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The dragonfly delusion: why it is essential to sample exuviae to avoid biased surveys

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Abstract Odonate populations and species numbers are declining globally. Successful conservation requires sound assessments of both odonate distributions and habitat requirements. Odonates have aquatic (larval) and terrestrial (adult) stages, but most surveys that are used to inform conservation managers are undertaken of the adult stage. This study investigates whether this bias towards adult records in odonate recording is misinterpreting the environmental quality of sites. The habitat focus is farmland ponds, a key feature of agricultural landscapes. We tested whether or not, adult, larval and exuvial surveys lead to similar conclusions on species richness and hence on pond quality. Results showed that pond surveys based upon larvae and exuviae are equally suitable for the reliable assessment of presence/absence of odonates, but that adult surveys are not interchangeable with surveys of larvae/exuviae. Larvae were also found at ponds with no emerging individuals due to changes in habitat quality, therefore presence of exuviae remains the only proof of life-cycle completion at a site. Ovipositing females were recorded at all ponds where exuviae were totally absent hence adult surveys over-estimate pond quality and low-quality ponds are functioning as ecological traps. Highly mobile and generalist species were recorded at more locations than other species. Adult surveys also bias recording towards genera, species and populations with non-territorial mate-location strategies. Odonate biodiversity monitoring would benefit from applying the best survey method (exuviae) to avoid wasting valuable financial resources while providing unbiased data, necessary to achieve conservation objectives.

Keywords Odonata · Survey methods · Exuviae · Ecological traps · Conservation

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Introduction

Odonates are declining worldwide due to the loss and deterioration of their habitat (Clausnitzer et al. 2009), and nearly 15% of known species are currently threatened with extinction (IUCN 2009). In Britain, three species became extinct in the 1950s, and of 43 resident species currently present, 12 are now included in the UK Red Data Book. Overall, declines in odonate populations are consistent with the increase of post-war intensive farming methods (Macdonald and Smith 1991). Given the dominant footprint of agricultural land, covering 76% of the UK in 2007 (FAOSTAT 2009), the challenge faced by policy makers is to reverse these negative trends by integrating efficient conservation of odonates—and biodiversity in general—into the dynamic landscapes that result from economically sustainable agricultural production methods (Scherr and McNeely 2008).

Odonates have a bipartite life history, with both aquatic and terrestrial (aerial) stages. This characteristic makes them valuable bio-indicators of both terrestrial and aquatic landscape quality (Clark and Samways 1996; Briers and Biggs 2003; Córdoba-Aguilar 2008; Catlin 2009). However, adults do occur, and even oviposit, at poor quality aquatic sites, where eggs may not develop and larvae may not be able to reach the final instar (Corbet 1999). As a result, the presence of adults, or even larvae, may not be indicative of successful odonate breeding. The importance of surveying for larvae or exuviae (cast-off skin) has recently been highlighted (Ott et al. 2007; Hardersen 2008; Samways et al. 2010) and indeed, even though certain landscape features (e.g., functional 'corridors') may encourage adult dispersal towards aquatic sites (McCauley 2006), recruitment rates may still be zero, or too low to result in viable (meta-)populations, if these sites are of poor quality. Additionally, the duration of the aquatic stage is typically much longer than is the adult stage, but worldwide, most surveys are undertaken of the adult stage. Data specifically obtained for this study from six national (regional) recording networks of five European countries (Belgium, France, Netherlands, Slovenia and UK) show this in detail: out of the total number of records ($N = 1{,}410{,}055$), adults comprised between 85 and 98% of records within these datasets, whereas larval and exuvial records only represented small proportions (0.06–15%; 0.7–6.5%, respectively). Although such datasets are a vital tool to assess species distributions and changes in population trends, which are pre-requisites to conservation planning (Sahlén et al. 2004), they generally suffer from coverage and recorder bias (Dennis and Shreeve 2003; Maes et al. 2003; Dennis et al. 2006). In this study, we show that this bias towards adult records in odonate datasets risks leading to misinterpretations of the environmental quality of sites. We focus specifically on farmland ponds, a key feature of lowland agricultural landscapes (Williams et al. 2003). Although numbers are currently increasing in England, they suffered a dramatic decline (*ca*. 50%) over the past century (Countryside Survey 2008). We hypothesise that possible discrepancies between adult, larval and exuvial records stem from a bias created by (1) the dispersal capacity during the adult stage, and (2) the difference between mere indicators of reproduction (e.g., copulation and oviposition, by adults) and a direct measure of reproductive success (i.e., presence of exuviae).

Evaluation of the (dis)advantages of adult, larval and exuvial surveys may predispose surveyors to choose the option that is easiest, most rapid and least costly, namely adult surveys (Table 1). Adult surveys are used worldwide and consist of identifications of flying or net-caught individuals while walking transects [e.g., perimeter of lentic/lotic (standing/running) waterbodies; i.e., modified Pollard Walk (Pollard and Yates 1993)] and recording species present, estimating their abundances and noting individual behaviours. These surveys are used by national recording schemes and, at least in the UK, by national and local wildlife organisations, to monitor reserve sites. They are also used by consultancy companies when assessing farmland biodiversity for Agri-Environment Scheme (AES) application reports. There is no consistent pattern of larval surveys for Odonata in the UK: patchy sampling is usually performed on ponds by the Pond Conservation Trust and on rivers by the Environment Agency, with Wildlife Trusts sampling on an ad hoc basis. All these surveys are a means of sampling communities of macroinvertebrates in general to assess the quality of waters through species presence/absence, and are not targeted towards odonates. Surveying requires the use of a pond-dipping net and allocating a given sampling time or space. Exuvial surveys are rarely used and require wading in water to check vegetation and substrates within the water and on the bank. Studies on exuviae are therefore scarce and have either only focused on single species (Foster and Soluk 2004) or have been used as a sideline of larger studies to determine species' presence, to assess habitat quality at very specific and small-scale locations (Chovanec and Raab 1997; D'Amico et al. 2004; Gaines 2006; Hardersen 2008), as part of seasonal emergence pattern studies (Corbet 1999), or for assessing exuviae persistence rates on substrates (Lubertazzi and Ginsberg 2009).

