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Multi-scale effects of farmland management on dragonfly and damselfly assemblages of farmland ponds

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ABSTRACT

Agricultural intensification has contributed to severe declines in odonate (dragonfly and damselfly) populations. Odonates require healthy waterbodies for their larval stages and resource-rich terrestrial landscapes as adults. As such, farmland management at both local and larger landscape scales may be needed to reverse population declines.

We sampled odonate adults and exuviae from lowland farmland ponds in England, to investigate relationships between odonate species richness and surrounding land-use. The more mobile dragonflies (Anisoptera) were influenced most strongly by landscape variables at the largest scale (i.e. 1600 m radius), while less mobile damselflies (Zygoptera) were affected by variables at more local scales (i.e. 100/400 m radii). A greater number of landscape variables affected exuvial species richness compared to adult species richness. Exuvial species richness was higher when 2 m wide cross-compliance buffer strips around ponds were present. However, no ponds in the study had buffer strips that were established through England's basic agri-environment scheme (Entry Level Scheme: ELS) agreements, and we observed a negative relationship between ELS area and exuvial species richness. Exuvial species richness increased with the amount of water, but not the number of ponds, in the landscape surrounding a focal pond. The observed odonate responses to local and surrounding land-use lend support to the development of agri-environment scheme policies that encourage landscape-scale, as well as local, scheme implementation and management. We predict that both landscape-scale and quality-targeted management of farmland ponds would benefit odonates, irrespective of mobility level and life-stage.

1. Introduction

The escalating worldwide demand for agricultural products is having a detrimental effect on biodiversity (Scherr and McNeely, 2008). In an attempt to reverse environmental degradation, most European countries have introduced agri-environment schemes (AES), which are considered the most realistic policy-tool to integrate biodiversity with economically sustainable production systems (Vickery et al., 2004; Scherr and McNeely, 2008), although their effectiveness remains uncertain (e.g. Kleijn et al., 2011).

In Britain, farmland covers 76% of the land area (FAOSTAT, 2009). Post-war agricultural intensification has resulted in habitat loss and fragmentation, reducing habitat connectivity. This, together with more intensive farm management practices and increased pollution and eutrophication, contributed to the extinction of three species of Odonata in the 1950s (British Dragonfly Society, 2010). Out of 40 native British odonate species, four are currently classified as 'Endangered' and two as 'Vulnerable' (Daguet et al., 2008). Odonates are also declining worldwide (Clausnitzer et al., 2009). Of 137 native European species, 15% are threatened and 24% are declining. Deterioration of the farmland biotope has been implicated in their declines (IUCN, 2010; Kalkman et al., 2010).

Ponds are the obligate habitat for at least 35% of British odonate species and secondary habitat for a further 38%. However, 50% of UK farmland ponds have been lost over the past century and only 8% of the remaining ca. 482,000 ponds are of good quality (Carey et al., 2008). Although ponds are still widespread, and regionally sustain the highest levels of aquatic biodiversity compared to other waterbodies (Williams et al., 2003), there is a paucity of financial incentives and policy frameworks to create, maintain or improve

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them. For example, ponds are not considered in the Water Framework Directive (Davies et al., 2008a).

Odonates are effective bio-indicators of both aquatic and terrestrial habitats and, therefore, of agricultural land, including farmland ponds (Clark and Samways, 1996; Briers and Biggs, 2003). Odonates have a bipartite life-cycle: at a local scale they depend on healthy waterbodies for growth and emergence during their larval stages, and egg deposition during their adult stages, and at a larger scale adults depend on the quality of the terrestrial landscape for dispersal, feeding and roosting (Corbet, 1999). As a result, the presence of odonates at ponds not only reflects pond quality but also reflects the quality of the surrounding farmed landscape, and a failure to consider aquatic habitats at the landscape-scale has exacerbated odonate declines (Declerk et al., 2006; Thompson and Watts, 2006). Ponds need to be considered within the landscape matrix (the ‘pondscape’: Boothby, 1997) as odonates benefit from shorter distances between ponds (Sherratt et al., 1999).

Dispersal is a fundamental aspect of the odonate life-cycle: after emergence, tenerals (immature adults) will move away from the waterbody to mature, forage and roost (Corbet, 1999). Movements between roosts and ponds will occur daily, while dispersal to other waterbodies will typically occur less often. Species size affects dispersal: the larger dragonflies will typically disperse longer distances in search of new resource patches, while the more slender damselflies tend to remain near the natal pond (Banks and Thompson, 1985; Conrad et al., 1999). Consequently, the pond's surrounding land-use may affect damselfly and dragonfly dispersal in different ways (Samways and Steytler, 1996).

Agri-environment schemes (AES) were launched in the UK in 1987 (Table S1 in Supplementary Information). They all include some pond-specific options that could potentially benefit odonates, such as buffering in-field ponds in improved grassland or arable land, maintenance of high quality ponds, and pond creation and restoration. Other non-pond options can also be beneficial; for example, areas with lower fertiliser input will have a positive effect on pond quality. Some species may benefit from matrix restoration through AES, particularly species whose ranges or wetland habitats are vulnerable to climate change, species of low mobility and high habitat specificity, and species with fluctuating populations (Donald and Evans, 2006). These features are common to many odonates (Hassall et al., 2007; Allen and Thompson, 2010).

