

# Mark recapture estimates of dispersal ability and observations on the territorial behaviour of the rare hoverfly, *Hammerschmidtia ferruginea* (Diptera, Syrphidae)

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**Abstract** In order to effectively manage habitat for fragmented populations, we need to know details of resource utilisation, and the capacity of species to colonise unoccupied habitat patches. Dispersal is vital in maintaining viable populations in increasingly fragmented environments by allowing re-colonisation of areas in which populations have gone extinct. In the UK, the endangered aspen hoverfly *Hammerschmidtia ferruginea* (Fallén 1817) (Diptera, Syrphidae) depends on a limited and transient breeding habitat: decaying aspen wood *Populus tremula* L. (Salicaceae). Conservation management for *H. ferruginea* involves encouraging aspen expansion across Scotland, and ensuring retention, maintenance and continuity of dead wood where *H. ferruginea* has been recorded and in areas that may link populations. In order to do this effectively we need to know how far *H. ferruginea* can disperse. By taking advantage of the tendency of adults to group on decaying aspen logs, we estimated dispersal ability through mark recapture techniques. In the first year, 1,066 flies were marked as they emerged from aspen logs and 78 were re-sighted at artificially-placed decaying aspen logs up to 4 km from the release site. In the second year, of 1,157 individually marked flies, 112 were re-sighted and one was observed 5 km from

the release site. Territorial behaviour was recorded at all (19) decaying aspen log locations. In total, 72 males were recorded defending territories, which overlapped with 68 % of recorded female oviposition sites. Among males only, wing length was positively associated with dispersal. While these results show *H. ferruginea* is capable of locating decaying logs up to 5 km away, most dispersing individuals (68 %) were recorded at 1 km, which should be taken into account in developing management protocols. If enough dead wood is available it should be distributed within a radius of 1–2 km, and where possible, as stepping-stones linking up aspen woodlands. We discuss the implications of our findings for the natural history of this species, and make recommendations for its conservation management.

**Keywords** Saproxylic · *Populus tremula* · Mate seeking · Distribution

## Introduction

Effective conservation management requires detailed knowledge of the natural history of a species, which includes its habits, habitat requirements and behavioural interactions. Where habitat is limited, information on dispersal ability informs management decisions aimed at maximising habitat connectivity and gene flow within the environment in which populations exist, and in new areas for colonisation. Here, we investigate the natural history and dispersal ability of the endangered aspen hoverfly, *Hammerschmidtia ferruginea*, to better inform vital conservation management protocols for this species.

*Hammerschmidtia ferruginea* is listed in the UK Red Data Book as a category 1 (endangered) species, and it is included in the UK Biodiversity Action Plan (UKBAP). It

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is listed as an indicator of internationally important forests, and is rare throughout its Holarctic distribution (Speight 1989; Speight et al. 2010). *H. ferruginea* is considered a flagship species for a group of 13 other rare and similarly endangered Diptera in Scotland that all depend on aspen, *Populus tremula* L. (Salicaceae) (Rotheray 2001).

Since 1999 the number of UK sites occupied by *H. ferruginea* has decreased from 15 to 8 (Rotheray et al. 2009). The main reason for this decline is probably that it is a specialist saprophage depending on a scarce and temporary resource: decaying cambial layers under bark of dead aspen wood. From the time a tree falls or a branch breaks off, it can take up to 2 years for the cambial layers to become suitable for larval development and, depending on its size and location, a piece of wood with cambial decay can last from just 1–3 years before drying out (Rotheray et al. 2009). During periods when habitat is in short supply, *H. ferruginea* can also develop in small pockets of decaying sap that exudes from damage on living aspen trees (Rotheray 1991). While this resource may be by its nature scarce, in the UK there are few aspen woodlands large enough (>100 trees) to maintain a constant supply of dead wood of the correct age, and in Scotland where some large groups of aspen stands exist, unpredictable winds and storms are the chief cause of fluctuations in the amount of dead wood present causing boom and bust periods.

As part of the UKBAP process, strategies must be designed for the restoration, protection and monitoring of *H. ferruginea*. Conservation management involves encouraging the expansion of aspen and insuring continuity of deadwood (Rotheray et al. 2009). This includes detecting the quantity and state of decay of dead aspen wood at all *H. ferruginea* sites and supplementing breeding habitat as necessary by severing branches or whole trees (Rotheray et al. 2009). In order to plan this effectively we need to know how far individuals can disperse. In 2006, a mark and recapture experiment estimated the dispersal ability of *H. ferruginea* at no less than 1 km (Rotheray et al. 2009). Therefore, we carried out a 2-year project to further investigate the dispersal ability of *H. ferruginea*, and measured adult morphological traits to assess whether any of them, for example wing length, affects dispersal. In addition to this, breeding sites were evaluated for their utilisation as mate-seeking sites. Knowing details of a species reproductive biology is an important part of effective conservation management, and this was a gap in the known ecology of this endangered hoverfly.

## Methods

### Field site

The study involved surveying *H. ferruginea* localities in Strathspey as described by Rotheray et al. (2009). Dispersal

experiments took place at Insh Marshes National Nature Reserve (NNR), Inverness-shire, Scotland (57°05' N, 3°58' W), which is owned and managed by the Royal Society for the Protection of Birds (RSPB). The reserve is primarily a wetland floodplain with wet woodland fringed by birch *Betula pubescens* and aspen at higher elevations.