The aim of our study is to test whether or not different survey methods for odonates lead to similar conclusions on species richness and hence on farmland pond quality. If significant discrepancies between survey methods are detected, this would imply that the current bias towards adult surveying may have important implications for conservation assessments. It has been stressed before that routine comparisons between technique effectiveness should be applied to all conservation issues (Franco et al. 2007). We believe that this study is the first to contrast, at a landscape-scale, these three different survey methodologies (larval, exuvial and adult surveys) for assessing presence/absence of dragonflies at farmland ponds, and to establish to what extent these three different methods are interchangeable.

Materials and methods

Study sites

A total of 29 farmland ponds (size range: 23–1,452 m^2) was sampled in four areas of the River Ray catchment (Buckingham- and Oxfordshire, UK). This is a catchment of alkaline waters and comprises ca. 283 km^2 of lowland agricultural land, mainly underlain by low permeability sedimentary rocks of Jurassic age (Neal et al. 2006), with clay as the main top substrate. After a preliminary pond survey, based on Ordnance Survey maps, had been undertaken, pond selection was based on discussions with landowners with regard to accessibility and knowledge of the area. The only selection requirement was that ponds

Table 1 Advantages (+) and disadvantages (−) of using adult (AD), larval (LA) and exuvial (EX) surveys

	AD	LA	EX	
Cost	+ +	+ −	− −	(AD) cheap: no specialist equipment required, rapid training; (LA) medium: rapid training but time consuming identifications; (EX) expensive: not cost-effective to pay someone for undertaking surveys/identifications. Health and safety issues when wading and kneeling in water
Surveying time	+	+	− −	(AD) rapid surveying on site; (LA) rapid surveying on site; (EX) time consuming
Invasive/destructive?	+ +	− −	−	(AD) no interference with the habitat/other organisms; (LA) wading and netting within vegetation can be detrimental to habitat and other organisms, especially in small waterbodies; (EX) moderate disturbance: regular wading can be invasive in small waterbodies, by stirring substrates and damaging vegetation
Identification	+	− −	+ +	(AD) on site: non-destructive/rapid; (LA) on-site: non-destructive but impossible to identify some species; off-site: very destructive, need to preserve sample in alcohol;. samples are slow to process and to identify; early instars cannot be identified but are killed; (EX) off-site: all disregarded skins allow for identification without damaging individuals; can be stored for later work
Expertise	+ −	−	−	(AD) can be obtained rapidly; females and immature individuals may be confusing to inexperienced surveyors; (LA) needed for larval identification; microscope may be required; (EX) needed for identification; microscope may be required
Seasonality dependence	−	+ −	−	(AD) high: flight period is time-restricted and species dependent; most immature adults will not be found near water; (LA) moderate: species present all year round; early instars may not be captured; univoltine synchronised species may be under-represented just after emergence; (EX) high: emergence period is short for synchronised species and species dependent but exuviae still found weeks after emergence
Weather-dependence	− −	+ +	+ +	(AD) high: restricted to non-windy conditions with >17°C and <50% cloud cover; (LA) low: larvae would be found even if they have moved away from the bank in adverse weather conditions; (EX) low: exuviae will wash off during heavy rain but can still be found under light rain and windy conditions
Sex ratio	− −	+	+	(AD) male biased due to territoriality near water bodies; (LA) both sexes are caught and individuals can be sexed; (EX) both sexes are caught and individuals can be sexed
Mate-location strategies	− −	N/A	N/A	(AD) bias towards perching individuals as these are easier to record than patrollers
Habitat quality/life-cycle completion	− −	+ −	+ +	(AD) presence does not proof good habitat quality as adults may have arrived from another waterbody, no proof of emergence; (LA) good habitat for larvae at the time of sampling but not proven life-cycle completion: adults may not reach emergence stages; (EX) sole proof of a successful habitat for emergence

were not completely surrounded by trees. We had no previous knowledge of odonate presence or absence, therefore pond selection was unbiased with regards to species richness.

Data collection

Larval sampling

Presence/absence of odonates was ascertained by larval sampling at all ponds using a pond-dipping net (1 mm mesh): ponds were scooped for 4-s at vegetation tussocks by the bank; the sample was immediately transferred into a white tray and examined for larvae. If odonates were present, Zygoptera (damselflies) and Anisoptera (dragonflies) numbers were estimated. If odonates were not present in the sample, the procedure was repeated up to ten times (at different mesohabitats) or until presence was recorded, whichever occurred first. Sampling took place from mid-April to the first week of June 2006. The larvae of most species have reached the final instar by this time, which facilitates collection and identification.

Exuvial collection

Presence/absence of exuviae was determined by collecting specimens from May to September in 2006 and 2008, and from June to September in 2007, as part of a larger study (E. M. Raebel, unpublished data). In each of these years, ponds were visited at least four times in a three-week rotation to allow for species turnover and to maximise sampling effort at each pond. Exuviae were sampled from: (1) emergent bank vegetation by wading in the water to vegetation level; (2) vegetation and ground within 1.5 m from the bank; and (3) emergent vegetation within the pond area. Species were identified and sexed, where possible, in the hand with the use of a hand lens and under the microscope for Zygoptera and for Anisoptera of the genus *Sympetrum*.

Adult surveys

Presence/absence of adults was determined on a rotational basis from May to September in 2006 and 2008 and from June to September in 2007. Visits took place every 3 weeks in order to allow for species turnover during the flight season. No surveys were undertaken under overcast, windy or rainy conditions. Individuals, together with copulating and ovipositing behaviours, were recorded for half an hour between 10 a.m. and 2 p.m. (before any pond disturbance). Anisoptera and Zygoptera were recorded differently. Species and sex of individual territorial Anisoptera were recoded by sight or with the use of close-focusing binoculars. This allowed observations of the number of resident species and of numbers of individuals holding a territory. During the remaining time at the pond, which involved Zygoptera recording (see below) and sometimes exuviae collection, newly observed species and visiting individuals (of both sexes) were also recorded. As Anisoptera are easy to count individually, a count was taken for each species with the exception of *Sympetrum* species, which being abundant at most ponds, were given an abundance code adapted from the one used by the British Dragonfly Society's recording scheme ($A = 1$; $B = 2–5$; $C = 6–10$; $D = 11–20$; $E = 21–50$; $F = 51–100$; $G = 100–500$; and $H > 500$).