This study presents the results of extensive exuvial (cast-off larval skin at emergence) and adult odonate surveys of farmland ponds in lowland England, in relation to characteristics of the surrounding landscape. The aims of the study were to: (i) identify the scale at which the surrounding landscape influences species richness of odonates most strongly, with the hypothesis that landscape affects dragonflies at a larger scale than damselflies, due to the latter being less mobile; (ii) test if, and at what scale, the presence of other waterbodies increases odonate species richness; (iii) test if some types of land-use and AES surrounding ponds affect odonate species richness; and (iv) suggest recommendations for odonate conservation in intensively farmed lowland landscapes.

2. Methods

2.1. Study sites

Twenty-nine farmland ponds (mean pond area ± SE: 353 ± 63.4 m^2) were randomly selected (with regard to location and size) in the River Ray catchment (Buckinghamshire/Oxfordshire, UK) and were treated separately purely for logistical purposes. The Ray is a 283 km^2 catchment of alkaline waters within lowland agricultural land, with clay as the main top substrate. Pond selection was unbiased with regard to odonate species richness levels, as these were unknown. The only selection requirement was that ponds were not completely surrounded by trees.

2.2. Data collection

2.2.1. Species richness of Odonata: exuviae

Exuviae were collected between May/June and September in 2006, 2007 and 2008. In each year, each pond was visited four times in a three-week rotation to allow for species turnover and to maximise sampling effort. Searching time was dependent on pond size as we aimed to collect every exuvia present by sampling the entire pond on each visit. The following habitats were searched for an unlimited time: emergent bank and within-pond vegetation; and vegetation and ground within 1.5 m from the bank. Vegetation was searched throughout every accessible area of the pond except for bramble (*Rubus* spp.) patches, as odonates avoid them for emergence (E.M. Raebel, pers. obs.). Exuviae were identified to species level in the laboratory, using a microscope for damselflies and *Sympetrum* individuals.

2.2.2. Species richness of Odonata: adults

Surveys of adult odonates were conducted between May/June and September in 2006, 2007 and 2008 on a three-week rotational basis to allow for species turnover during the flight season. These surveys took place on the same days as the exuviae sampling. Individuals were recorded prior to any pond disturbance. No surveys took place during overcast, windy or rainy conditions. Species were recorded by sight (sometimes using close-focus binoculars) whilst walking the accessible parts of the pond perimeter. Damselfly species were also identified in the hand as part of another study (see Raebel et al., 2010).

2.3. Landscape variables

2.3.1. Sampling design

Landscape variables were obtained from the UK's Ordnance Survey (OS) digital database (Centre for Ecology and Hydrology), LandCover 2000 and Defra records (Defra, unpublished data) (see Section 2.3.3). Data were projected within a GIS environment (ArcView 9.2). Landscape composition was overlayed and feature class data extracted at five spatial scales. Each scale was circular, and covered an area with a radius of 100 m, 200 m, 400 m, 800 m and 1600 m (Fig. 1). The maximum radius of 1600 m was chosen to cover for the farthest estimated distance of 1.5 km travelled by some non-territorial damselflies (coenagrionids), as estimated by mark-recapture studies on damselfly dispersal (Rouquette and Thompson, 2007a). Circles were centred at each of the 29 ponds' polygons, corresponding to surface areas of 0.03, 0.13, 0.50, 2.01 and 8.04 km^2, respectively (Fig. 1). A given variable calculated for any of the scales is referred to as: ‘variable + scale’ (e.g. ‘ELS100m’).

2.3.2. Water and land-use

Water records were obtained from OSMasterMap data downloaded from Digimap (©Crown Copyright/database right 2009 – OS/EDINA supplied service). OSMasterMap contains polygons representing different land-use classes. Data from all waterbodies within the catchment area were downloaded (OS tiles SP61/62/71/72) (Fig. S1). Ditches and running water of <1 m width were not provided by the database. We calculated two landscape variables: ‘number of ponds’ [POND] and ‘percentage water’ [WATER] (Table 1) and an area for each waterbody was obtained. ‘Number of ponds’ within a given radius for each pond was determined by filtering out all lotic and lentic waters over 1 ha, leaving only ponds (Fig. S1). ‘Percentage water’ was obtained by dividing the catchment into a 1 km^2 grid and calculating the percentage water of lentic and lotic waterbodies within each square (Fig. S1).