### Distribution and habitat quality

All aspen woodland sites were located using aerial photographs of the area, which effectively identify aspen due to its tendency to flush later in the year than more common species such as *Betula* spp. (Kouki 2008). These were searched for decaying aspen wood, and larval and pupal stages of *H. ferruginea* (for detailed methods see Rotheray et al. 2009), in order to avoid any bias within the experimental areas, and build a basic distribution map of Strathspey populations.

### Dispersal experiments

Two experiments were carried out between May and August 2009 and 2010. The first sought to investigate dispersal ability using decaying aspen logs set out from a central point at 1 km intervals to a maximum of 4 km. The second experiment was designed to estimate dispersal ability from 1 to 7 km without 1 km stepping-stones (Fig. 1), to assess morphological differences between dispersers (those observed at 1 km +) and non-dispersers (those only observed at the release location), and to compare the morphologies of winners and losers of territorial contests on logs. Emergence, size differences and sex ratio over time was also recorded in both years to identify the peak abundance period for adults, and to compare these data with observations at the logs.

### Experiment 1: stepping-stone dispersal ability

In 2008, nine aspen trees were felled on private land local to Insh Marshes, and donated to the reserve to provide habitat for *H. ferruginea*. These were cut into twenty logs of similar length (mean  $\pm$  SD; 113  $\pm$  26.7 cm) and width (32  $\pm$  7.4 cm). In 2009, two 3 km and one 4 km long transects were set up using decaying aspen logs extending out from a central location at  $\sim$ 120° angles from each other, pointing south, northwest and northeast (Fig. 1). Two logs were positioned at the central meeting point of the transects, and at 1, 2 and 3 km “stepping stone” points along each transect. One additional log was positioned at 4 km on the NE transect. We conducted extensive searches to confirm that no other decaying aspen branches or logs were within 1 km of the experimental area.



**Fig. 1** Maps (<http://maps.google.co.uk/maps>) of experimental areas in Strathspey, Scotland for experiment 1 (on left) and experiment 2 (on right). Black circles indicate where the aspen logs were

positioned. The number within each circle indicates kilometres distance from the *H. ferruginea* release point, R

From 14th May until 24th June, emergence traps were constructed over six decaying fallen or severed aspen on and around Insh marshes but outside the experimental area. The traps were simple constructions using pesticide-free mosquito netting and malleable fence wire (see Rotheray et al. 2009). Each trap was checked for emergence every morning and afternoon, between 7 am and 8 pm. All *H. ferruginea* caught in traps were removed individually using a  $3 \times 10$  cm collection tube, and marked on the thorax using a dry grass stem and non-toxic enamel paint (Humbrol™) using a different colour or combination of colours for each day of emergence. Flies were not individually marked in Experiment 1 due to time constraints and concern over damaging the insects. Marking was carried out in the tube, or within a marking cage made from a plastic open-ended  $3 \times 10$  cm tube with a cork plunger and flexible netting over one end where the insect could be gently immobilised (Bonduriansky and Brooks 1997). Occasionally, marking required moving adults into cool bags with freezer blocks wrapped in a towel for several minutes to reduce activity. Each adult was photographed on laminated lined paper for scale, and the length of the thorax, from where the neck meets the pronotum to the apex of the scutellum, and the length between two wing veins (landmarks 1 and 3 in Milankov et al. 2010) were measured using ImageJ software (Abràmoff et al. 2004). Adults were released the same day at the central meeting point of the transects.

From 16th May until 5th July, 60-min observation sessions were spent at each group of decaying logs in succession throughout the day, with the starting location rotated each day (from 9/10 am to 7/8 pm depending on weather). We noted the local wind direction, and recorded

the number of marked and unmarked *H. ferruginea* individuals throughout each session.

Experiment 2: dispersal ability in the absence of stepping-stones

In 2010, similar techniques were used as in experiment 1, however this time two decaying logs were placed at eight points from 0 to 7 km from one central release location with no intermediately placed stepping-stones (Fig. 1). Logs were sourced from a local golf course where three aspen trees had fallen naturally and snapped at the base at least 1 year previous to the experiment. These were cut into similar lengths ( $128 \pm 26.7$  cm) and were of similar width ( $28 \pm 6.8$  cm).

From 17th May until 22nd June, we constructed emergence traps over seven decaying logs or trees in and around RSPB Insh Marshes, and one west of Newtonmore ( $57^{\circ}04'$  N,  $4^{\circ}07'$  W). We used the same methods as described above for experiment 1 to collect and mark *H. ferruginea* caught in the traps, however each individual was this time given a unique mark using a combination of colours and locations on the thorax.

From 4th June until 14th July, each log was observed as described in experiment 1, except that adult activity, location on the aspen log, territorial behaviour and oviposition were also recorded. Behaving territorially was defined as males chasing passing insects and repeatedly returning to a similar location on the aspen log. 'Contests' were defined as events involving two males in physical contact. A male was considered to have 'won' a contest if it returned to the original location and continued territorial behaviour, while a 'losing' male would either leave the site

or take up a territory elsewhere. Oviposition was defined as when the female ovipositor could be observed probing cracks in the bark. Territory and female oviposition locations were recorded on basic illustrative representations of the logs. Territories were described as including oviposition locations if they were within 20 cm on the log.