All species of Zygoptera were given an abundance code as per *Sympetrum* species. Species were coded by estimating their abundance at the end of the survey and after walking the accessible parts of the pond perimeter. To help estimate density of each species, whilst avoiding potential misidentification of species which are hard to distinguish by sight (e.g., 'blue coenagrionids' *Enallagma cyathigerum* and *Coenagrion puella* (Brooks 1993)), a sample of 30 individuals was taken, marked and released at each pond. The percentage of each of these species in this sample was then applied to the total 'blue coenagrionids' populations, estimated by codes. This method prevents lumping of low density species into the more abundant species. Every captured individual Zygoptera was marked with a dot on the left forewing using a permanent water-proof marker (Staedtler Lumocolor), ensuring that no individual was counted twice.

Analysis

Fisher's Exact Test was used to test for associations in presence/absence of adults, larvae and exuviae in 2006 (Table 2; SAS 9.1). Data from all 3 years (2006–2008) were combined to assess how many ponds contained a given species. This meant that a species was counted as 'present' in a pond even if only recorded in one of the years (Fig. 1). Comparisons of adult and exuvial surveys in terms of population abundance (Fig. 2b) were conducted by separating 'flier' and 'percher' species of Anisoptera (Table 3) (Corbet and May 2008). Calculations for adult 'flier' species of the genera *Aeshna* and *Anax* and for adult 'percher' species of the genera *Libellula* and *Orthetrum* were performed by summing total numbers recorded at each survey, separately for each year, with visits at least 3 weeks apart. Abundance of adult 'percher' species of Zygoptera and Anisoptera of the genus *Sympetrum* was estimated by summing the means of the range within each code (see above), when surveys had taken place at least 3 weeks apart. Total abundance was used for all genera in order to estimate exuvial abundance. All abundances were

Table 2 Contingency tables showing the relationship (in 2006) between presence (P) and absence (A) of (a) larvae versus exuviae; (b) larvae versus adults; and (c) exuviae versus adults

	Larvae	
	P	A
(a)		
Exuviae		
P	17	1
A	1	10
(b)		
Adults		
P	18	11
A	0	0
	Exuviae	
	P	A
(c)		
Adults		
P	18	11
A	0	0

$\log_{10}$-transformed prior to analysis and are referred to subsequently as log-adults (logad) and log-exuviae (logex). GLM Univariate analysis was used to test whether adult numbers increased in line with numbers of exuviae, depending on sub-order (Anisoptera/Zygoptera) or genus, and assuming that exuvial numbers found at a pond should be related to the number of adults that would be present that season. We excluded non-pond dwellers (*Calopteryx splendens*), species with less than ten observations of Zygoptera (*Erythromma viridulum*, *E. najas*) and less than twenty for Anisoptera (*Aeshna mixta*), and species for which no more than five individuals of exuviae were found over the 3 years period (*Lestes sponsa, Orthetrum cancellatum*). SPSS 17.0 was used for the analysis.

Results

Survey bias

Data from 2006 showed that larval and exuvial surveys are interchangeable (Fisher's exact; $P > 0.5$). However, adult surveys gave different results, implying that this method is not interchangeable with larval or exuvial surveys (Fisher's exact; $P < 0.0001$). Although adults were recorded at all ponds, only 18 of these had larvae (Table 2b) and exuviae (Table 2c). Both larvae and exuviae were present at 17 ponds and both were absent at ten ponds (Table 2a). Differences between the surveys for larvae and exuviae occurred at only two ponds (Table 2a).

Ovipositing success

A total of 17 species was recorded as adults in each of the three study years. Ovipositing was recorded for all these species, with a minimum of 7% ($N = 2$) of the total number of ponds ($N = 29$) oviposited by *Erythromma najas* and *E. viridulum*, and a maximum of 93% of ponds ($N = 27$) by *Ischnura elegans* and *Sympetrum sanguineum* (Table 3). Overall, 11,025 exuviae were collected (2006: $N = 3{,}316$, 12 species; 2007: $N = 2{,}325$, 13 species; 2008: 5,384, 16 species). We observed ovipositing behaviour at all ponds, in each of the 3 years. Nevertheless, a significant

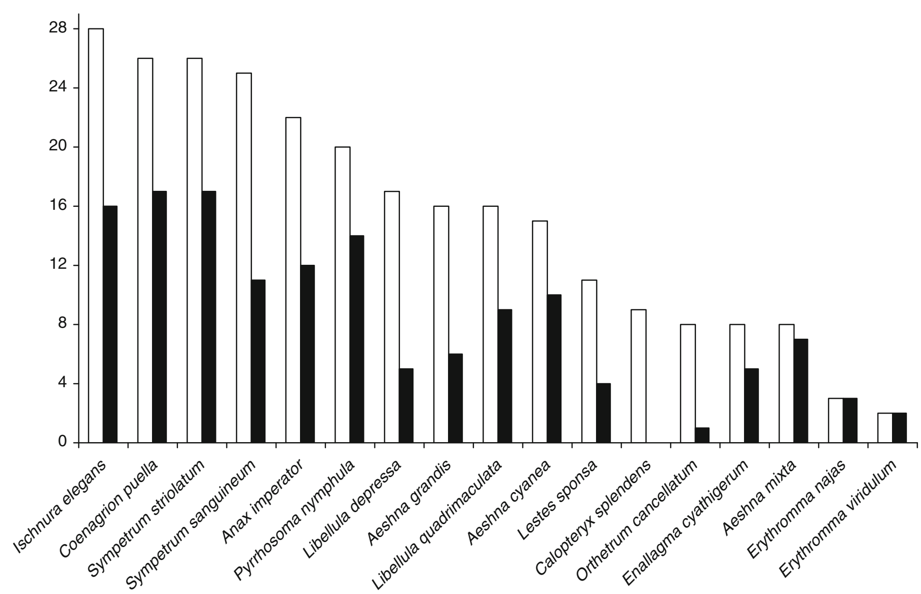

Fig. 1 Number of ponds ($N_{max} = 29$) at which each species was found. Adult presence is depicted in *white* and exuviae presence in *black*. Species are considered as present at a pond if found in at least one of the three study years

