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Identifying high-quality pond habitats for Odonata in lowland England: implications for agri-environment schemes

EVA M. RAEBEL,[1,2] THOMAS MERCKX,[1] RUTH E. FEBER,[1] PHILIP RIORDAN,[1] DAVID W. MACDONALD[1] and DAVID J. THOMPSON[2]

[1]Wildlife Conservation Research Unit, The Recanati-Kaplan Centre, Department of Zoology, University of Oxford, Tubney, Abingdon, UK and [2]School of Biological Sciences, University of Liverpool, Liverpool, UK

Abstract. 1. Agricultural intensification has contributed to severe declines in odonate (dragonfly and damselfly) populations. The objective of our study is to benefit current measures for the conservation of odonates by establishing the conditions favourable to Odonata and focusing on ponds within agricultural land.

2. Our landscape-scale study used exuvial counts and habitat measurements from 29 ponds across a catchment in England, over 3 years, to determine key factors affecting odonate abundance and species richness.

3. Ponds dominated by floating and submerged vegetation were the most transparent, supported the highest abundance and species richness of exuviae, and were always fully or partially surrounded by buffer strips. Ponds lacking vegetation were turbid, yielding no exuviae even if they were buffered. English agri-environment schemes (AES) currently support pond and buffer strip creation and management.

4. Abundance of exuviae was higher in recently created ponds compared to older ponds, whereas ponds that had dried out the previous summer had fewer exuviae.

5. Species richness of exuviae decreased with increasing distance to the nearest viable pond, falling by more than 40% for distances over 100 m.

6. We conclude that odonate conservation would be more effective if AES would consider the spatial scale at which ponds are created and the location, type, and quality of ponds targeted for buffer strips.

Key words. Agricultural landscapes, buffer strips, exuviae, farmland ponds, freshwater conservation, odonates, pond quality.

Introduction

The overall decline of odonates [dragonflies (Anisoptera) and damselflies (Zygoptera)] in Western Europe correlates well with the post-war uptake of intensive agricultural practices (Corbet & Brooks, 2008). Despite recent increases in range and populations of certain species owing to climate change, of a total of 46 species recorded in Britain, three have become extinct, four are classified as 'endangered', two as 'vulnerable', and six as 'near threatened' (Daguet *et al*., 2008). The main causes of these Western European and British declines are somewhat interrelated but can be attributed mainly to habitat loss and fragmentation, changes in farm management practices (e.g. drainage, neglect, and infilling of ponds) and pollution and eutrophication (e.g. increased use of agrochemicals). Furthermore, the paucity of financial incentives and policy frameworks to create, maintain, or improve waterbodies and the lack of a landscape-scale consideration of aquatic habitats (Declerck *et al*., 2006; Davies *et al*., 2009) are preventing the current situation from improving.

Odonates have a bipartite life cycle, depending both on waterbody quality for growing, emerging, and oviposition during larval and adult stages and on the quality and connec-

Correspondence: Eva M. Raebel, Wildlife Conservation Research Unit, The Recanati-Kaplan Centre, Department of Zoology, University of Oxford, Tubney House, Abingdon Road, Tubney, Oxfordshire OX13 5QL, UK.
E-mail: evamraebel@gmail.com

tivity of terrestrial landscape features for resource use and dispersal during the aerial adult stage. Odonates are thus considered valuable bioindicators for assessing both aquatic and terrestrial aspects of landscape quality (Clark & Samways, 1996; Briers & Biggs, 2003). Furthermore, odonates play predatory and prey roles that influence trophic and biomass cascades across ecosystems (Knight *et al*., 2005; Turner, 2007; McCoy *et al*., 2009).

In Britain, a large proportion of odonate species live in lentic (standing) waters: ponds are the obligate habitat for at least 35% of all species and a secondary biotope for a further 38%. Ponds in Britain have been strongly affected by changes in agricultural practices: there has been an estimated 50% loss during the 20th century (Carey *et al*., 2008), although numbers have increased by 12.4% in the last decade to a current level of ca. 487 000 (Carey *et al*., 2008). Ponds support more plant and macroinvertebrate species than rivers, streams, and ditches (Williams *et al*., 2003; Davies *et al*., 2008). This situation is especially worrying for odonates, as ponds make a higher contribution than other waterbodies to their taxonomic richness and other macroinvertebrates (Biggs *et al*., 2005; Williams *et al*., 2008). Despite this, conservation management has, until recently, focused on lotic (running) waters, while ponds have largely been neglected by policies such as the Water Framework Directive (Cereghino *et al*., 2008). In 2008, 'High Ecological Quality' ponds were added as a priority habitat to the UK Biodiversity Action Plan (UKBAP, 2007). Ponds in lowland Britain are deteriorating and only 8% are in good condition (as determined by aquatic plants: Carey *et al*., 2008).

Policy makers face the challenge of reversing these negative trends by integrating effective conservation measures into the farmed landscape (Scherr & McNeely, 2008). Agri-environment schemes (AES) are the main instrument introduced in the late 1980s by the European Union (EU) agricultural policy to achieve this, by providing financial support for farmers and land managers to improve environmental quality (Natural England, 2009a). AES were optional until 1992, when European regulation required all EU members to apply agri-environment measures (European Commission, 2011). Environmental Stewardship (ES), the current AES in England, opened for applications in 2005, aiming to conserve, enhance, and promote sustainable agriculture to deliver farmland biodiversity, *inter alia* (Natural England, 2009a). Some of the options within ES address pond management: both conventional and organic Entry Level Stewardship (ELS and OELS, respectively) encourage pollution mitigation and restrict cattle access through buffer strips (Natural England, 2010a,b) and/or fencing (Natural England, 2009b,c), and Higher Level Stewardship (HLS) provides payments for maintenance and creation of ponds of 'high wildlife value' (Natural England, 2010c). European AES have shown a mixture of effects depending on taxa (Kleijn & Sutherland, 2003), and recent studies have reinforced the need for targeted, landscape-scale AES approaches (e.g. Rundlöf *et al*., 2008; Davies *et al*., 2009; Marini *et al*., 2009; Merckx *et al*., 2009). The extent to which these options are benefitting odonates is not known.