Males and females appear to darken in colour as they age (Rotheray et al. 2009). To test the accuracy of thorax colour or shade as a prediction of age, we compared each re-sighted marked individual to a strip of paper with seven progressively darker shades taken from photographs of actual *H. ferruginea* thoraces, labelled 1–7, and assigned each individual to the most similar colour category (Fig. S1). This category was later regressed on known adult ages based on dates of emergence.

### Statistical analysis

Chi squared tests were used to assess deviations from the unity sex ratio over the emergence period. We used linear models to assess differences in adult thorax and wing length between sexes, associations between thorax and wing length and day of emergence, and associations between the direction of dispersal and local wind direction. Direction data were taken in degrees. To compare these data, 360 was added to the smaller of the two vectors in cases where the corresponding vector was more than 180 i.e. the difference between the two vectors gave the obtuse rather than the acute angle. We then used a linear model to compare the difference in angle between the direction of displacement and the prevailing wind direction at the time of capture.

We used generalised linear models (GLMs) (with quasibinomial error distribution, where appropriate, to account for under-dispersion of data) to model the influence of wing and thorax length on dispersal (a binomial response, with individuals recaptured at 1 or more km away from their capture site as dispersers compared with all other flies). We also conducted a second analysis featuring only the subset of marked flies that were re-sighted to control for any effects of morphology on re-sighting probability. We similarly conducted logistic regressions predicting the outcome of territorial contests between males (a binomial response, with individuals either winning or losing contests) as a function of morphology. We assessed possible variance inflation in models including morphological variables using the ‘car’ package (Weisberg and Fox 2010) for R. Finally, we used a linear model to predict thorax shade as a function of adult age. In this analysis, we ranked the shades in terms of their darkness, with higher ranks assigned to darker shades (Fig. S1). All statistical analyses were carried out using the statistical package R (version 2.13.1) (R Team 2011).

## Results

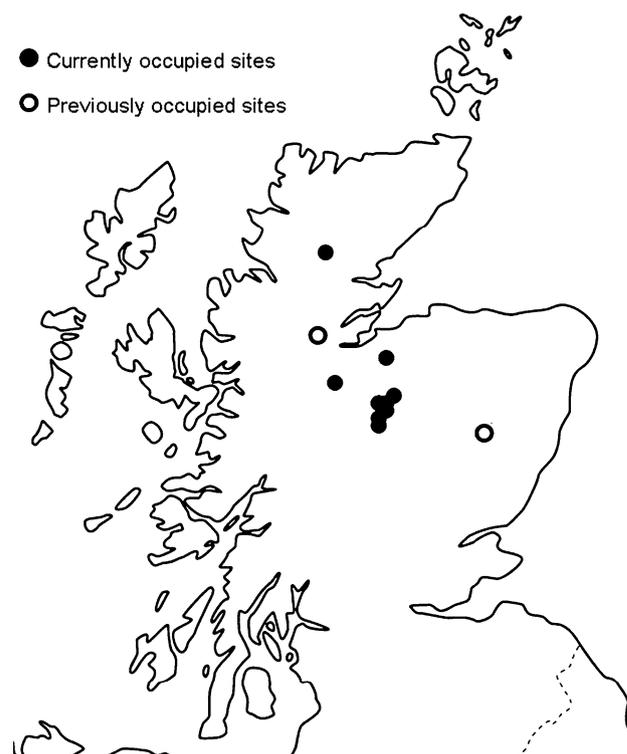
### Distribution and habitat quality

In June 2011, decaying aspen wood and newly fallen trees and branches were found at all known *H. ferruginea* sites in Strathspey (see Rotheray et al. 2009). Empty puparia were found in one fallen aspen tree at Creagan Bruegach (57°05' N, 3°58' W), two at Kinveachy (57°05' N, 3°58' W) and one at Newtonmore (57°05' N, 3°58' W). Each site, including *H. ferruginea* localities pre and post 2006 (Rotheray et al. 2009), was mapped to indicate areas where breeding habitat supplementation should be focussed to link up sites (Fig. 2).

### Experiment 1: stepping-stone dispersal ability

#### Emergence

Between 15th May and 14th June 2009, 1,066 individuals were caught in six emergence traps, most of which came from one severed tree (664). Overall the sex ratio was female biased (M = 465, F = 573,  $\chi^2 = 11.24$ ,  $df = 1$ ,  $P < 0.001$ ). The sex ratio was almost equal in the first 15 days (15th until 29th May) of the emergence period



**Fig. 2** Map of Scotland indicating *H. ferruginea* localities for where it was recorded from 2006–2011 (solid circles) and at previously occupied (pre-2006) sites (hollow circles)

**Table 1** Male and female thorax and wing measurements in 2009 and 2010, and separately for the subsets of dispersing individuals (1 km +) in 2010 (Dispersers), and males that ‘won’ and ‘lost’ in territorial contests