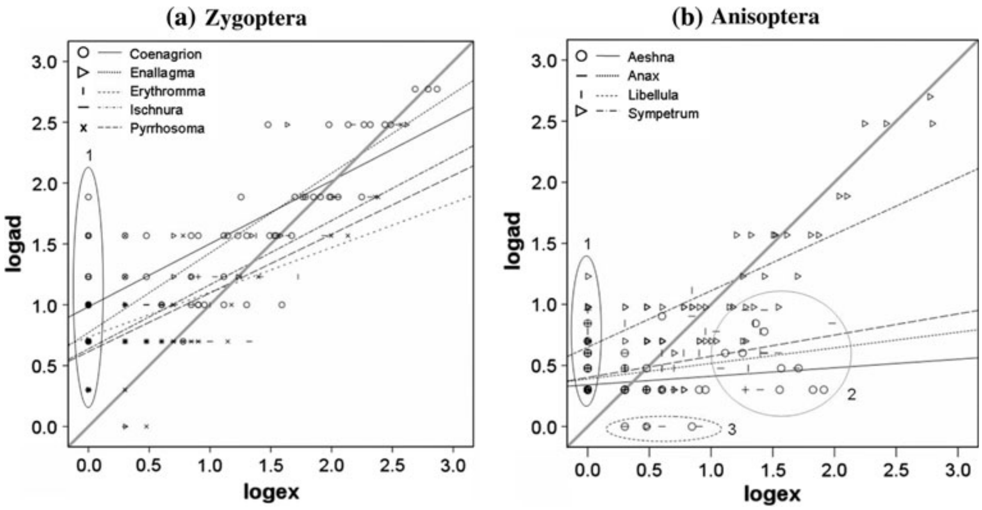

Fig. 2 Adult abundance plotted against exuviae abundance at ponds over a 3 years period (2006–2008) for different genera of the odonate suborders: **a** Zygoptera: *Coenagrion*, *Enallagma*, *Erythromma* and *Ischnura*; and **b** Anisoptera: *Aeshna*, *Anax*, *Libellula* and *Sympetrum*. Abundances have been log transformed. 'Best fit' linear correlations are given for each genus, which are represented by *different symbols*. A reference line representing a perfect linear correlation has been provided. *Individual symbols* can refer to more than one observation. *Symbols* grouped within a *numbered ellipse* are referred to within the text to highlight similarities

Table 3 Mating strategy (*T* territorial, *NT*, non-territorial, *s&w* sit-and-wait), voltinism and ovipositing versus exuviae records of all odonate species recorded as adults during the study; Univoltine (UV) species have a 1-year life-cycle, whereas semi-voltine (SV) species generally complete their life-cycle in 2 years, unless specified otherwise

Family	Species	Mating strategy	Life-cycle	Ovipositing (%)	Failure (%)
Zygoptera					
Coenagrionidae	*Coenagrion puella*	NT: s&w	UN	90	42% ($N = 26$)
Coenagrionidae	*Enallagma cyathigerum*	NT: s&w	UN	24	57% ($N = 7$)
Coenagrionidae	*Erythromma najas*	NT: s&w	SV	7	0% ($N = 2$)
Coenagrionidae	*Erythromma viridulum*	NT: s&w	SV	7	0% ($N = 2$)
Coenagrionidae	*Ischnura elegans*	NT: s&w	UN	93	52% ($N = 27$)
Coenagrionidae	*Pyrrhosoma nymphula*	T: s&w	SV	55	31% ($N = 16$)
Lestidae	*Lestes sponsa*	NT: s&w	UN	38	82% ($N = 11$)
Anisoptera					
Aeshnidae	*Anax imperator*	T: flier	UN/SV	24	57% ($N = 14$)
Aeshnidae	*Aeshna cyanea*	T: flier	SV	41	42% ($N = 12$)
Aeshnidae	*Aeshna grandis*	T: flier	SV (up to 4ys)	34	100% ($N = 10$)
Aeshnidae	*Aeshna mixta*	T: flier	UN	14	75% ($N = 4$)
Libellulidae	*Libellula depressa*	T: percher	SV/UN	45	77% ($N = 13$)
Libellulidae	*Libellula quadrimaculata*	T: percher	SV	21	50% ($N = 6$)
Libellulidae	*Orthetrum cancellatum*	T: percher	SV	17	80% ($N = 5$)
Libellulidae	*Sympetrum sanguineum*	T: percher	UN	93	67% ($N = 27$)
Libellulidae	*Sympetrum striolatum*	T: percher	UN	72	43% ($N = 21$)

Oviposting percentages refer to the percentage of ponds ($N_{total} = 29$) where ovipositing for each species was recorded in 2006. Failure percentages refer to the percentage of ponds (number of ponds is given between brackets) at which ovipositing was recorded in 2006 but which failed to produce any exuviae in 2007, or 2008, depending on the specific life-cycle. Species known to have both UN and SV life-cycles in the study area include exuvial records for both 2007 and 2008. Only pond odonate species are included

percentage of ponds did not yield any exuviae at all, even not from the univoltine species observed ovipositing at all ponds in 2006 and 2007. For example, only 18 ponds yielded *Coenagrion puella* exuviae in 2007 and only 19 in 2008, which shows that 38% ($N = 11$) and 34% ($N = 10$) of ponds, respectively, were not suitable for the development of eggs and/or larvae (i.e., successful reproduction). Overall, the percentage of ponds where a species was observed ovipositing but without producing exuviae in consecutive years, ranged from 31 to 100%, depending on the species (and excluding two species which were only found ovipositing at two ponds that yielded exuviae hence percentage failure was 0%) (Table 3).