Guidelines for the creation of good-quality ponds (Pond Conservation, 2010) and for ponds targeting odonates (British Dragonfly Society, 2011) focus on various pond parameters believed to be important for sustaining and enhancing pond biodiversity.

These guidelines are derived from several studies which have detected correlations between variables of lentic waterbodies and species/numbers of odonate adults/larvae. For example, higher odonate numbers were correlated with greater macrophyte coverage (Carchini *et al*., 2007) and abundance of other macroinvertebrates (Foote & Hornung, 2005); conversely, odonate numbers and species richness were lower with increased turbidity (D'Amico *et al*., 2004), nutrient loads (Carchini *et al*., 2007), and cattle grazing (Foote & Hornung, 2005). Either positive or negative relationships were found, depending on specific species, with shade, reed cover, bank height (Steytler & Samways, 1995; Hofmann & Mason, 2005), presence of fish (Morin, 1984), pond size, and pond age (Kadoya *et al*., 2004). However, many of these studies have been based on either small sample sizes, single species or macroinvertebrates as a whole, a limited number of abiotic variables, or presence of adults or larvae only (neither of which provide definitive evidence of breeding odonate populations).

Our study is, we believe, the first to take a landscape-scale approach to assess which pond parameters most influence species richness and abundance of odonates, and whether current AES measures are likely to sustain pond quality and benefit odonate populations. We surveyed farmland ponds in four study areas within a lowland agriculture catchment in England [agricultural land currently covers 76% of the UK (FAOSTAT, 2009)] and used the Information Theoretic (IT) approach to consider which of a range of local (a)biotic variables (and interactions) best explained observed differences in odonate abundance and species richness. Unlike other studies, extensive surveys of exuviae (discarded larval casings) were conducted to assess abundance and species richness of odonates in farmland ponds. Only the presence of exuviae proves life cycle completion; data obtained with exuvial survey methods do not correlate with data on adults (Raebel *et al*., 2010). The few studies that have used exuviae to assess habitat quality conducted surveys only at specific or small-scale locations, or during one emergence season, or only from the pond bankside (Chovanec & Raab, 1997; D'Amico *et al*., 2004; Gaines, 2006; Hardersen, 2008).

Materials and methods

Study sites

A sample of 29 farmland ponds (size range: 23–1452 m^2) was randomly selected, in regard to size and location, within four discrete areas of the River Ray catchment (Buckinghamshire and Oxfordshire, UK). The Ray is a catchment of alkaline waters, comprising ca. 283 km^2 of lowland agricultural land, with clay as the main top substrate, and located in a Nitrate Vulnerable Zone (Defra, 2009a). This region is typical of lowland England. Odonate presence/absence was unknown, so pond selection was unbiased with regard to species occurrence. As odonates do not occupy completely tree-shaded ponds, the only selection requirement was that ponds were not surrounded by trees on their entirety.

Data collection

Odonata. Exuviae were collected in each of 3 years: from May to September in 2006 and 2008 and from June to September in 2007. Possible effects of the absence of data for May 2007 include underestimating abundance for early species, but this was minimised by surveying same ponds on the previous and following years. Each pond was visited at least four times in a 3-week rotation each year to allow for species turnover and to maximise sampling effort. Although sampling every 3 weeks would allow for assessing all species at a pond, we acknowledge the limitations in terms of abundance of sampling every 3 weeks, as some exuviae were probably lost in between surveys. However, we aimed to obtain every exuvia present by searching the following habitats: (i) emergent within-pond vegetation; (ii) emergent bank vegetation; and (iii) vegetation and ground within 1.5 m of the bank. Emergent vegetation was searched by wading throughout every accessible area of the pond. Bramble patches were not searched, as odonates avoid them for emergence (E. M. Raebel, pers. obs.). Unrestricted time-wise, we collected and counted all exuviae per pond for each survey visit. This quantitatively precise approach is better than approaches with limited search periods as the latter may not always differentiate between ponds characterised by large, but different, population sizes. Exuviae were identified to species level, using a microscope for Zygoptera and Sympetrum individuals (Hammond, 1983; Miller, 1995; Brooks & Lewington, 1997; Cham, 2007).