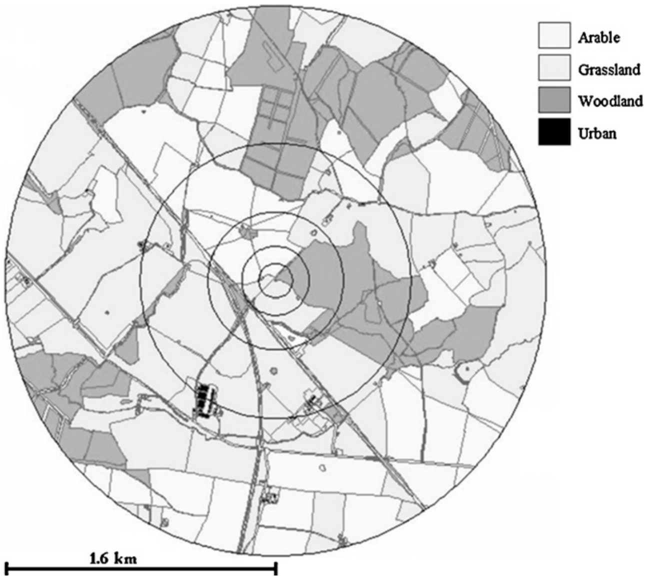

Fig. 1. Example of digital map of the area surrounding a pond. Circles represent the five spatial scales of 100 m, 200 m, 400 m, 800 m and 1600 m radius for which land-use composition was quantified. Map produced from Ordnance Survey data ©Crown Copyright/database right 2009 (OS/EDINA supplied service).

The final water percentage surrounding a pond within a given radius was obtained by averaging the percentages of all squares with which the radius overlapped (Fig. S1).

Land-use data were obtained from Land Cover Map 2000 (CEH 2000). Four land-use variables were considered: 'woodland' [WOOD], 'arable' [ARABLE], 'grassland' [GRASS] and 'urban' [URBAN] (Table 1: see Fuller et al. (2002) for full description of categories). Total area for each variable was calculated within each radius for each pond and percentages calculated. In addition, about 75% of the total study area was mapped in the field to corroborate digital data obtained from the Land Cover Map.

2.3.3. Agri-environment schemes (AES)

Data regarding land under AES between 1995 and 2004 were obtained from Defra (Table S2). Agreements were included in each of the three study years only if they started in the previous year or earlier, as it was assumed that effects would not be measurable during the first year. Environmentally Sensitive Area (ESA) and Countryside Stewardship Scheme (CSS) agreements (Table S1) were considered as old [ESAold; CSSold] when the agreement had started ≥6 years ago, and new [ESAyou; CSSyou] when they were ≤5 years old (see Table S1 for explanation of agreements). This cut-off was chosen to allow for more than half of identified species to potentially colonise ponds as adults (Moore, 1991) assuming that pond conditions had been enhanced by improvements to surrounding land. The percentage of land area within each radius for each pond was calculated for old and new Environmentally Sensitive Area and Countryside Stewardship Scheme agreements. In 2005, Environmentally Sensitive Area and Countryside Stewardship Schemes had been replaced by the Entry Level Scheme (ELS), Organic Entry Level Stewardship (OELS) and Higher Level Scheme (HLS): Table S1. The percentage land under these schemes was similarly calculated but with no age distinction.

Presence or absence of a buffer strip was recorded in the field. A buffer [BUFFER] was an unfertilised grass strip (which could include scrub or part of a hedge) established around a pond, of at least 2 m width (minimum cross-compliance requirement [Defra, 2009]). A full buffer refers to a buffer strip running the full perimeter of the pond and a partial buffer refers to a buffer strip that only ran around part of the pond's perimeter.

Table 1
Description of the twelve variables used in the landscape analysis.

Variables	Description
BUFFER	Unmown, grassy, ≥2 m wide margin; 3 classes: 0 = absent; 1 = partially surrounding; 2 = fully surrounding
WAT	% of lentic and lotic water within a given radius
POND	Number of ponds within a given radius
WOOD	% woodland[a] within a given radius: 1.1 Broad-leaved woodland; 2.1 Coniferous woodland
ARABLE	% arable land[a] within a given radius: 4.1 Arable cereals; 4.2 Arable horticulture; 4.3 Non-rotational horticulture
GRASS	% grassland[a] within a given radius: 5.1 Improved grassland; 5.2 Set-aside grass; 6.1 Neutral grassland; 7.1 Calcareous grassland
URBAN	% urban[a] development within a given radius: 17.1 Suburban/rural developed; 17.2 Continuous urban
ESA	Old: % land on ESA for ≥6 years; young: % land on ESA for ≤5 years; within a given radius
CSS	Old: % land under CSS for ≥6 years; young: % land on ESA for ≤5 years; within a given radius
ELS	% land under ELS within a given radius
OLS	% land under OLS within a given radius
HLS	% land under HLS within a given radius

[a] As classified by Land Cover Map 2000 (CEH 2000).

2.4. Analyses

To calculate the six response variables, the number of species of exuviae (STOTEX) and of adults (STOTAD) were totalled for each pond and for each of the three consecutive years. In addition, the number of dragonfly (SANIEX, SANIAD) and damselfly (SZYGEX, SZYGAD) species were totalled separately, since dragonflies typically move larger distances than damselflies. Methods were adapted from Marini et al. (2009). Simple Poisson regressions, using Generalised Linear Models (GLM) with Poisson error distributions and log-link functions, were preliminary used (Proc Genmod SAS 9.2), allowing the most important spatial scale to be established for each parameter. Since landscape variables are typically highly correlated when using nested spatial scales, only the scale that best explained the variation for each of the six response variables was used for further analyses (Steffan-Dewenter et al., 2002; Cozzi et al., 2008; Marini et al., 2009).