Species composition

Species composition at single ponds (combining the 3 years) differed when using adult versus exuvial surveys (Fig. 1). For example, the sequence of species most frequently observed as adults (ad) does not match the same sequence for exuviae (ex) (four most common species in declining order; number of ponds between brackets): (1) ad: *Ischnura elegans* (28)—ex: *Coenagrion puella* (17); (2) ad: *Coenagrion puella* (26)—ex: *Sympetrum striolatum* (17); (3) ad: *Sympetrum striolatum* (26)—ex: *Ischnura elegans* (16); (4) ad: *Sympetrum sanguineum* (25)—ex: *Pyrrhosoma nymphula* (14) (Fig. 1). Another example of the mismatch between surveys for adults versus exuviae is the presence as adults of the mobile, riverine species *Calopteryx splendens* at seven ponds, whereas no exuviae were recorded at these or any other pond (Fig. 1). Similarly, adults of *Orthetrum cancellatum*—a species mainly found in lakes and slow-flowing rivers—were recorded at eight ponds, but exuviae were found only at one of the largest ponds (512 m^2) (Fig. 1).

Adult: exuviae relationships

At single ponds, adults of both Zygoptera and Anisoptera were often recorded even when no exuviae were found (Fig. 2a, b, Group 1). Although adult numbers, overall, tended to be higher than those of exuviae, Zygoptera adult abundance increased in line with exuvial abundance (Fig. 2a), this being the case for all genera of Zygoptera (interaction: $F_{4,\ 241} = 0.885$, $P > 0.5$) (Fig. 2a). Consequently, exuvial numbers explained a larger amount of variation in Zygoptera adult abundance than did genus, although both variables are highly significant in explaining adult abundance (exuvial abundance: $F_{1,\ 241} = 173.43$, $P < 0.001$; genus: $F_{4,\ 241} = 8.97$, $P < 0.001$).

This strong pattern between adult and exuvial abundance for Zygoptera was different for the other odonate suborder (i.e., Anisoptera) (interaction: $F_{1,\ 599} = 24.80$, $P < 0.001$; Fig. 2a,b).

For the Anisoptera, slopes differed between genera ($F_{3,\ 344} = 19.46$, $P < 0.001$), which was mainly explained by the higher slope for the genus *Sympetrum*. Indeed, when excluding this genus from the analysis, the differences in slope between the three remaining genera disappeared (interaction: $F_{2,\ 214} = 0.04$, $P > 0.5$), and slopes are lower if compared to the Zygoptera (Fig. 2a, b). For example, aeshnids (genera *Aeshna* and *Anax*) often remained below ten individuals even when exuvial records were up to 95 individuals (Fig. 2b, Group 2), and these aeshnid adults were not always found at ponds that yielded exuviae (Fig. 2b, Group 3). Similarly, libellulids showed the largest numbers of exuviae (18–24 individuals) corresponding to adult sightings of fewer than ten individuals (Fig. 2a, Group 2). Slopes did not significantly differ between genera of Zygoptera ($F_{4,\ 241} = 0.89$, $P = 0.47$).

Discussion

Adult surveys over-estimate pond quality

Our study shows that farmland pond surveys based upon larvae and those based upon exuviae are equally suitable for the reliable assessment of presence/absence of odonates (Table 2). This finding corroborates a study, focused on only one odonate species (i.e., *Somatochlora hineana*), in which no differences were found between population estimates based on larval or exuvial surveys (Foster and Soluk 2004). However, our data additionally show that adult surveys are not interchangeable with surveys of larvae and exuviae (Table 2). Indeed, not only were adults recorded on all ponds where exuviae were totally absent, but we also recorded ovipositing females on these ponds. For example, the univoltine *Coenagrion puella*, *Ischnura elegans* and *Sympetrum striolatum* were present as adults at 72–93% of ponds in 2006, whereas 42–52% of these ponds produced not a single exuvia in 2007 (Table 3). Overall, a total of 14 out of 16 species oviposited at ponds that turned out to be unsuitable for successful development of eggs and/or larvae. These unsuitable quality ponds where egg development failed, represented between 31 and 100% of ponds, depending on the species, were females were observed ovipositing (Table 3).

Based on these findings, and in order to improve adult survey methodologies which are currently widely used, we recommend to combine and contrast adult surveys with either larval or exuvial surveys. In cases when cost-efficiency is paramount, we would advise larval surveys, since exhaustive surveys of exuviae are more time consuming (Table 1). It should also be taken into account that exuviae could be under-recorded depending on frequency of surveys (Lubertazzi and Ginsberg 2009) and loss due to them being washed off in bad weather or blown off in high winds. However, despite what seems a strong association between the results of surveys of exuviae and larvae (Table 2), we have shown that some larvae are found at ponds at which completion of the whole life-cycle fails to be successful, for example as a result of changes in habitat quality (see also Foster and Soluk 2004). This was the case, in our study, for a pond which only yielded exuviae of the semi-voltine species *Aeshna cyanea* in 2006 ($N = 81$) and in 2008 ($N = 66$), but which lacked exuviae in 2007, although oviposition was recorded at each of the 3 years. Larvae at various instar stages were found in early June 2006, but the pond dried out from mid-July to the end of August that year. Consequently, first-year larvae in 2006 did not survive, explaining the absence of exuviae in the following year. However, endophytic eggs laid in 2006 would have retained enough moisture to survive, resulting in larvae during 2007 and emerging as adults in 2008. Furthermore, Benke and Benke (1975) compared larval abundance estimates with numbers at emergence, and concluded that at least 80% of final instar larvae die before emergence, with other studies suggesting that larvae are affected by pesticides and general pollution (Hardersen et al. 1999; Chang et al. 2007), cattle grazing (Foote and Rice Hornung 2005), the presence of fish (Dorn 2008), and parasites (Braune and Rolff 2001). As a result, surveys based on exuviae, though more costly, will provide a more precise assessment of odonate pond occupancy, as exuviae remain the only evidence for life-cycle completion success.