Total in year	Total	Thorax length (cm) (mean ± SD)		Wing length (cm) (mean ± SD)	
		M	F	M	F
2009	1066	0.373 ± 0.034	0.337 ± 0.029	0.72 ± 0.06	0.67 ± 0.059
2010	1157	0.379 ± 0.04	0.35 ± 0.028	0.75 ± 0.05	0.69 ± 0.05
Dispersal 2010					
Dispersers	28	0.365 ± 0.028	0.337 ± 0.034	0.784 ± 0.052	0.693 ± 0.066
Re-sighted at 0 km	50	0.370 ± 0.032	0.344 ± 0.025	0.747 ± 0.053	0.691 ± 0.048
Contests 2010					
Winners	24	0.379 ± 0.041	–	0.789 ± 0.043	–
Losers	19	0.360 ± 0.023	–	0.776 ± 0.039	–

**Table 2** Total number of marked *H. ferruginea* individuals re-sighted at each distance from the release site in 2009 and 2010, and for each distance: total marked and unmarked individuals, maximum number observed over a 1 h session, fraction of total males and females observed, fraction of visiting females observed ovipositing per site

Km	Number of re-sighted individuals per site				2010 total observed <i>H. ferruginea</i> and fraction of total at each site					
	2009 (total)	2010 (total)	Male	Female	Total	Maximum no. per hour	Males	Females	Visiting females ovipositing	
0	45	87	51	36	163	9	0.40	0.44	0.39	
1	11	19	10	9	60	6	0.14	0.17	0.64	
2	4	4	1	5	16	5	0.01	0.11	0.29	
3	12	2	0	2	18	3	0.06	0.02	1.0	
4	1	2	1	1	46	6	0.13	0.05	0.43	
5	–	1	1	0	21	3	0.06	0.05	0.50	
6	–	0	0	0	58	7	0.14	0.16	0.43	
7	–	0	0	0	18	4	0.05	0.02	0.50	

(M = 327, F = 333) and significantly female biased over the final 15 days (M = 138, F = 240,  $\chi^2 = 27.52$ ,  $df = 1$ ,  $P < 0.001$ ). The average daily emergence was 34 flies ( $\pm 30.37$  SD) with a peak of 107 on May 30th. Males had significantly longer wings ( $F_{1,995} = 196.64$ ,  $P < 0.001$ ) and thoraces ( $F_{1,995} = 316.36$ ,  $P < 0.001$ ) than females (Table 1).

*Dispersal*

In total, 105 h were spent observing aspen logs (~ 10 h at each) during which 78 (7.3 %) marked *H. ferruginea* were re-sighted. Most individuals were re-sighted at the release location (54, 69 %). Of those that dispersed, 39 % (11) were re-sighted at 1 km, 43 % (12) at 3 km, and one individual was re-sighted at 4 km (Table 2). More individuals were observed at logs extending northeast from the release point (18) than the southwest (3) and south (7) ( $\chi^2 = 12.9$ ,  $df = 2$ ,  $P < 0.005$ ). This bias in direction did not appear to relate to the prevailing wind direction at the time of recapture (effect of wind in a model of angular displacement; Parameter estimate =  $0.44 \pm 0.25$ ,  $F_{1,19} = 3.21$ ,  $P = 0.09$ ). However, a plot of the data did indicate a trend, and when one outlying data point was

removed a bias in direction was evident, with flies tending to disperse downwind (Parameter estimate =  $0.9 \pm 0.23$ ,  $F_{1,18} = 14.7$ ,  $P = 0.001$ ).

Male and female maximum adult longevity (estimated as the latest recapture date) was 41 ( $11 \pm 14.67$ ) and 28 ( $11 \pm 8.64$ ) (mean ± SD) days respectively, but there was no significant difference in mean age at the time of the last sighting ( $F_{1,34} = 0.79$ ,  $P = 0.38$ ). There was also no significant difference between the number of males (20) and females (23) dispersing ( $\chi^2 = 0.21$ ,  $df = 1$ ,  $P = 0.65$ ).

Experiment 2: dispersal ability in the absence of stepping-stones

*Emergence*

From 17th May until 20th June 2010, eight emergence traps constructed over decaying aspen logs caught 1,157 *H. ferruginea* adults, 94 % of which emerged from one fallen tree located near Newton more. Overall the sex ratio was male biased (M = 592, F = 519,  $\chi^2 = 4.79$ ,  $df = 1$ ,  $P < 0.05$ ). The sex ratio was significantly male biased in the first fifteen days of the emergence period (M = 431, F = 254,  $\chi^2 = 45.7$ ,  $df = 1$ ,  $P < 0.001$ ) and significantly

female biased in the final 15 days ( $M = 161$ ,  $F = 265$ ,  $\chi^2 = 25.39$ ,  $df = 1$ ,  $P < 0.001$ ). There was an average daily emergence of 37 ( $\pm 56.2$  SD) with a peak of 247 individuals on 23rd May.