To show simple relations between response variables and each predictor, we ran a Pearson correlation analysis on the variable predictors for each of the six groups to evaluate the degree of collinearity, but only for the significant ($P \leq 0.05$) or trend ($P > 0.05 < 0.1$) variables as assessed from the GLM Poisson regressions. The number of explanatory variables was then reduced by excluding factors strongly correlated with another factor (Pearson correlation coefficient >0.6) (Table S3).

Finally, multiple Poisson regression models were run (Proc Glimmix SAS 9.2). The variable 'year' (three classes: 2006; 2007; 2008) was included as a categorical blocking variable in all models. 'Pond' (29 classes) nested within 'area' and 'buffer' was always included as a random factor. Although the four areas were the same, and were all sampled equally exhaustively, 'area' is part of the analysis because some ponds within each 'area' had small overlapping areas when analysing for the 1600 m scale, and therefore spatial autocorrelation was hence compensated for by blocking study 'area' within the pond. For each of the six groups, the models were started with all main effects at the most significant spatial scale (both significant and trend effects) for that group, but without those main effects excluded due to strong correlation (see Table S3). Models did not converge when including interactions, and hence full models only contained main effects. In order to build the minimum adequate model, backward selection of non-significant factors was applied, but non-significant factors with a P-value <0.2 were conservatively retained within models. We then included all

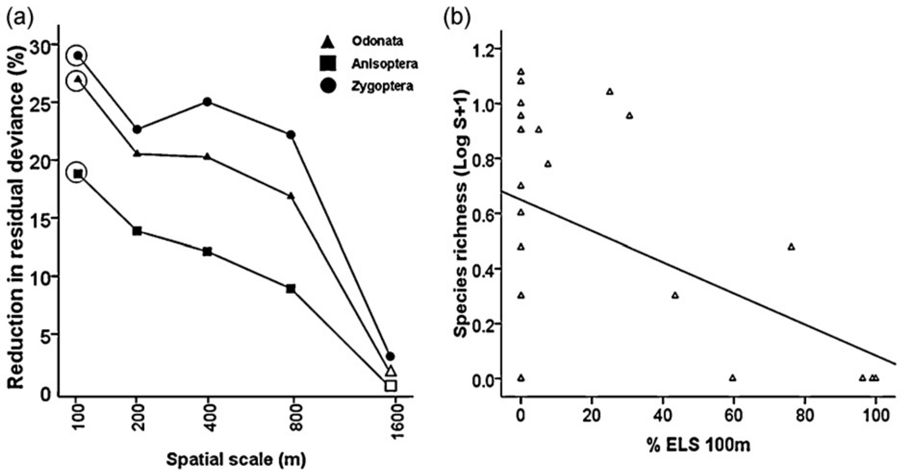

Fig. 2. Scale-dependent effect of the uptake of Entry Level Scheme (ELS) on species richness of exuvial odonates: (a) Percentage drop in residual deviance of Poisson regressions between species richness and the proportion of ELS land at five spatial scales (significant: filled symbols; non-significant: empty symbols). Scales with largest drops in residual deviance are marked with circles. (b) Log-transformed species richness for the scale with the largest drop in residual deviance, i.e. 100 m, with a line of 'best fit' for visual reference. Anisoptera refers to dragonflies and Zygoptera to damselflies.

interactions of these remaining variables with the variable 'buffer' (3 classes). Again, backward selection of non-significant factors was applied to build the final models. Improvement of model's goodness-of-fit was corroborated at each step, as indicated by a reduction in the '-2 RES log pseudo-likelihood' of the models.

3. Results

3.1. Overall species richness: adults and exuviae

A total of 17 species was recorded as adults in each of the three study years (Table S4), comprising eight damselfly and nine dragonfly species. Overall, 11,025 exuviae were collected (2006: 3316; 2007: 2325; 2008: 5384), from seven damselfly and nine dragonfly species (Table S4). The maximum species richness at a pond was: (i) Total exuviae: 12; (ii) Total adults: 15; (iii) Dragonflies-exuviae: 7; (iv) Dragonflies-adults: 9; (v) Damselflies-exuviae: 7; (vi) Damselflies-adults: 6. Minimum species richness at a pond was zero for all categories.

3.2. Exuviae: Odonata, dragonflies and damselflies

The Poisson regression between species richness of odonates overall, dragonflies and damselflies and the percentage of land under Entry Level Scheme at the five spatial scales showed a scale-dependent effect, with the largest drop in residual deviance at the scale of 100 m. Damselflies showed a more pronounced response to this variable (29%) than did dragonflies (19%) (Fig. 2a). At the 100 m scale, species richness was lower in areas with higher amounts of Entry Level Scheme around a pond (overall: $F_{1,55} = 18.35$; $P < 0.0001$; dragonflies: $F_{1,53} = 12.50$; $P = 0.0009$; damselflies: $F_{1,55} = 9.93$; $P = 0.003$) (Fig. 2b). The direction of the Entry Level Scheme effect at scales 200 m to 800 m was the same than at 100 m and significant.

