence interval (CI) for concurrent adult and exuvial odonate surveys at natural and restored lakes of south-west France.

Species	Adult survey		Exuvial survey	
	$p$	95% CI	$p$	95% CI
<b>Zygoptera (damselflies)</b>				
<i>Ceriagrion tenellum</i>	0.900	0.794–1.0	0.574	0.359–0.789
<i>Chalcolestes viridis</i>	0.335	0.0–0.722	0.398	0.127–0.669
<i>Coenagrion puella</i>	0.413	0.178–0.648	0.221	0.0–0.508
<i>Coenagrion scitulum</i>	0.147	0.0–0.437	0.100	0.0–0.206
<i>Enallagma cyathigerum</i>	0.718	0.544–0.892	0.413	0.178–0.648
<i>Ischnura elegans</i>	0.975	0.918–1.0	0.750	0.596–0.904
<i>Lestes virens</i>	0.175	0.039–0.311	0.335	0.0–0.722
<b>Anisoptera (dragonflies)</b>				
<i>Anax imperator</i>	0.776	0.615–0.937	0.639	0.381–0.897
<i>Cordulia aenea</i>	0.300	0.067–0.533	0.189	0.0–0.546
<i>Crocothemis erythraea</i>	0.776	0.615–0.937	0.413	0.178–0.648
<i>Libellula quadrimaculata</i>	0.452	0.169–0.735	0.335	0.0–0.722
<i>Orthetrum cancellatum</i>	0.780	0.613–0.947	0.368	0.033–0.703
<i>Orthetrum coerulescens</i>	0.545	0.330–0.760	0.266	0.0–0.596

undoubtedly limited in this small sample of 10 lakes, but sample size doubled in the analysis by site. Exuvial species were potentially overlooked in seven lakes (Fig. 1). In five lakes, the estimated number of exuvial species was one or two greater than the number observed. In the remaining two lakes, six and 13 species may have been missed, the latter suggesting that all species from the regional pool were present. Interestingly, the number of species observed as adults was equal to or less than the estimated exuvial richness in four sites (Fig. 1), suggesting there was no dragonfly delusion in those sites.

## Conclusions

Controlling for species detection probability is crucial in making unbiased inferences on how many species occupy a site (Dorazio *et al.*, 2006; van Strien *et al.*, 2010) and, by extension, comparing



**Fig. 1.** Number of odonate species potentially overlooked in exuvial surveys based on imperfect detection probabilities, and the cumulative exuvial species found across sites (indicated by the dashed line).

adult and exuvial odonate richness. If exuviae are harder to detect than adult stages, the dragonfly delusion as presented by Raebel *et al.* (2010) becomes exaggerated. Raebel *et al.* (2010) concluded from limited exuvial surveys (triweekly) and detection-naïve analysis that adult richness is biased high. But our detection-corrected example found detectability was generally lower in 1-h exuvial searches than in 20-min adult searches and that exuvial surveys may lead to strong negative bias in richness estimation. Raebel *et al.* (2010) probably overstated the dragonfly delusion. Their data should be reanalysed to more accurately measure the positive bias of adult surveys, and their study should be replicated in other habitats and especially other climates. They also did not consider that adult surveys in lotic systems may result in negative bias because some species (e.g. large river gomphids, crepuscular *Neurocordulia*) in certain geographical areas are rarely seen as adults (Hunt *et al.*, 2010).

Daily or near-daily exuvial collections recommended for documenting abundances (e.g. Benke & Benke, 1975; Wissinger, 1988) may not be necessary for capturing a representative spectrum of species for conservation (sensu Schmidt, 1985). However, our personal experience combined with the current analysis suggests that infrequent visits, as used by Raebel *et al.* (2010), will miss some exuvial species, which is not a trivial matter if those species are rare or threatened (Mao & Colwell, 2005; Bried *et al.*, 2011a). Raebel *et al.* (2010) observed that '...exhaustive exuvial searches are essential when dealing with protected species'. Weekly visits may generally suffice for documenting odonate richness from exuviae, but this is still twice the effort suggested for gathering a representative spectrum of species from adult surveys (Bried *et al.*, 2011a).

Raebel *et al.* (2010) are correct in asserting that adults are not good indicators of reproductive success at a particular site and that exuvial data may be critical to conservation of populations (although to be clear, exuviae do not indicate long-term viable populations, only completion of the life cycle at that point in time). Regardless, adults still have value for important conservation work such as restoration monitoring (Roush &

Anon, 2003; D'Amico *et al.*, 2004; Kadoya & Washitani, 2007; Kadoya *et al.*, 2008; Mabry & Dettman, 2010; Magoba & Samways, 2010; Samways & Sharratt, 2010) and large-scale faunistic surveys or status assessments (Clausnitzer *et al.*, 2009; Kadoya *et al.*, 2009; Simaika & Samways, 2009; Bried & Mazzacano, 2010; van Strien *et al.*, 2010; Dijkstra *et al.*, 2011; Hassall, 2011). This is especially true in species-rich tropical or subtropical areas where the exuviae are poorly known and heavy rainfall patterns cause high rates of exuviae loss (e.g. Reels, 2011). Deciding which stage to use depends on such factors as the goal of the assessment, time constraints for sampling, denseness of vegetation, frequency of heavy rainstorms, accessibility and safety concerns (e.g. wading in many parts of Africa is simply too dangerous), and level of taxonomic knowledge (e.g. for many tropical species only the adult is known). We suggest that more work is needed on developing conceptual guidelines and quantitative criteria for when to use each stage. We predict that sampling multiple stages at the appropriate effort level will produce the most reliable assessment of odonate communities and habitat quality.

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