The linear model showed a significant interaction between morphological traits and time of emergence ( $t = -2.72$ ,  $P = 0.007$ ), sex and morphological traits ( $t = 6.334$ ,  $P < 0.005$ ), and between sex and time ( $t = 2.11$ ,  $P = 0.03$ ). As in 2009, males had longer wings ( $0.75 \pm 0.05$ ) and thorax lengths ( $0.379 \pm 0.04$ ) than females (wing:  $0.691 \pm 0.048$  and thorax:  $0.35 \pm 0.028$ ) (Table 1), and while males showed no change in morphology as a function of emergence date, females had significantly shorter wings and thoraces later in the emergence period (Slope estimate for wing as a function of day of year =  $-0.001 \pm 0.0004$ ,  $F_{1,436} = 9.4$ ,  $P = 0.002$ ; for thorax =  $-0.001 \pm 0.0003$ ,  $F_{1,436} = 3.87$ ,  $P = 0.05$ ).

Adult *H. ferruginea* caught in emergence traps in 2010 had significantly larger thoraces (male:  $F_{1,1089} = 6.2$ ,  $P < 0.001$ , female:  $F_{1,1110} = 24.51$ ,  $P < 0.001$ ) and wing lengths (male:  $F_{1,1001} = 89.32$ ,  $P < 0.001$ , female:  $F_{1,1027} = 53.63$ ,  $P < 0.001$ ) than those captured in 2009 (see Table 1 for means).

### Dispersal

In total, 249 h were spent observing aspen logs ( $\sim 31$  h each) during which 115 hoverflies (10 %) were re-sighted. The release site at 0 km had the greatest number of individuals recorded (87 marked and 76 unmarked) (Table 2). Of those that dispersed (28), nineteen (68 %) were observed at 1 km, and one male (4 %) was observed at 5 km (Table 2). Males were found to repeatedly visit logs, as part of their territorial behaviour, whereas females were recorded visiting infrequently ( $M = 252$  visits,  $F = 131$ ,  $\chi^2 = 38.2$ ,  $df = 1$ ,  $P < 0.005$ ). There was no significant difference between the proportion of males ( $n = 58$ , 10 %) and females ( $n = 49$ , 9 %) dispersing ( $\chi^2 = 0.05$ ,  $df = 1$ ,  $P = 0.82$ ). Maximum male and female longevity was 45 (mean  $30.7 \pm 7.2$ ) and 45 ( $25.7 \pm 8.2$ ) days respectively, and re-sighted males on average were significantly older than females ( $MS = 1204.6$ ,  $F_{1,194} = 20$ ,  $P < 0.005$ ). Finally, we found a significant effect of local wind direction (at the time of recapture) on the direction of dispersal, with flies tending to disperse downwind (Parameter estimate =  $0.6 \pm 0.2$ ,  $F_{1,11} = 7.3$ ,  $P = 0.02$ ).

### Mate seeking

Between 4th June and 13th July, we recorded 72 males defending territories and 58 females ovipositing on the aspen logs. Females observed ovipositing were between 10 and 42 days old ( $25.46 \pm 8.05$ ). Of visiting females

observed (131), 44 % were ovipositing (Table 2). Of all male territorial locations on aspen logs, 68 % (49) were near ( $< 20$  cm distance) female oviposition locations. Males were infrequently (recorded 3 times) observed hovering over females briefly, landing on them and immediately carrying them away from the oviposition resource and out of sight. Females were also observed ovipositing within 20 cm of male territories while territorial males were present. The maximum number of individuals at a log during one hour was nine at 0 km (Table 2).

### Morphological associations with dispersal, contest outcome, and age

Our two morphological traits, thorax length and wing length, were very weakly positively associated in both sexes, albeit nonsignificantly for males (for males: Pearson's  $R = 0.04$ ,  $N = 599$ ,  $P = 0.3$ ; for females  $R = 0.1$ ,  $N = 500$ ,  $P = 0.02$ ). Unsurprisingly, then, we found no evidence of variance inflation due to multicollinearity in

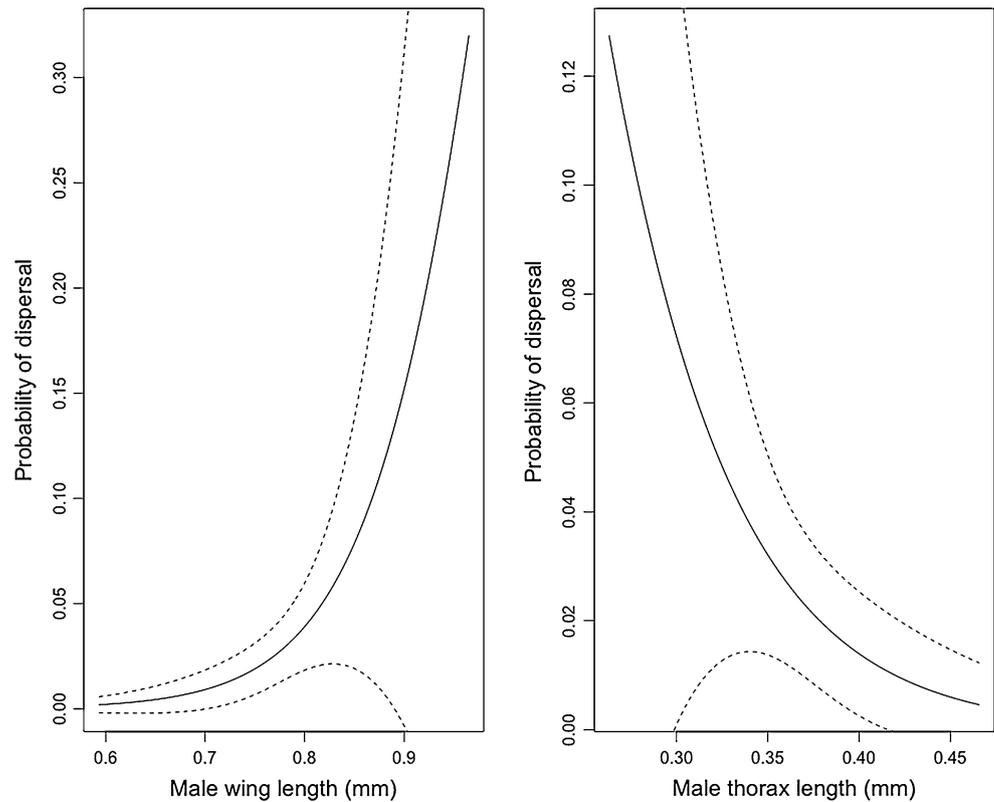
**Table 3** Parameter estimates for generalised linear models with quasibinomial error distribution modelling the influence of wing and thorax length on dispersal in 2010