The number of Environmentally Sensitive Area scheme agreements in place for more than 6 years coincided with a decrease of overall species richness. This effect was strongest at the largest spatial scale (1600 m) ($F_{1,55} = 8.57$; $P = 0.005$). Although the positive main effect of proportion of water present at the 1600 m scale on exuvial species richness was only a trend ($F_{1,55} = 3.97$; $P = 0.051$), water at this scale was significantly, and positively, correlated with overall species richness for ponds without a buffer ($F_{1,55} = 3.70$; $P = 0.031$), while ponds with buffers were not affected by the amount of surrounding water (Fig. 3).

The amount of land under Countryside Stewardship Scheme for more than 6 years (Table S1) was positively correlated with dragonfly species richness, especially at the 1600 m scale ($F_{1,53} = 5.34$; $P = 0.024$), while the amount of Environmentally Sensitive Area schemes in place for more than 6 years, at the same scale, had a negative effect ($F_{1,53} = 9.73$; $P = 0.003$). Species richness of damselflies increased with an increasing percentage of water in the surrounding land, and mostly so at the largest scale (i.e. 1600 m) ($F_{1,55} = 7.42$; $P = 0.009$). Species richness of dragonflies was higher when ponds were characterised by full or partial buffers compared to ponds without a buffer (class 0 vs. 1–2) ($F_{1,24} = 10.48$; $P = 0.0005$), while the species richness of damselflies was higher only at ponds with a full buffer (class 0–1 vs. 2) ($F_{1,23} = 8.89$; $P = 0.0005$) (Fig. 4).

There were no effects of ESAyou1600m on exuvial dragonfly species richness ($F_{1,53} = 1.90$; $P = 0.174$) or of ESAold1600m

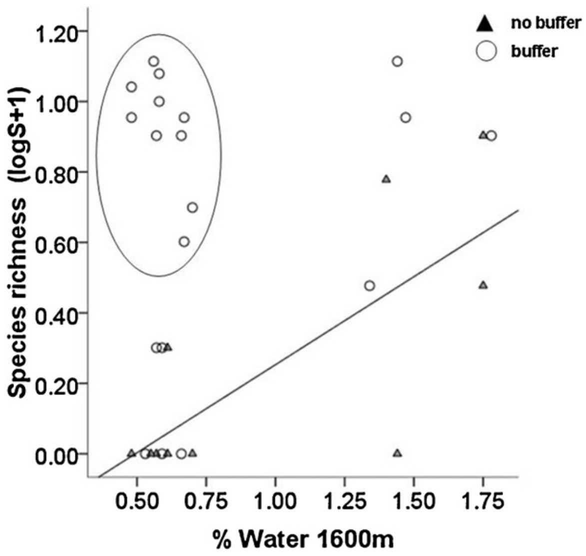

Fig. 3. Log-transformed overall species richness of exuvial odonates in relation to percentage water at the 1600 m scale, for ponds with and without buffers. 'Buffer' refers to ponds with a partial or full buffer. A line of 'best fit' has been given for ponds without a buffer. Symbols grouped within an ellipse are referred to within the text to highlight similarities.

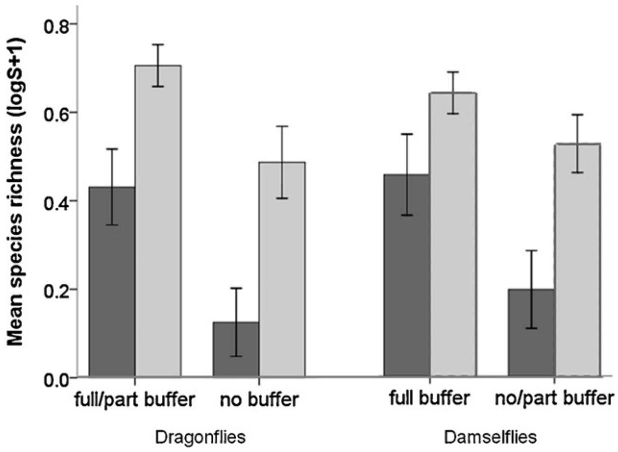

Fig. 4. Effect of pond buffers on odonate species richness (±SE). Bar colours refer to exuviae (dark grey) and adults (light grey). Species richness has been log-transformed (see Sections 3.2 and 3.3 for buffer groups).

($F_{1,55}$ = 2.52; P = 0.118) or POND100 m ($F_{1,55}$ = 2.02; P = 0.161) on exuvial damselfly species richness. No year effects were found.

3.3. Adults: dragonflies and damselflies

Overall, odonate species richness increased with larger areas of land under Higher Level Scheme at the 1600 m scale ($F_{1,54}$ = 4.50; P = 0.038). Odonate species richness decreased with increasing amounts of woodland, especially at the 200 m scale ($F_{1,54}$ = 4.57; P = 0.037) (Table S3).