Ponds. Ten (a)biotic variables (Table 1) were recorded at three visits for all ponds, for each of the three study years. Variables were chosen because of their biological and current AES relevance, and it was decided that pond managers should be able to test parameters in the future without the need of electronic equipment. It was therefore decided that the vegetation community of a pond would be a good reflection of its water quality, and hence, large chemical analysis was avoided. Water level variation between May and September was recorded as the difference between maximum and minimum percentage water area. Percentage water area was in turn measured at each visit as the percentage of the total pond area (at winter maximum) covered by water (Biggs *et al*., 1998). This variation was relevant to odonates in Britain, which emerge and oviposit in spring and summer only. Transparency (of water > 0.5 m away from the margin) was recorded by visual assessment using a scale of 1 (best) to 4 (total turbidity), hence avoiding the use of equipment whose measures were being affected by the shallowness of most banks. For every pond, the median was calculated for each year. Pond age (years) was obtained after discussion with landowners in 2006 and using maps. We also ascertained (from discussion in 2006, and by visual field assessment in the following years) whether ponds had dried out. We then had information to determine whether the pond had dried out in the previous year, as this variable was considered more important than recording dryness during the current year, owing to the effect on species with a life cycle longer than 1 year. We recorded presence/absence/partial presence of a buffer, defined as an unfertilised grass strip ≥2 m around a pond [Natural England, 2010a; cross-compliance (Defra, 2009b)]. Full/partial buffers refer to buffers surrounding the entire/partial pond perimeter. Cattle trampling intensity was recorded as zero/low/high. Percentage cover of deciduous trees over land within 5 m of the pond edge – an indicator of shade and potential roosting sites – was recorded. Data on fish and amphibian species were collected by visual assessment, pond dipping with a net, egg searching, and landowner information. Aquatic plants were identified twice during each of the three field seasons for any case over 5% pond cover within the outer edge (upper level of water in winter) of a pond. Vegetation records were based on percentage cover of major structural types of plant groups of submerged, floating-leaved and emergent macrophytes and were classified into seven distinct vegetation types depending on dominant structure (Table 2). Distances between ponds and nearest viable pond (defined as distance in metres to the nearest pond with exuviae being present) were calculated using GIS (ArcGIS 9.2) and converted into four distance classes as to be able to set up spatial scale cut-off points.

Analysis

For each pond, and for each of the three consecutive years, we totalled the number of individual exuviae and the number of species recorded. Values of both abundance and species richness

Table 1. Description of the 10 biotic and abiotic variables used to classify each pond. See text for details.

Variable	Description
Pond age	Pond created ≤3 years ago or > 3 years ago
Water area variation	Yearly variation in water surface area; 4 classes: 0–10%; 10–20%; 20–50%; > 50%
Buffer	Unmown, grassy, ≥2 m wide margin; 3 classes: absent; partially surrounding; fully surrounding
Cattle	Cattle trampling intensity; 3 classes: zero; low; high
Distance	Distance to nearest viable pond; 5 classes: 0–100 m; 100–200 m; 200–300 m; 300–400 m; > 400 m
Dry	Pond did or did not dry out the summer before sampling
Fish	Fish present vs. absent
Transparency	Water transparency; 4 classes: transparent > 0.5 m from bank; transparent on shallow bank only; low turbidity; high turbidity
Trees	Percentage of deciduous trees within an area of 5 m around the pond; 7 classes: 0–5%; 5–10%; 10–30%; 30–40%; 40–50%; 50–70%; > 70%
Vegetation type	Pond vegetation type; 7 classes: see Table 2

Table 2. Pond vegetation types and respective overall odonate abundance (N) and species richness (S). Vegetation types are based on the presence of major plant groups and their relative abundance: Dominant (D: >35%); Abundant (A: 25–35%); Frequent (F: 10–25%); Occasional (O: <10%).

Type	Species composition and structure	N ± SE	S ± SE
Callitriche	*Callitriche* spp. (F); other spp. (O)	147.8 ± 82.1	5.0 ± 0.7
Emergent dicotyledonous	Emergent dicotyledonous: *Rorippa nasturtium-aquaticum, Apium nodiflorum, Veronica beccabunga, Mentha aquatica* (D); *Sparganium erectum* (A); *Alisma plantago-aquatica*, *Typha* spp. (O). (Ponds dried out at least once)	5.9 ± 3.5	0.7 ± 0.2
Floating	Floating spp. (*Potamogeton natans*) (D); emergent spp.: *Myosotis scorpioides, R. nasturtium-aquaticum, Typha* spp., *Callitriche* spp., *Nymphaea* spp. (A); *Lemna* spp. (F); Blanket weed, *Ceratophyllum demersum* (O)	278.2 ± 90.5	6.6 ± 0.6
Floating and submerged	Submerged spp. (e.g. *C. demersum*, *Elodea* spp.) (D); Blanket weed (A); floating vegetation: *P. natans* (D); *Typha*, *Callitriche* spp., *Nymphaea* spp., *M. scorpioides* (F); *Lemna* spp. (O)	466.0 ± 170.6	9.7 ± 0.6
Glyceria	*Glyceria fluitans*, *Typha* spp. (D); *S. erectum* (A); *Lemna* spp. (O)	54.8 ± 18.5	2.3 ± 1.6
Lemna	Any vegetation type with *Lemna* spp. (D)	39.1 ± 18.9	3.2 ± 0.7
Limited/absent vegetation	Floating and submerged spp. absent. Limited representation of species on marginal zone [*Callitriche* spp. (O)]	0.0 ± 0.0	0.0 ± 0.0