Ecological traps

Odonata mainly recognise habitat resources by visual cues. This reliance may make them inherently vulnerable to ecological traps, as the presence of conspecifics (Corbet 1999), structural features such as vegetation (Wildermuth 1992), and linear polarised light reflected from waterbodies (Bernáth et al. 2002), have all been identified as cues. Light polarisation plays a significant role in attracting odonates to oviposit, not only on waterbodies, but even on clearly unsuitable substrates, such as oil lakes, glass buildings, and certain colours of gravestones and cars (Horváth et al. 1998, 2007; Kriska et al. 2006, 2008). These observations, together with our finding that odonates oviposited in all ponds irrespectively of pond quality, imply that their evolutionary cues for habitat selection encourage odonates to make what are currently poor habitat choices (Schlaepfer et al. 2002; Van Dyck 2009). Given that the presence of conspecifics can also act as a further cue to attract individuals, we advance the hypothesis that low-quality ponds are functioning as ecological traps.

Some authors are sceptical as to the significance of the ecological trap concept for conservation because such traps are believed to be rare (Robertson and Hutto 2006). However, here we show that the low-quality variant of a common habitat (*ca*. 487,000 ponds in Britain; Carey et al. 2008) may act as an ecological trap. We therefore believe that the ecological trap concept is significant within this conservation context as ponds of low quality are currently a widespread feature within intensively managed agricultural landscapes. We demonstrate that the reason why this has gone unnoticed is that pond quality has been overestimated by standard odonate survey methods: if solely relying on adult surveys, our study would have classified all ponds as suitable habitats, ignoring that at least a third of them might have been functioning as ecological traps.

Ecological strategies bias adult records: generalists and dispersers

Highly mobile and generalist species may be recorded at more locations than other species. Within our study, the three most frequently found species as adults and exuviae were generalists, able to breed in eutrophic conditions and relatively good dispersers (Fig. 1). However, there were great discrepancies among some species. For example, *Libellula depressa* is an early-coloniser which adults were recorded at 59% of ponds but since this species usually breeds in ponds of early successional stages (Brooks and Lewington 1997), exuviae were only found at 17% of ponds. Similarly, *Sympetrum sanguineum*, a species associated with woodland (Brooks and Lewington 1997) appeared to be present at 86% of ponds as adults, but only at 38% as exuviae. Since Anisoptera are known to disperse away from their natal pond by several kilometres, unsuitable ponds possibly acted as 'sinks' for this species as they often produced zero exuviae, and never more than five. Kokko and Sutherland (2001) have highlighted that the absence of an aversion for such 'sinks' may lead to population extinctions in areas that would otherwise be capable of sustaining populations, putting species, in this case highly mobile ones, at risk of a behaviourally mediated Allee effect.

Ecological strategies bias adult records: territoriality and mating

Our study also shows that different territorial strategies can affect adult survey results. Adult surveys are most suited to situations with medium and high populations of Zygoptera, regardless of genera (Fig 2a), due to their mating strategy: males arrive at a pond and 'sit and wait' for females, adopting a scramble competition strategy (Corbet 1999). This implies that zygopteran adults are more likely to be recorded than territorial Anisoptera, which disperse more frequently to find new territories. Males of territorial Anisoptera 'fliers' (e.g., *Aeshna*, *Anax*) patrol in flight to deter other males and attract females (Corbet and Brooks 2008), while guarding territories in a hierarchical manner: a dominant male patrols the territory while satellite/visiting males await his departure in order to take over. Corbet (1999) showed that *Aeshna cyanea* could visit a pond one to eight times in slots of 40 min at a time per day, allowing temporal niche partitioning with other individuals. As a result, small ponds will only be able to hold one *alpha* male at a time. Territorial Anisoptera 'perchers' (e.g., *Libelulla*), will also hold such territories but from a perch. Consequently, our results show that Anisoptera adults were generally under-recorded, or even missed, in relation to exuviae presence (Fig. 2b). Similar results were observed by Brooks (1993) in a small study to validate the modified Pollard Walk for monitoring adult odonates, with the author concluding that adult surveys were less suitable for mobile hawker odonates (Aeshnidae) than for Zygoptera and perching dragonflies (Libellulidae). However, our study also shows that it would be misleading to consider all territorial 'perchers' as following the same pattern because species can have different territorial strategies depending on population densities, and are even able to switch from territorial to non-territorial behaviour when male density is high (Ottolenghi 1987). We show that territorial 'perchers' at high densities (*Sympetrum*) were characterised by a significantly steeper slope than other Anisoptera genera, implying a better correlation between adult and exuvial numbers, similar to the relationship for non-territorial Zygoptera (Fig. 2b). We conclude that adult surveys bias recording towards genera, species and populations with non-territorial mate-location strategies.

Bias due to rarity and voltinism

For Anisoptera, a lack of exuviae where adults are found can be explained by their strong dispersal ability but most Zygoptera (e.g., Coenagrionidae) are known to prefer their natal pond (Corbet 1999), with most individuals only likely to move a short distance (Conrad et al. 1999; Rouquette and Thompson 2007). This would imply that ponds with no exuviae, do not have natal populations hence adult numbers would depend solely on dispersing individuals, which would be low. Our study found that when adult records did not exceed ten individuals per zygopteran species, no exuviae were found. This corroborates a previous study which showed that scarce species as adults were also scarce as exuviae (D'Amico et al. 2004). In our case, adults of *Lestes sponsa* were always coded between one and five, whereas exuviae were zero or one (Fig. 2a), suggesting that species present in very low numbers may need targeting in order to avoid being mis-recorded as individuals of more abundant species. One also needs to take into account that they may be emerging from places not included in the searching area (Lubertazzi and Ginsberg 2009) and instead, a combination of methods, including larval sampling, may be needed to ascertain their presence.