The Poisson regression between dragonfly species richness and the percentage of land under Higher Level Scheme at the five spatial scales showed a scale-dependent effect, with the largest drop in residual deviance at 1600 m (Fig. 5a). The amount of Higher Level Scheme around a pond at the largest spatial scale was positively correlated with dragonfly species richness ($F_{1,55}$ = 6.20; P = 0.016) (Fig. 5b).

Damselfly species richness decreased with increasing percentage of land under Entry Level Scheme ($F_{1,55}$ = 6.67; P = 0.013), and increasing percentage of water in the surrounding land, especially at the 400 m scale ($F_{1,55}$ = 5.24; P = 0.026). Overall species richness was higher when ponds were characterised by full or partial buffers ($F_{1,24}$ = 9.11; P = 0.0004), as was dragonfly species richness ($F_{1,24}$ = 10.02; P = 0.0007), compared to ponds without a buffer (class 0 vs. 1–2) (Fig. 4). For damselflies, however, this was only a trend ($F_{1,23}$ = 2.90; P = 0.075). The coverage of Entry Level Schemes at the 1600 m scale had no effect on odonates species richness ($F_{1,54}$ = 2.15; P = 0.15). The number of ponds in the surrounding area had no effect on species richness of dragonflies (best scale: 1600 m) ($F_{1,55}$ = 1.68; P = 0.20).

4. Discussion

4.1. Landscape responses depend on sub-order and life-cycle stage

Species richness of adult and exuvial dragonflies was more influenced by variables at a larger scale (1600 m) compared to damselflies (100/400 m); similarly, Kadoya et al. (2008) found the occurrence of dragonflies to depend more on landscape composition than damselfly occurrence. Current strategies for odonate conservation are most likely to benefit the less mobile damselflies, by focusing on increasing pond quality and their immediate surroundings (such as establishing pond buffer strips). This can more easily be achieved given the small areas that usually characterise pond catchments (Davies et al., 2008b) than the landscape-scale approach required for the more mobile dragonflies, and other mobile groups (Merckx et al., 2009a, 2010).

Our study also showed different responses to landscape use depending on the life-cycle stage. The number of landscape variables affecting exuviae (and hence larvae) was greater than that for adults. Odonates spend the longest period of their life-cycle in ponds (aquatic), and presence of exuviae, which proves at least one-generation life-cycle completion, is a measure of surrounding landscape quality, which in turn affects the catchment and quality of the pond. By contrast, the effects of different management options were less pronounced for adults; although the quality of the landscape might be crucial for dispersal, this stage only lasts for a few weeks and the requirements for roosting sites and insect prey may more easily be met. However, even for adults of common species, there may be specific habitat requirements which differ between sexes (Foster and Soluk, 2006), between adults at different reproductive stages (Corbet, 1999) and vary with time of day (Kortello and Ham, 2010).

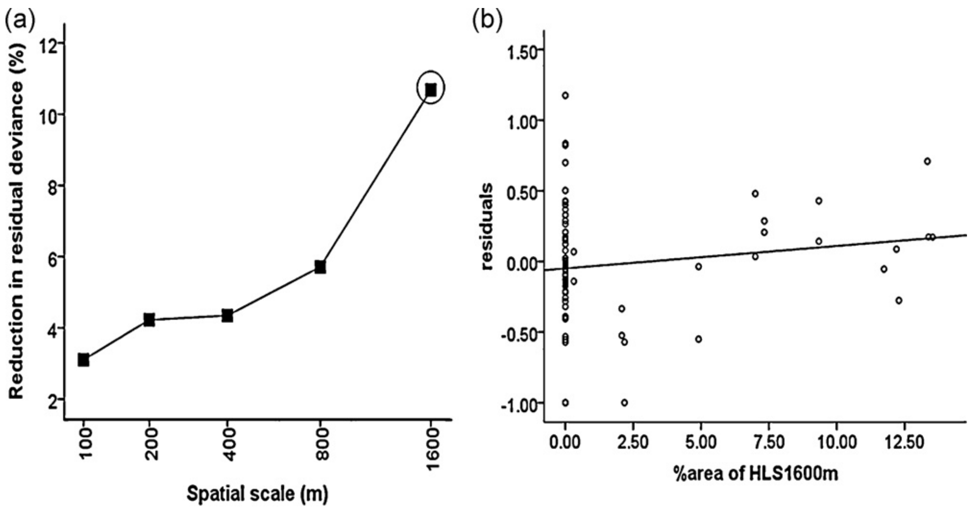

Fig. 5. Scale-dependent effect of Higher Level Scheme (HLS) uptake on the species richness of adult dragonflies: (a) Percentage drops in residual deviance of the Poisson regressions between species richness and the proportion of land under HLS at five spatial scales. The scale with the largest drop in residual deviance is marked with a circle. (b) Residuals for the scale with the largest drop in residual deviance, i.e. 1600 m. A line of 'best fit' has been given as a visual reference.