	Parameter estimate $\pm$ SE	z-value	p value
<i>Females</i>			
(1) Disperse v all others			
Intercept	$-0.35 \pm 4.08$	-0.085	0.932
Thorax length	$-12.26 \pm 8.33$	-1.471	0.142
Wing length	$2.09 \pm 4.86$	0.431	0.666
<i>Males</i>			
(2) Disperse v all others			
Intercept	$-8.62 \pm 4.22$	-2.043	0.059
Thorax length	$-17.05 \pm 7.64$	-2.233	0.025*
Wing length	$14.86 \pm 5.09$	2.918	0.003*
(3) Disperse v re-sighted at 0 km			
Intercept	$-9.07 \pm 5.69$	-1.596	0.111
Thorax length	$-9.06 \pm 10.76$	-0.842	0.399
Wing length	$14.45 \pm 6.43$	2.248	0.025*
(4) Winner v Loser			
Intercept	$-13.69 \pm 8.33$	-1.641	0.1007
Thorax length	$19.8 \pm 11.72$	1.689	0.09
Wing length	$8.6 \pm 8.43$	1.02	0.3

The four separate panels summarize models for (1) dispersing females (1 km +) and total emerged females; (2) dispersing males (1 km +) and total emerged males; (3) dispersing (1 km +) and re-sighted males (at 0 km only); and (4) winning and losing males in territorial contests. Data from 2010

\*  $< 0.05$  significance

**Fig. 3** Plots showing fitted logistic curves with 95 % confidence interval (dotted lines) for the effect of male wing (left) and thorax (right) length on probability of dispersal. The data in this analysis include all emerged individuals, including those that were never re-sighted



any of our models. We built two models to assess how morphology affected dispersal. In the first model, we compared the subset of males captured away from the release site to all marked individuals. In this case, we found a strong positive effect of male wing length and negative effect of thorax length on dispersal probability (GLM,  $P < 0.05$ , Table 3, Fig. 3). However, we reasoned that this analysis might conflate morphological effects on survival to recapture with morphological effects on dispersal. To evaluate this possibility, we performed a second model including only the subset of re-sighted individuals (rather than all individuals released). Although the positive effect of wings persisted in this model (GLM,  $P < 0.05$ , Table 3), the parameter for thorax (although still negative) was smaller and nonsignificant. No effect was found of female wing or thorax length on dispersal in an analysis comparing dispersing females to all marked individuals (GLM,  $P > 0.05$ , Table 3), and consequently there was no need to explore any effect using a smaller subset of cases.

In total, 21 intersexual contests were recorded involving 23 uniquely identified males. Twelve of these contests involving 14 males took place at the release location. We attempted to fit a generalized linear mixed model to account for the presence of individual males more than once in this dataset, but unfortunately this model did not converge, perhaps due to the low sample size. Consequently we built a model with fixed effects only to explore

the effects of morphology on contest outcome, knowing that any significant effect should be interpreted with caution due to pseudo replication. This generalised linear effects model showed no effect of male wing or thorax length on the outcome of territorial contests (GLM,  $P > 0.05$ , Table 3), in spite of the trend for winning males to have larger mean thorax and wing lengths (Table 1).

Finally, we evaluated the effect of adult age on colour to assess whether older individuals could be discerned photometrically. In the linear model, adult age was positively associated with thorax shade (parameter estimate =  $0.12 \pm 0.01$  SE,  $F_{1,99} = 62$ ,  $P < 0.001$ ).