It should also be considered that exuvial surveys can under-record the presence of rarely present species, and it is often rare species that are of conservation interest. In Ott et al.'s (2007) study of the threatened *Oxygastra curtisii*, exuvial surveys proved to be the most relevant to understand the ecology of this species. Exuvial results showed that areas of emergence did not correspond with adult territories and that they were restricted to specific microhabitats. Such studies should increase awareness of the need to understand requirements at each stage of the life-cycle when dealing with threatened species. It also highlights the need to include exuvial surveys in management plans (e.g., Red List species).

Adult surveys can also be misleading with regard to semi-voltine or parti-voltine species. In this study, and over 3 years, exuviae of *Erythromma viridulum* were always found at two ponds where adults had also been recorded. However, yearly analysis shows that although ovipositing adults were present during 3 years (Table 3), there were no records of exuviae in the first year at both ponds and in the second year at one of them. This suggests that ponds had just been colonised with exuvial patterns reflecting the year of colonisation of this semi-voltine species. However, adult records alone would have suggested that reproductive success had occurred from year one, hence caution should be taken when surveying species with life-cycles longer than 1 year, as they are likely to be most affected by changes in habitat quality and stochastic events. Consequently, semi-voltine and parti-voltine species may be valuable bio-indicators, as their presence would imply that a good habitat quality has been sustained for at least the developmental period of these species (e.g., up to 4 years for *Aeshna grandis*).

Conclusions

Although extended exuvial surveys are costly and time consuming, we recommend that at least presence/absence of species should be ascertained when the aim is to deliver quality biodiversity assessments. On the contrary, exhaustive exuvial surveys are essential when dealing with protected species. Since costs and time are always constraints, concentrating exuvial survey efforts to particular species could be a valuable option.

Both countryside-wide and site-specific monitoring of odonate biodiversity would benefit from applying the best survey methods. In addition to birds, the EU has recently accepted butterflies as a small-scale terrestrial bio-indicator (EEA 2007). We suggest that including Odonata would benefit this set of indicator taxa, as odonates may act as bio-indicators for the quality of semi-aquatic environments (Briers and Biggs 2003; Córdoba-Aguilar 2008; Catlin 2009). Odonate surveys will then give an indication of the quality of both terrestrial and aquatic ecosystems at both small and larger spatial scales. Monitoring using exuvial surveys would avoid wasting valuable financial resources while providing the unbiased data that is necessary for informing on sound conservation options.

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References

Benke AC, Benke SS (1975) Comparative dynamics and life histories of coexisting dragonfly populations. Ecology 56:302–317

Bernáth B, Szedenics G, Wildermuth H, Horváth G (2002) How can dragonflies discern bright and dark waters from a distance? The degree of polarisation of reflected light as a possible cue for dragonfly habitat selection. Freshw Biol 47:1707–1719

Braune P, Rolff J (2001) Parasitism and survival in a damselfly: does host sex matter? P Roy Soc Lond B Biol 268:1133–1137

Briers RA, Biggs J (2003) Indicator taxa for the conservation of pond invertebrate diversity. Aquat Conserv 13:323–330

Brooks SJ (1993) Review of a method to monitor adult dragonfly populations. J British Dragonfly Soc 9:1–4

Brooks S, Lewington R (1997) Field guide to the dragonflies and damselflies of Great Britain and Ireland. British Wildlife Publishing, Hampshire

Carey PD, Wallis S, Chamberlain PM, Cooper A, Emmett BA, Maskell LC, McCann T, Murphy J, Norton LR, Reynolds B, Scott WA, Simpson IC, Smart SM, Ullyett JM (2008) Countryside survey: UK results from 2007. NERC/Centre for ecology and Hydrology. (CEH Project Number: C03259)

Catlin PA (2009) A potential for the use of dragonfly (Odonata) diversity as a bioindicator of the efficiency of sewage lagoons. Can Field Nat 119:233–236

Chang X, Zhai B, Wang M, Wang B (2007) Relationship between exposure to an insecticide and fluctuating asymmetry in a damselfly (Odonata, Coenagriidae). Hydrobiologia 586:213–220

Chovanec A, Raab R (1997) Dragonflies (Insecta, Odonata) and the ecological status of newly created wetlands: examples of long-term bioindication programmes. Limmologica 27:381–392

Clark TE, Samways MJ (1996) Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa. J Appl Ecol 33:1001–1012

Clausnitzer V, Kalkman VJ, Ram R, Collen B, Baillie JEM, Bedjanic M, Darwall WRT, Dijkstr KB, Dow R, Hawking J, Karube H, Malikova E, Paulson D, Schüte K, Suhling F, Villanueva RJ, von Ellenrieder N, Wilson K (2009) Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. Biol Conserv 142:1864–1869

Conrad KF, Willson KH, Harvey IF, Thomas CJ, Sherratt TN (1999) Dispersal characteristics of seven odonate species in an agricultural landscape. Ecography 22:524–531

Corbet PS (1999) Dragonflies: behaviour and ecology of odonata. Harley Books, Colchester

Corbet PS, Brooks SJ (2008) Dragonflies. The New Naturalist Library. HarperCollins Publishers, London

Corbet PS, May ML (2008) Fliers and perchers among Odonata: dichotomy or multidimensional continuum? A provisional reappraisal. Int J Odonatol 11:155–171

Córdoba-Aguilar A (ed) (2008) Dragonflies and damselflies. Model organisms for ecological and evolutionary research. Oxford University Press, Oxford

Countryside Survey (2008) Countryside survey: UK results for 2007, Chap. 8: rivers, streams and standing waters. http://www.countrysidesurvey.org.uk/reports2007.html

D'Amico F, Darblade S, Avignon S, Blanc-Manel S, Ormerod SJ (2004) Odonates as indicators of shallow lake restoration by liming: comparing adult and larval responses. Restor Ecol 12: 439–446

Dennis RLH, Shreeve TG (2003) Gains and losses of French butterflies: tests of predictions, under-recording and regional extinction from data in a new atlas. Biol Conserv 110:131–139

Dennis RLH, Shreeve TG, Isaac NJB, Roy DB, Hardy PB, Fox R, Asher J (2006) The effects of visual apparency on bias in butterfly recording and monitoring. Biol Conserv 128:486–492