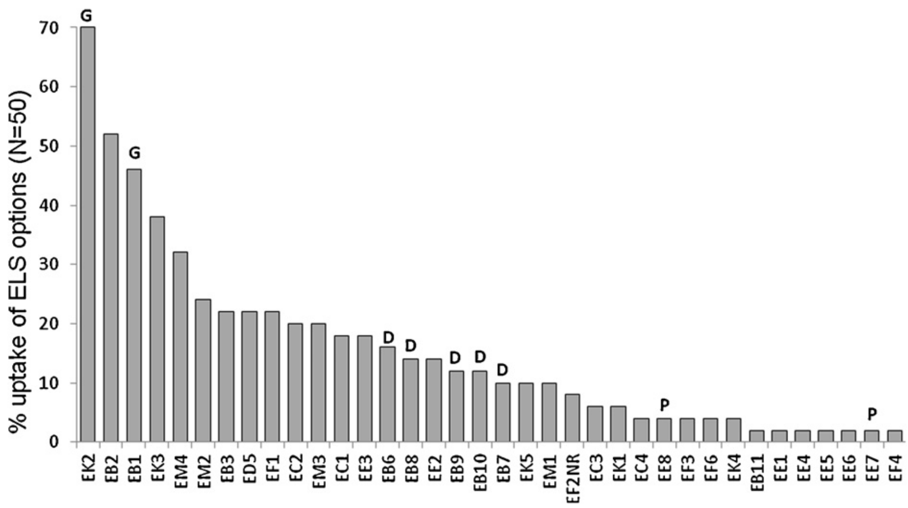

Fig. 6. Percentage uptake of Entry Level Scheme options in the study area (1600 m) (N = 50 agreements). Uptake refers to the percentage of agreements taking a given management option. See Table S2 for description of codes. Bars marked with symbols are referred to within the text as pond (P), ditch (D) and grass (G) options.

4.2. Agri-environment schemes

Overall species richness of both dragonfly and damselfly exuviae decreased with greater area of land under the most basic AES, the Entry Level Scheme (ELS), especially at the smallest spatial scale (i.e. within 100 m of a pond). From the 11 ponds that had Entry Level Scheme within 100 m, the six ponds with >40% of surrounding land under ELS100m always yielded low levels of exuviae species (0–2). Although the Entry Level Scheme has specific options related to pond management (buffering in-field ponds in improved grassland and in arable land) these options were not chosen by farms in our study (Table S2). Landowners have always tended to opt for the easiest and cheapest Entry Level Scheme options (Wilson et al., 2007; Dobbs and Pretty, 2008), with continuing poor uptake of pond options (Hodge and Reader, 2010). Of 50 Entry Level Scheme agreements (within 1600 m of each pond) in our study area, only 2–4% selected a pond option (Fig. 6P). The most popular Entry Level Scheme options relate to low fertiliser inputs and linear features (Davey et al., 2010). Ponds in this study were not situated within fields that were in Environmentally Sensitive Areas or Countryside Stewardship Scheme agreements. Differing effects of the presence of these schemes in the surrounding landscape on odonates in this study may have been due to the particular land management options chosen, none of which related to ponds.

Compared to the Entry Level Scheme, the Higher Level Scheme (HLS) concentrates on more complex management that can deliver more specific conservation targets. Adult odonates showed a positive response to the Higher Level Scheme, especially at the 1600 m scale. Although only 12% of agreements in the area were Higher Level Schemes, pond options were taken by three out of seven agreements, suggesting that farmers were more likely to undertake pond management at Higher Level Schemes. The creation of high quality ponds is an option currently only available within the Higher Level Scheme.

Besides pond neglect, which is more likely to occur under Entry Level Scheme than under Higher Level Scheme, it is difficult to explain why Entry Level Scheme agreements had a negative impact on odonate exuviae within 100 m, without testing the effects of individual Entry Level Scheme options. Management in the immediate vicinity of the ponds may have contributed to the effect. Other studies have reported negative effects of harvesting and hay cutting on a variety of organisms (Humbert et al., 2009; Marini et al., 2009; Dover et al., 2010). AES prescriptions on grassland have been largely driven by the need to protect nesting birds and may be inappropriate for other groups such as odonates. These options have high uptake within Entry Level Scheme (Fig. 6G). Odonates, especially damselflies, will roost in grassland on adjacent fields and standard mowing in June and July would coincide with peak numbers of adult coenagrionids. Incentives to leave field margins ungrazed/unmown could help to reduce impacts of removal of roosting sites. Such a measure would not only reduce direct mortality but also provide extra habitat resources (e.g. shelter, food) for many other arthropods (e.g. bees, beetles, butterflies, grasshoppers, spiders) (Humbert et al., 2009; Dover et al., 2010).