per pond were $\log_{10}$-transformed. Analysis was not performed for individual species as not many single species were present at enough ponds for this type of analysis. In addition, our approach was meant to be general and complementary and aimed to give general insights valuable for AES, as general agreements (ELS) aim to increase overall biodiversity rather than specific species. The IT approach (Burnham & Anderson, 2002) was used to compare a large set ($N = 1081$) of biologically plausible models that captured key elements of the system under study. This approach aspires to find the best of a suite of models, with the fewest parameters necessary (Johnson & Omland, 2004). The models were generalised linear models that contrast the effects of 10 class variables (i.e. fixed effects) on both abundance and species richness of exuviae in ponds. All possible combinations of these fixed effects give a total of 1023 different models. An additional set of models included biologically plausible two-way interactions of the variables 'age' and 'vegetation type' with all other variables. The variable 'year' was included as a categorical blocking variable in all models as study years could not be selected at random. The variable 'pond' (29 classes) was nested within 'area' (four classes), together with within-pond variables that did not change over the 3 years: 'buffer' (three classes), 'fish' (two classes), and 'distance to viable pond' (five classes). The minimum adequate model was selected using Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2002), and we determined Akaike's weights of evidence for each model given the other models considered. Using the COMPMIX macro (RD Wolfinger; SAS 9.1), the models were ranked from lowest to highest AICc. For each model i, the difference in AICc values between a model and the best model (Δi) was calculated. Models with $\Delta i > 7$ (abundance) and $\Delta i > 9$ (richness) were not retained in the final set of models as these high Δi values indicate a poor fit compared to the best model (Burnham & Anderson, 2002). These cut-off values corresponded with a 90% cumulative weight for each final set of models (abundance and richness). Model-averaging for these final sets of models is recommended to reduce bias that would arise if results were based on just one model (Burnham & Anderson, 2002; Johnson & Omland, 2004). We averaged the estimated coefficients of each explanatory variable (and for each class) for all models containing that variable and weighted this average in relation to the weight of each model as calculated by the AICc procedure. We then calculated the model-averaged estimates and the unconditional SE using a 95% confidence interval, both for abundance and species richness and for single variables as well as interactions. *A posteriori*, mixed models that included high weight variables (i.e. vegetation type, age, and buffer) were run, separately for each buffer level, to explain relevant interactions.

Results

A total of 11 025 exuviae were collected (2006: 3316; 2007: 2325; 2008: 5384), consisting of seven species of Zygoptera and nine species of Anisoptera. Abundance varied substantially between species (Table 3). Minimum and maximum numbers of species per pond were 0 and 12, respectively. The species found were all generalists that are widespread in south-east England; none is of conservation concern at the national level.

Abundance

Overall, ponds with floating and submerged vegetation supported the largest number of exuviae, followed by ponds of the floating vegetation and *Callitriche* types (Tables 2 and 4). Ponds with limited/absent vegetation had the lowest numbers of exuviae, as did ponds with emergent dicotyledonous plants only (Tables 2 and 4). Recently created ponds were characterised by higher exuviae abundance than older ponds (Table 4). Exuviae abundance decreased with pond turbidity (Fig. 1), and especially so for older ponds (Table 5). Ponds that dried out the summer before sampling contained fewer exuviae than ponds that retained water the whole year through

Table 3. Numbers of exuviae, totalled over 3 years, for each of the recorded odonate species.

Family	Species	Scientific name	*N*
Coenagrionidae	Azure Damselfly	*Coenagrion puella*	4232
Coenagrionidae	Common Blue Damselfly	*Enallagma cyathigerum*	543
Coenagrionidae	Red-eyed Damselfly	*Erythromma najas*	91
Coenagrionidae	Small Red-eyed Damselfly	*Erythromma viridulum*	25
Coenagrionidae	Blue-tailed Damselfly	*Ischnura elegans*	1415
Coenagrionidae	Large Red Damselfly	*Pyrrhosoma nymphula*	1192
Lestidae	Emerald Damselfly	*Lestes sponsa*	5
Aeshnidae	Emperor Dragonfly	*Anax imperator*	367
Aeshnidae	Southern Hawker	*Aeshna cyanea*	383
Aeshnidae	Brown Hawker	*Aeshna grandis*	10
Aeshnidae	Migrant Hawker	*Aeshna mixta*	53
Libellulidae	Broad-bodied Chaser	*Libellula depressa*	42
Libellulidae	Four-spotted Chaser	*Libellula quadrimaculata*	124
Libellulidae	Black-tailed Skimmer	*Orthetrum cancellatum*	1
Libellulidae	Ruddy Darter	*Sympetrum sanguineum*	508
Libellulidae	Common Darter	*Sympetrum striolatum*	2034

Table 4. Final model-averaged estimates, unconditional standard errors (SE) and 95% upper and lower limits of each estimate for odonate abundance and species richness for each single parameter of the best set of models (90% cumulative weight) as ranked by Akaike's Information Criterion (vegtype refers to vegetation type).

		Abundance				Species richness			
Single variables/class		Average estimate	SE	95% lower	95% upper	Average estimate	SE	95% lower	95% upper
Pond age < 3 years	1	0.729	0.484	1.678	−0.221	−0.112	0.108	−0.324	0.101
Pond age > 3 years	2	0	0	0	0	0	0	0	0
Water area variation	1	−0.026	0.029	0.030	−0.083	−0.001	0.001	−0.004	0.002
Water area variation	2	−0.004	0.012	0.019	−0.027	0	0.001	−0.001	0.002
Water area variation	3	−0.018	0.021	0.022	−0.059	−0.001	0.001	−0.003	0.001
Water area variation	4	0	0	0	0	0	0	0	0
Buffer: absent	0	−0.038	0.046	0.051	−0.128	−0.006	0.007	−0.020	0.008
Buffer: partial	1	0.040	0.051	0.141	−0.060	0.003	0.006	−0.009	0.016
Buffer: full	2	0	0	0	0	0	0	0	0
Distance: 0–100	1	–	–	–	–	0.027	0.027	−0.025	0.080
Distance: 100–200	2	–	–	–	–	0.008	0.010	−0.012	0.028
Distance: 200–300	3	–	–	–	–	0.003	0.009	−0.013	0.020
Distance: 300–400	4	–	–	–	–	−0.009	0.011	−0.031	0.014
Distance: > 400	5	–	–	–	–	0	0	0	0
Dried: no	0	0.177	0.146	0.462	−0.108	0.010	0.011	−0.012	0.033
Dried: yes	1	0	0	0	0	0	0	0	0
Fish: preset	0	0.011	0.021	0.053	−0.030	0.001	0.002	−0.003	0.005
Fish: absent	1	0	0	0	0	0	0	0	0
Transparency: > 0.5 m	1	0.601	0.325	1.238	−0.035	0.027	0.026	−0.025	0.079
Transparency: shallow	2	0.402	0.243	0.879	−0.075	0.020	0.021	−0.020	0.061
Transparency: low turbidity	3	0.203	0.150	0.497	−0.091	0.015	0.015	−0.015	0.044
Transparency: very turbid	4	0	0	0	0	0	0	0	0
Vegtype: limited/absent	1	−0.673	0.212	−0.257	−1.088	−0.638	0.157	−0.946	−0.330
Vegtype: emergent dicots	2	−0.592	0.278	−0.046	−1.137	−0.423	0.138	−0.694	−0.152
Vegtype: floating	3	0.318	0.246	0.799	−0.164	0.128	0.092	−0.053	0.309
Vegtype: glyceria	4	0.006	0.475	0.937	−0.925	−0.311	0.138	−0.581	−0.041
Vegtype: floating/submerged	5	0.747	0.387	1.505	−0.011	0.244	0.112	0.025	0.463
Vegtype: callitriche	6	0.522	0.267	1.044	−0.001	−0.174	0.148	−0.464	0.116
Vegtype: lemna	7	0	0	0	0	0	0	0	0