## Discussion

In Scotland, six of eight remaining *Hammerschmidtia ferruginea* sites are located in Strathspey (Rotheray et al. 2009). Each known site is separated by up to 5 km along a 40 km length of Strathspey, from the most southern at Creagan Bruegach to the most northern at Grantown-on-Spey (Rotheray et al. 2009). The findings in this study imply that *H. ferruginea* is capable of dispersing at least 5 km, suggesting the network of sites in Strathspey probably form a metapopulation, i.e. a group of unstable, local populations occupying discrete habitat patches linked by dispersal (Hanski 1998). Although large aspen stands (>5

Ha) are rare in Scotland, aspen is widely distributed, and recent surveys using aerial photographs have identified several small pockets of aspen woodland outside previously mapped areas in Strathspey (Worrell 1993; MacGowan 1997; Kouki 2008). *H. ferruginea* can probably detect and locate decaying aspen in these more isolated areas, using them as stepping-stones between larger woodlands, and as habitat availability fluctuates through space and time. This may explain how populations have survived in Strathspey while elsewhere they have declined.

A lack of deadwood can cause abrupt local extinctions, possibly isolating populations across the landscape. Current conservation management efforts aim to link up fragmented habitat for this hoverfly (*H. ferruginea* UKBAP Steering Group pers. comm.), and the findings from this study broaden the management options by enabling exploitation of more isolated aspen woodlands. However, it is important to note that fewer individuals will locate breeding habitat at greater distances. While as many individuals were observed at 3 km as there were at 1 km in 2009, in 2010 most dispersing individuals (68 %) were observed only at 1 km from the release location. Moreover, despite more than double the observation effort, fewer decaying logs to observe, and ~100 more marked individuals in 2010, the same number (28) were observed dispersing in both years. It is likely that stepping-stones augment *H. ferruginea* dispersal, but this result could also be due to several other factors. For example, differences in quality between the decaying logs within and between the two experiments may alter detection and attraction, or the location and direction of transects may have an effect. Indeed in 2009, the number of re-sighted individuals observed on the transect extending northeast was greater than those found to the south and southwest, which appeared to correspond with on-site prevailing wind directions. While wind direction will have an effect on dispersal propensity, it is also probably strongly affected by the landscape. Transects in 2009 extended south toward valleys where there are no aspen woodland. In 2010, more activity was observed at logs closer to and around Insh Marshes reserve, 4 and 6 km southwest from the release site. Breeding habitat has been continuous at the reserve for at least the last 20 years (Rotheray and MacGowan 2000; Rotheray et al. 2001, 2009) and may attract individuals from further north, perhaps by way of volatiles evaporating from the decay. Further investigation into movement patterns and processes of *H. ferruginea* in a landscape, and molecular, context could be informative both in terms of this species conservation management, and movement research.

For *H. ferruginea*, greater wing length may be important for dispersing to scarce and fluctuating resources. The first model, which included all emerged individuals caught that year, showed a strong positive effect of male wing length, and a negative effect of thorax length on dispersal. This

trend was evident from the second model, which included only re-sighted individuals, but the thorax effect was smaller and non-significant. This may suggest that both morphological traits are important (in opposite directions) for dispersal. However the reduced effect of the thorax coefficient in the second model may also suggest that part or all of its effect has to do with re-sighting probability (survival), rather than dispersal. Dispersal ability often positively correlates with indices of body size and wing length (Denno 1994; Hoffmann et al. 2007; Sekar 2011; Stevens et al. 2012). The sex difference in how morphology affects dispersal is unexplained, but it may relate to sex-specific selection on flight performance associated with intrasexual contests in males. Any such selection for performance could likewise feedback into dispersal ability. For example, dispersal ability to locate new sites may be advantageous if competition for territorial space is high (as observed in this study, and reported in Rotheray et al. 2009). The ability to disperse can have direct consequences on mating success in other insects (for example, the planthopper *Prokelisia dolus* (Hemiptera: Delphacidae) has a flightless morph which outcompetes those that are capable of flight in mating success; Langellotto et al. 2000). However, whether this is a factor affecting *H. ferruginea* is yet to be investigated.

We found no effect of morphological traits on winning contests, but it is important to note that our sample size was small and we had limited power in the analysis. We did find that wing and thorax lengths were on average, albeit non-significantly, larger in males that won contests, and this very preliminary observation warrants further study of the mating systems for these flies. Territorial behaviour in flies commonly involves male defence of oviposition sites to monopolize incoming females (Maier and Waldbauer 1979; Preston-Mafham 2001). Gravid females are attracted to the breeding site, and presumably to the particular areas that offer the best conditions for larval development. The hypothesised resource-dependant polygyny in this system was supported by the number of territories that overlapped with oviposition sites on the logs, and by males repeatedly defending these areas. While we could not directly study paternity success in the current experiment, we expect that males who patrolled and won contests for high quality territories achieve better insemination success with gravid females visiting the site (Thornhill and Alcock 1983).

If sexual selection based on resource defence polygyny is strong in *H. ferruginea*, it may have implications for the conservation genetics of this species. For example, if just a few males secure most of the copulations, this could dramatically reduce the effective population size. Current habitat management for *H. ferruginea* often involves cutting pieces off live aspen trees in an attempt to extend the time one aspen provides breeding habitat (Rotheray et al.

2009), but this results in reducing the area available for males to set up territories, potentially increasing the intensity of sexual selection and the resulting skew in mating and paternity success. This may have knock-on effects on genetic variation in *H. ferruginea* populations, a question deserving more scrutiny in future work.