4.3. Buffer strips and water

Buffer strips increased the species richness of odonates in both adult and exuvial data. Buffers can increase pond quality by reducing surface run-off (Lovell and Sullivan, 2007) and provide roosting resources for adults (Rouquette and Thompson, 2007b). However, while partial buffers seemed to have the same positive effect on adult and exuviae of dragonflies as full buffers, they did not increase damselfly species richness. Male adult damselflies rely heavily on vegetation surrounding ponds to wait for females, in contrast to dragonfly males, which tend to guard territories on the wing or by perching within the pond. Our results also suggest that damselfly larvae preferred full buffers, probably because, when coupled with the right larval habitat factors (pond vegetation, transparency), they contribute to better pond quality (Raebel et al., 2012). This reinforces our previous finding that damselflies are more reliant on the good quality of small-scale landscape components (full buffers) than dragonflies.

The amount of water, especially within 1600 m of a pond, also increased species richness of exuviae, but only for ponds without a buffer. Ponds with buffers did not depend on surrounding water to have high species richness of exuviae (Fig. 3-ellipse). Nevertheless, some ponds with buffers did not produce any exuviae (30%), suggesting that, in these ponds, species richness may depend on other factors, e.g. presence of floating/submerged vegetation within ponds (Raebel et al., 2012).

Buffers were present at 66% of the ponds under study, but they were not established under Entry Level Scheme agreements. Most were 2 m buffers created under current cross-compliance buffer-guidance, which may not be wide enough to increase biodiversity levels. Entry Level Scheme recommends an option of 7–10 m wide buffers, but it has been suggested that 25–30 m would be most beneficial for freshwater biodiversity (Davies et al., 2009). However, since buffers can be managed at a local scale (pond catchments are generally small, Davies et al., 2008b), buffer creation beyond cross-compliance would have positive effects on odonates across sub-groups and at all stages of their life-cycle.

The high contribution of ponds to regional biodiversity has already been highlighted (Biggs et al., 2005; Davies et al., 2008a), but our study did not find any effect of the number of ponds on species richness, probably because it is the number of viable ponds that is more important for odonate conservation than the number of ponds themselves. However, the amount of water within 1600 m of a pond did increase species richness of exuviae, especially for damselflies. Most damselflies in this study have waterbodies other than ponds as secondary habitats (Smallshire and Swash, 2004), and habitat connectivity has been proven to be vital for maintaining their populations (McCauley, 2006). Even a suboptimal habitat might be able to support certain species if a sufficient abundance of habitat in the vicinity can provide a surplus of individuals available to recolonise ponds (Moore, 1991), and facilitate gene flow between populations.

Previous studies on agricultural lowland have found that, in cultivated areas, general water availability and deep ditches encouraged odonate species (Tessier et al., 2009). In our study, 10–16% of Entry Level Scheme and 14–29% of Higher Level Scheme agreements had taken a ditch-related option within the 1600 m scale (Fig. 6D). Although applying the correct ditch management has shown great benefits to odonate populations (Painter, 1998; Rouquette and Thompson, 2005), most ditches in the study area were too small, temporary or covered in too great an amount of vegetation to be detected by odonates or to allow for completion of their life-cycle. Water amount did not seem to have an effect on dragonfly species richness, suggesting that this sub-group does not rely on water density due to its long-distance dispersal ability, or that they rely on a larger scale than the maximum chosen for this study.

The reliance of damselflies on the amount of water at a large scale highlights the need for connectedness between these waterbodies. Non-territorial species (e.g. coenagrionids in this study: *Coenagrion puella*, *Ischnura elegans*, *Enallagma cyathigerum*) will spend most of their life away from water (Conrad et al., 1999), only commuting to ponds to breed. Damselfly dispersal largely depends on chance wandering and so ponds, fields and hedgerows need to form a functionally continuous biotope (Conrad et al., 2002). The amount of woodland, especially within 400 m, seemed to have a negative effect on adult coenagrionids; woodland may decrease their movement, speed and dispersal distance compared to pastures (Pither and Taylor, 1998). In contrast, positive effects have been found for highly mobile damselflies (e.g. calopterygids: Jonsen and Taylor, 2000), implying that management should focus on overall species richness but also needs to be tailored to individual species of interest.

5. Conclusions

Odonate species richness is affected by land-use at different spatial scales, and conservation needs to focus on creating more heterogeneous landscapes (Foster and Soluk, 2006). Odonate responses to land-use, while varying with the mobility of sub-orders and life-stages, support the argument for the development of policies that encourage contiguous farms to apply for AES (Merckx et al., 2009b) in order to form continuous managed landscapes. AES can play an important part in achieving this, if pond-related options are encouraged as well. Maximum benefits would be delievered by targeting individual species, focusing on restoration and quality management of specific areas (Sutherland, 2002), and encouraging pond-related options. We believe that this could be achieved under AES if the current non-cost-effective trend of untargeted and scattered uptake of schemes and options is replaced by landscape-scale agreements. Higher-level schemes should be aimed at specific areas (e.g. areas with ponds with large number of plant or macro-invertebrate species) that would promote hotspots of high ecological value (e.g. new approach of 'Higher-level schemes targeting maps' in the UK (NE, 2011)). AES would then encourage contiguous farmland to connect these 'best' areas in the wider landscape by means of non-focused, broad, and easy management options, hence providing for the whole range of odonate species, irrespective of their mobility levels.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2012.07.015.

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