(Table 4). There were no differences in exuviae abundance depending on water area variation, presence/absence of fish or buffer (Tables 4 and 5).

The most-supported model had a relatively low Akaike weight (0.25), indicating uncertainty in relation to alternative models and hence encouraging the use of model-averaging. The

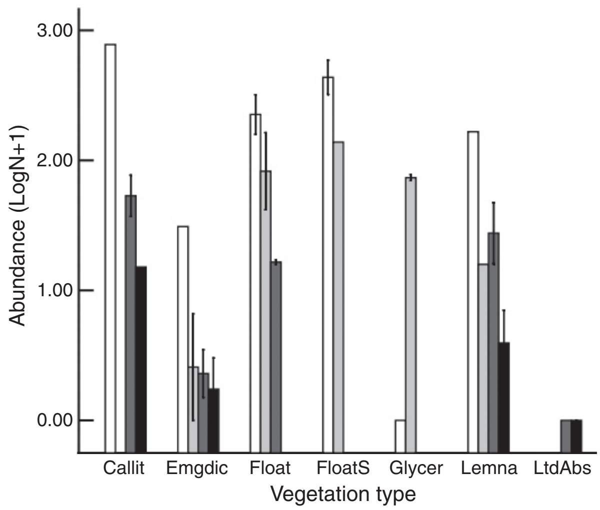

Fig. 1. Effect of pond transparency and vegetation type on odonate abundance (±SE) ($\log_{10}$). Bar colours refer to transparency levels, from white (highly transparent) to black (highly turbid). See Tables 1 and 2 for description of transparency levels and vegetation types.

top-ranked model was closely followed by two other well-supported models ($\Delta i < 2$). These three best-fitting models accounted for a cumulative weight of 47%, and they shared a consistent and identical set of variables: pond vegetation type, water transparency, and pond age; therefore, it was decided not to decrease the number of models in the study. There were additional variables to this core set: pond age × transparency and pond age × vegetation type in the best and third model; 'dry' in the second-best model; and vegetation type × transparency in the third-best model.

In total, 23 models had a $\Delta i \leq 7$, which accounted for 90% cumulative weight (see Materials and methods). Six of the nine predictor variables were present in this final set of models.

Cattle, tree cover and distance from nearest viable pond were not included. Vegetation type was included in all models, and the high sum of Akaike weights for this variable ($\Sigma W_i = 0.90$) indicated that vegetation type was the most important variable explaining abundance of exuviae. Additional variables and interactions that explained variation in abundance of exuviae in farmland ponds included: pond age ($\Sigma W_i = 0.70$), transparency ($\Sigma W_i = 0.52$), pond age × transparency ($\Sigma W_i = 0.37$), and 'dry' ($\Sigma W_i = 0.35$) (Fig. 2).

Species richness

Ponds with limited/absent vegetation had zero species richness, independent of buffer presence (full buffer: -0.75 ± 0.14, t-value$_{26} = -5.42$, $P < 0.0001$; partial buffer: -0.69 ± 0.17, t-value$_{4} = -4.11$, $P = 0.01$; absent buffer: -0.26 ± 0.04, t-value$_{18} = -5.27$, $P < 0.0001$) (Table 5). Similarly, ponds with emergent dicots only had low species richness, regardless of buffer presence (full buffer: -0.49 ± 0.17, t-value$_{26} = -2.92$, $P = 0.007$; absent buffer: -0.26 ± 0.07, t-value$_{18} = -3.71$, $P = 0.002$) (Table 5). Ponds with floating vegetation always had high levels of species richness, even in the absence of buffers (absent buffer: 0.46 ± 0.07, t-value$_{18} = 6.66$, $P < 0.0001$) (Table 5). 'Floating/submerged' and 'Glyceria' ponds were all characterised by a full buffer (Fig. 3). There was a trend for ponds with full buffers to result in lower species richness of exuviae when being recently created (-0.20 ± 0.14; t-value$_{26} = -1.48$; $P = 0.15$) (there were no recently created ponds without buffers). Ponds within a distance of 100 m from a viable pond had slightly higher species richness than those further away (Table 4). There were no differences in exuviae species richness depending on transparency, water area variation, and presence/absence of fish.