Dorn NJ (2008) Colonization and reproduction of large macroinvertebrates are enhanced by drought related fish reductions. Hydrobiologia 605:209–218

European Environment Agency (EEA) (2007) Halting the loss of biodiversity by 2010: proposal for a first set of indicators to monitor progress in Europe. European Environment Agency, Denmark 180 pp

FAOSTAT (2009) Food and agriculture organization of the United Nations—FAO Statistics Division 2009. http://faostat.fao.org

Foote AL, Rice Hornung CL (2005) Odonates as biological indicators of grazing effects on Canadian prairie wetlands. Ecol Entomol 30:273–283

Foster SE, Soluk DA (2004) Evaluating exuviae collection as a management tool for the federally endangered Hine's emerald dragonfly, *Somatochlora hineana* Williamson (Odonata: Cordulidae). Biol Conserv 118:15–20

Franco AM, Palmeirim JM, Sutherland WJ (2007) Comparing effectiveness of research techniques in conservation and applied ecology. Biol Conserv 134:96–105

Gaines KH (2006) Does the equilibrium theory of island biogeography apply to dragonfly breeding ecology in a desert skinhole complex? In: Davies B, Thompson S (eds) Water and the landscape: the landscape ecology of freshwater ecosystems. Proceedings of the fourteenth annual IALE (UK) conference. Oxford Brookes University, Colin Cross Printers, Ltd, Garstang, pp 64–71

Hardersen S (2008) Dragonfly (Odonata) communities at three lotic sites with different hydrological characteristics. Ital J Zool 75:271–283

Hardersen S, Wratten SD, Frampton CM (1999) Does carbaryl increase fluctuating asymmetry in damselflies under field conditions? A mesocosm experiment with *Xanthocnemis zealandica* (Odonata: Zygoptera). J Appl Ecol 36:534–543

Horváth G, Bernáth B, Molnár G (1998) Dragonflies find crude oil visually more attractive than water: multiple-choice experiments on dragonfly polarotaxis. Naturwissenschaften 85:292–297

Horváth G, Malik P, Kriska G, Wildermuth H (2007) Ecological traps for dragonflies in a cemetery: the attraction of *Sympetrum* species (Odonata: Libellulidae) by horizontally polarizing black gravestones. Freshw Biol 52:1700–1709

IUCN (2009) IUCN red list of threatened species. Version 2009.1. www.iucnredlist.org. Downloaded on 2 June 2009

Kokko H, Sutherland WJ (2001) Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evol Ecol Res 3:537–551

Kriska G, Csabai Z, Boda P, Malik P, Horvath G (2006) Why do red and dark-coloured cars lure aquatic insects? The attraction of water insects to car paintwork explained by reflection-polarization signals. P Roy Soc Lond B Biol 273:1667–1671

Kriska G, Malik P, Szivak I, Horvath G (2008) Glass buildings on river banks as "polarized light traps" for mass-swarming polarotactic caddis flies. Naturwissenschaften 95:461–467

Lubertazzi MA, Ginsberg HS (2009) Persistence of dragonfly exuviae on vegetation and rock substrates. Northeast Nat 16:141–147

Macdonald DW, Smith HE (1991) New perspectives on agro-ecology: between theory and practice in the agricultural ecosystem. In: Firbank LG, Carter N, Darbyshire JF, Potts GR (eds) The ecology of temperate cereal fields (32nd symposium of the british ecological society). Blackwell Scientific Publications, Oxford, pp 413–448

Maes D, Gilbert M, Titeux N, Goffart P, Dennis RLH (2003) Prediction of butterfly diversity hotspots in Belgium: a comparison of statistically focused and land use-focused models. J Biogeogr 30:1907–1920

McCauley SJ (2006) The effects of dispersal and recruitment limitation on community structure of odonates in artificial ponds. Ecography 29:585–595

Neal C, Jarvie HP, Neal M, Hill L, Wickham H (2006) Nitrate concentrations in river waters of the upper Thames and its tributaries. Sci Total Environ 365:15–32

Ott J, Schorr M, Trockur B, Lingenfelder U (2007) Artenschutzprogramm Fur Die Gekielte Smaragdlibelle (Oxygastra Curtisii) in Deutschland an Der Our/Species Protection Programme for the Orange-spotted Emerald (Oxygastra Curtisii) in Germany. The Example of the Our River Population. Invertebrate Ecology and Conservation Monographs, vol 3. Pensoft Publishers

Ottolenghi C (1987) Reproductive behaviour of *Sympetrum striolatum* (Charp.) at an artificial pond in northern Italy. Odonatologica 16:297–306

Pollard E, Yates TJ (1993) Monitoring butterflies for ecology and conservation. Chapman & Hall, London

Robertson BA, Hutto RL (2006) A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085

Rouquette JR, Thompson DJ (2007) Patterns of movement and dispersal in an endangered damselfly and the consequences for its management. J Appl Ecol 44:692–701

Sahlén G, Bernard R, Cordero-Rivera A, Ketelaar R, Suhling F (2004) Critical species of Odonata in Europe. Int J Odonatol 7:385–398

Samways MJ, McGeoch MA, New TR (2010) Insect conservation: handbook of approaches and methods. Oxford University Press, Oxford

Scherr SJ, McNeely JA (2008) Biodiversity conservation and agricultural sustainability: towards a new paradigm of 'ecoagriculture' landscapes. Philos T Roy Soc B 363:477–494

Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. Trends Ecol Evol 17:474–480

Van Dyck H (2009) Are animals fooled in modern landscapes? The ecological trap as a new concept for conservation. Natuur focus 8:28–31

Wildermuth H (1992) Visual and tactile stimuli in choice of oviposition substrates by the dragonfly *Perithemis mooma* Kirby (Anisoptera, Libellulidae). Odonatologica 21:309–321

Williams P, Whitfield M, Biggs J, Bray S, Fox G, Nicolet P, Sear D (2003) Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. Biol Conserv 115:329–341