The top-ranked model had a relatively low Akaike weight (0.26), which encouraged model-averaging, and was followed closely by another well-supported model ($\Delta i < 2$). These two models accounted for a cumulative weight of 50%, and they shared an identical set of three main effects (pond age, vegetation type, and buffer) and one interaction effect (buffer × vegetation type). Additional variables to this core set, both within the best model, were pond age × buffer and pond age × vegetation type. The final set of models, with a cumulative weight of 90% ($\Delta i \leq 9$) (see Materials and methods), included 21 models in total. Seven of the nine predictor variables were present in this final set of models, with cattle and tree cover absent. Vegetation type was included in all models, and with a ΣW_i of 0.90, indicating that vegetation type was the most important variable explaining the observed variation in species richness of exuviae among farm ponds (Fig. 2). Additional variables and interactions were ranked as follows: pond age ($\Sigma W_i = 0.78$), buffer × vegetation type ($\Sigma W_i = 0.77$), and pond age × vegetation type ($\Sigma W_i = 0.30$) (Tables 3 and 4; Fig. 2).

Discussion

Vegetation and transparency

Vegetation type and amount clearly affected odonate abundance and species richness.

These findings support other studies showing that aquatic vegetation increases odonate abundance and diversity by providing refuges from predators (Thompson, 1987; Braccia *et al.*, 2007), promoting macroinvertebrate presence (i.e. prey) (Foote & Hornung, 2005), acting as a habitat selection cue (Wildermuth, 1992), and encouraging oviposition for endophytic species (Corbet, 1999).

Pond transparency increased overall odonate abundance (Fig. 1). This may be due to better water quality (D'Amico *et al.*, 2004), with the most transparent ponds being characterised by the presence of submerged and floating plants, which provide resources for odonates and their prey. Transparency has also been linked to low levels of suspended sediment/algae, and therefore to low pollution conditions, although clouded ponds sometimes occur under low pollution (Williams *et al.*, 1999). Nonetheless, highly transparent ponds did not necessarily imply high odonate abundance. For instance, we showed that ponds that did not retain water

Table 5. Final model-averaged estimates, unconditional standard errors (SE) and 95% upper and lower limits of each estimate for odonate abundance and species richness for each interaction of the best set of models as ranked by Akaike's Information Criterion (vegtype refers to vegetation type).

		Abundance				Species richness			
Interaction/class		Average estimate	SE	95% lower	95% upper	Average estimate	SE	95% lower	95% upper
Pond age × transparency	1 × 1	−0.030	0.206	0.373	−0.433	0.000	0.001	−0.003	0.002
Pond age × transparency	1 × 2	−0.286	0.296	0.295	−0.867	−0.002	0.002	−0.006	0.002
Pond age × transparency	1 × 3	0	0	0	0	0	0	0	0
Pond age × transparency	2 × 1	0.305	0.235	0.766	−0.157	0.001	0.001	−0.001	0.004
Pond age × transparency	2 × 2	0.210	0.169	0.542	−0.122	0.001	0.001	−0.001	0.003
Pond age × transparency	2 × 3	0.089	0.086	0.257	−0.080	0.001	0.001	−0.001	0.002
Pond age × transparency	2 × 4	0	0	0	0	0	0	0	0
Transparency × vegtype	1 × 2	0.141	0.142	0.419	−0.137	–	–	–	–
Transparency × vegtype	1 × 3	0.138	0.126	0.386	−0.110	–	–	–	–
Transparency × vegtype	1 × 4	−0.230	0.213	0.187	−0.647	–	–	–	–
Transparency × vegtype	1 × 5	0.048	0.075	0.194	−0.099	–	–	–	–
Transparency × vegtype	1 × 6	0.085	0.128	0.336	−0.165	–	–	–	–
Transparency × vegtype	1 × 7	0.193	0.181	0.548	−0.161	–	–	–	–
Transparency × vegtype	2 × 2	0.019	0.054	0.124	−0.086	–	–	–	–
Transparency × vegtype	2 × 3	0.077	0.076	0.227	−0.072	–	–	–	–
Transparency × vegtype	2 × 7	0.068	0.085	0.234	−0.099	–	–	–	–
Transparency × vegtype	3 × 1	0.010	0.058	0.124	−0.104	–	–	–	–
Transparency × vegtype	3 × 2	0.015	0.053	0.119	−0.090	–	–	–	–
Transparency × vegtype	3 × 6	0.069	0.089	0.238	−0.099	–	–	–	–
Transparency × vegtype	3 × 7	0.075	0.075	0.221	−0.072	–	–	–	–
Pond age × vegtype	1 × 3	−0.014	0.017	0.019	−0.047	−0.016	0.018	−0.051	0.020
Pond age × vegtype	2 × 3	0	0	0	0	0	0	0	0
Pond age × vegtype	1 × 6	–	–	–	–	−0.039	0.093	−0.222	0.144
Pond age × vegtype	2 × 6	–	–	–	–	0	0	0	0
Buffer × pond age	1 × 1	–	–	–	–	0.078	0.075	−0.070	0.225
Buffer × pond age	2 × 1	–	–	–	–	0	0	0	0
Buffer × vegtype	0 × 1	–	–	–	–	0.000	0.063	−0.124	0.124
Buffer × vegtype	0 × 2	–	–	–	–	−0.200	0.116	−0.428	0.028
Buffer × vegtype	0 × 3	–	–	–	–	−0.123	0.087	−0.294	0.048
Buffer × vegtype	0 × 6	–	–	–	–	0.249	0.121	0.011	0.487
Buffer × vegtype	0 × 7	–	–	–	–	−0.384	0.123	−0.624	−0.144
Buffer × vegtype	1 × 1	–	–	–	–	0.000	0.093	−0.182	0.182
Buffer × vegtype	1 × 2	–	–	–	–	0.032	0.107	−0.178	0.242
Buffer × vegtype	1 × 6	–	–	–	–	0.277	0.133	0.017	0.538
Buffer × vegtype	1 × 7	–	–	–	–	−0.027	0.112	−0.247	0.192
Buffer × vegtype	2 × 1	–	–	–	–	0	0	0	0
Buffer × vegtype	2 × 2	–	–	–	–	0	0	0	0
Buffer × vegtype	2 × 3	–	–	–	–	0	0	0	0
Buffer × vegtype	2 × 6	–	–	–	–	0	0	0	0
Buffer × vegtype	2 × 7	–	–	–	–	0	0	0	0

throughout the year had lower abundance of exuviae, regardless of water quality/transparency. For example, one of the highly transparent ponds, characterised by *Glyceria fluitans*, yielded semivoltine *Aeshna cyanea* exuviae in 2006 ($N = 81$) and in 2008 ($N = 66$), but produced no exuviae in 2007. This species has a 2-year cycle, and the absence of exuviae can be explained by the pond drying out in late summer 2006, probably killing all 1-year-old larvae. Similarly, ponds characterised by emergent dicotyledonous plants had very low species richness and abundance of exuviae, probably as a result of all drying out in at least one of the seasons, increasing mortality for species ovipositing before the drought events.

The lack of aquatic vegetation and exuviae in turbid ponds supports previous studies showing turbidity to reduce adult abundance as well as exuviae abundance (D'Amico *et al*., 2004) (Fig. 1). The mechanism is partly that high turbidity results in low photosynthetic activity, resulting in less vegetation and fewer associated prey, and also that high turbidity directly affects some odonate species, particularly those whose larvae rely on visual stimuli to forage (Corbet, 1999).

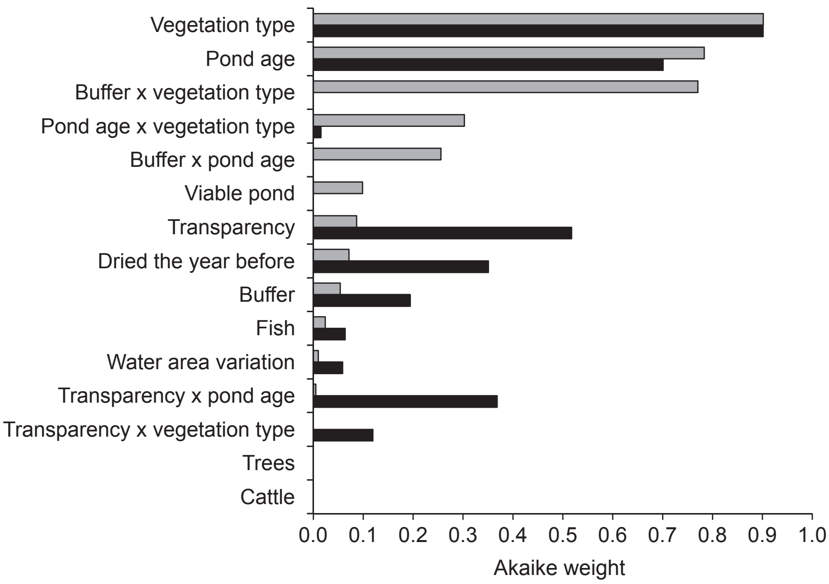

Fig. 2. Ranking (cumulative Akaike weights) of pond variables included in final set of models (90% cumulative weight) in line with their ability to explain the variation in exuviae species richness (grey bars) and abundance (black bars) among farmland ponds.

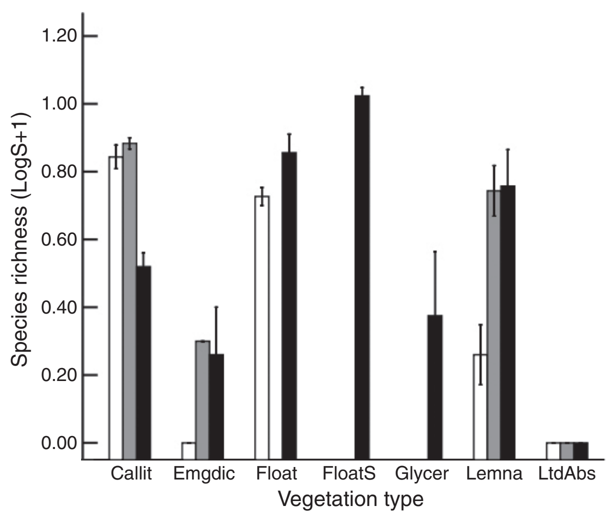

Fig. 3. Effect of pond buffers and vegetation type on odonate species richness (±SE) ($\log_{10}$). Bar colours refer to ponds with no buffer (white), partial buffer (grey), and full buffer (black). See Table 2 for description of vegetation types.

Vegetation and buffers

Ponds with submerged and floating vegetation, and 'Glyceria' ponds, were always fully buffered. This suggests that ponds with these vegetation characteristics are more likely to have been subjected to AES management by buffering and that buffers encourage these vegetation types, which supported the highest levels of odonate species richness and abundance. In general, buffer presence increased overall odonate species richness but did not affect abundance, suggesting that the latter mainly depends on other factors. Buffers provide roosting resources for larvae and adults (Rouquette & Thompson, 2007) and increase water quality by reducing surface run-off (Lovell & Sullivan, 2007).

The overall positive effect of buffers on odonate species richness, however, only applied to ponds with certain vegetation types; ponds that mainly lacked submerged and/or floating macrophytes yielded no exuviae, regardless of buffer presence. Overall, 30% of ponds without exuviae were fully buffered, suggesting that buffers alone are not enough to provide good-quality pond habitats for odonates.

Pond creation: age and nearest viable pond

Recently created ponds (< 3 years) had almost eight times more exuviae than older ponds, but lower species richness. As opposed to macroinvertebrates with an entirely aquatic life cycle, adult odonates can disperse rapidly to other ponds, regardless of pond habitat quality (Raebel *et al*., 2010). Our data show that exuviae of early colonising, univoltine species were already present in the second year after pond creation, and semi-voltine species appeared in the third year. It has already been noted that abundance of certain species (e.g. *Anax imperator*) can be greatest directly after colonisation (Brooks & Lewington, 1997) and then levels off, probably due to increased intra- and inter-specific competition (Moore, 1991), allowing for non-pioneer species to settle at ponds at later seral stages.

Our study showed that species richness decreased with increasing distance from the nearest viable pond. Whereas inter-pond distances < 100 m correlate with relatively high species richness, this level strongly drops (−40%) when distances between viable ponds exceed 100 m, and gradually decreases further with increasing distances. These findings should be taken into account during pond creation planning, especially because poor-disperser species will benefit from pond proximity. Although some odonates are clearly able to disperse large distances, here we demonstrate that there is a need to conduct pond and odonate conservation at a functional spatial scale, where ponds may act as 'stepping stones' to sustain local (meta)populations.

Fish and cattle

Odonates were present in ponds with predators (fish and amphibians), showing that odonates can indeed coexist with predators, at least in high-quality ponds; indeed, there was no overall effect of fish on odonate species richness and abundance. In lentic waters with stable populations of top predators (i.e. fish), dispersal costs for odonates are larger than the costs associated with remaining in the natal pond, as dispersal is associated with an increased mortality risk and decreased mating opportunity (McPeek, 1998). Also, Wittwer *et al*. (2010) suggest that fish species composition affects odonate community structure, with certain species being positively correlated with specific fish species. Cattle did not appear to affect odonate abundance or species richness, but further investigation would be needed to assess whether there are differential impacts among types of cattle and/or grazing pressure.

Implications for agri-environment schemes

Agri-environment schemes payments for buffers created indiscriminately across the landscape, without targeting the most effective locations (Davies *et al*., 2009) and without encouraging long-term sustainability of other interacting variables (e.g. vegetation, low fertilisers), may not be effective. Buffers that are 7–10 m wide are supported through ELS options. Although ELS recommends expansion of these uncropped areas, financial incentives are not in place to encourage wider buffers, which other studies have shown to be most beneficial (> 25 m: Davies *et al*., 2009; 30 m: Williams *et al*., 1999). In fact, most buffers in this study were only 2 m wide, following cross-compliance requirements (Defra, 2009b). However, given that ponds often have very small catchments (Davies *et al*., 2009), we suggest that better results will not necessarily be achieved by assigning larger and hence more costly buffers, but rather by cleverly positioning buffers, so that only areas minimising run-off are converted into buffer areas (e.g. partial uphill buffers). Although such an approach will be most effective for increasing pond water quality, it needs to be tempered with (i) EC requirements to check cross-compliance in a standardised way, (ii) high administrative costs of targeting, and (iii) acknowledging the limitations imposed by generic written guidance for ELS.

Pond creation is an AES option in the English HLS. Additionally, a Pond Conservation project to create a million ponds in the English countryside within 50 years is ongoing (Pond Conservation, 2010). These frameworks offer an unprecedented opportunity for odonate habitat creation, as we show that creation of good-quality ponds will entail swift colonisation; at the same time, they will provide other biodiversity benefits (Williams *et al*., 2008). However, HLS currently only comprises < 10% of AES agreements (Natural England, 2011). This coincides with European uptakes of basic single schemes [> 40% of the total area covered by AES (Kleijn & Sutherland, 2003)]. Additionally, most farmers opt for margin-related options that are perceived to be easier to undertake. For example, in south-east England, the uptake of pond options within ELS and HLS was low relative to other options (Defra, 2008). In the Upper Thames area, for example, only 4% of agreements ($N = 806$) included a pond option by the end of 2008 (Natural England, unpubl. data). This study strengthens the view that more attention needs to be paid to the benefits that are to be gained from in-field and non-linear landscape features. Surveys of farmers' attitudes in the Upper Thames suggest that 73% of farmers would consider pond creation, and positive attitudes towards pond creation score highly (80% of farmers in favour) (Riordan, 2009). Furthermore, of all landowners that had created ponds, over half were doing so outside AES agreements. We therefore predict a high uptake of pond creation options within HLS if they were to be coupled with appropriate encouragement, advice, and financial incentives.

Conclusions

Ponds with a complex vegetation structure are associated with increased odonate diversity and abundance. Such ponds, mostly transparent, can be maintained in intensive agricultural landscapes, both for new and existing ponds (see also Declerck *et al*., 2006). Our study emphasises that various factors need to be taken into account when planning for effective pond and odonate conservation within AES. Considerable improvements could be obtained by targeting a particular combination of pond options. Important factors are maximised pond-catchment cover by buffers (i.e. low agrochemical input) and encouragement of native submerged/floating vegetation, maintenance of open pond surface areas for ovipositing, and creation and maintenance of a viable pond within close proximity.

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