#### Comparing adult fly measurements between years

All individuals had significantly smaller wings and thoraces in 2009 than those in 2010. The primary source tree in 2010 was fairly isolated at 8 km from known localities for *H. ferruginea*, and the tree had fallen and snapped at the base, whereas the main source for individuals in 2009 was a severed tree in the middle of a known locality for this species. Both sources were large whole trees that had been decaying and therefore available as breeding habitat for 3 years, and were not suitable as breeding habitat in subsequent years after the experiments as the rotting layer had dried out. The difference in fly size measurements between years i.e. the smaller individuals in 2009 may be a result of the poorer larval resource due to severing which appears to dry the rot faster. Testing this hypothesis would require experiments that assess the effects of severing trees on the rot layer.

#### Estimating adult age by thorax colour

For a detailed study of populations, it is advantageous to be able to estimate the age of individuals. Our work has confirmed that thorax shade provides a rough estimate of adult age in *H. ferruginea*, with our categorical assignments of thoracic shade capturing 38 % of the variation in adult age. Because this effect may vary in different climatic conditions, care should be taken when comparing between sites. However, this technique could be used to help monitor local populations, by indicating when, where and how adults are active, mating and ovipositing, and in which part of their flight period they may be.

#### Conservation management

Current *H. ferruginea* population declines have probably resulted from a lack of periodic storms that boost deadwood input (Rotheray et al. 2009). Due to the small size of aspen woodlands, enough dead wood is frequently not available for saproxylic insects that specialize on aspen. Functional connectivity among populations will depend on the natural tendency of flies to disperse which may in turn depend on population density. While *H. ferruginea* is rare, due to its dependence on a characteristically varying level of breeding resource, it may have evolved to cope with fluctuating levels of suitable fallen wood. When

breeding habitat is scarce, *H. ferruginea* have been found in sap runs, which occur on live, damaged aspen trees (Rotheray and MacGowan 2000). However, patch abundance and distribution may alter such that population dynamics break down, and continuity of breeding habitat within colonisation distance and through time is crucial (Grove 2002). In addition, the distribution and availability of floral resources may affect dispersal, and this will vary throughout the lifetime of individual flies, which can expand the flight period of *H. ferruginea* from May through to July (Rotheray et al. 2009). Studies of how breeding habitat quality, landscape elements and composition affect *H. ferruginea* dispersal may clarify factors limiting colonisation. Investigating movement dynamics at the landscape level could be achieved through non-invasive molecular techniques (Jonsson et al. 2003; Vinatier et al. 2011; Rotheray 2012).

While very little is known of the status of *H. ferruginea* outside the UK, these findings have implications across its Holarctic distribution. In continental Europe, trees are taller and thicker, and deadwood usually becomes available when they reach their natural age limit, rather than intermittent stormy conditions in Scotland (Rotheray et al. 2009). However, aspen is threatened throughout Europe (Kouki et al. 2004), and populations are likely to face similar circumstances where they need to disperse to locate deadwood within and between woodland, and where forest management has isolated populations. Conservation management should focus on maintaining breeding habitat continuity by supplementing gaps in dead wood in addition to creating new habitat by planting aspen within colonisation distance of about 5 km. It is also important to preserve existing aspen networks where natural dynamics can be relied on to produce new suitable breeding habitat.

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#### References

- Abràmoff MD, Magalhães PJ, Ram SJ (2004) Image processing with ImageJ. *Biophotonics Int* 11:36–42

- Bonduriansky R, Brooks RJ (1997) A technique for measuring and marking live flies. *Can Entomol* 129:827–830
- Denno RF (1994) The evolution of dispersal polymorphisms in insects: the influence of habitats, host plants and mates. *Res Popul Ecol* 36:127–135
- Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. *Annu Rev Ecol Syst* 33:1–23
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Hoffmann A, Ratna E, Sgro C, Barton M, Blacket M, Hallas R et al (2007) Antagonistic selection between adult thorax and wing size in field released *Drosophila melanogaster* independent of thermal conditions. *J Evol Biol* 20:2219–2227
- Jonsson M, Johannesen J, Seitz A (2003) Comparative genetic structure of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. *J Insect Conserv* 7:111–124
- Kouki J (2008) Aspen and forest biodiversity in North European boreal forests. In: Proceedings from 2008 HAG aspen conference, pp 1–6
- Kouki J, Arnold K, Martikainen P (2004) Long-term persistence of aspen—a key host for many threatened species—is endangered in old-growth conservation areas in Finland. *J Nat Conserv* 12:41–52
- Langellotto G, Denno R, Ott J (2000) A trade-off between flight capability and reproduction in males of a wing-dimorphic insect. *Ecology* 81:865–875
- MacGowan I (1997) The entomological value of aspen in the Scottish Highlands. Unpublished Malloch Society Research Report
- Maier CT, Waldbauer G (1979) Diurnal activity patterns of flower flies (Diptera: Syrphidae) in an Illinois sand area. *Ann Entomol Soc Am* 72:237–245
- Milankov V, Francuski L, Ludoški J, Stahls G, Vujic A (2010) Genetic structure and phenotypic diversity of two northern populations of *Cheilosia aff. longula* (Diptera: Syrphidae) has implications for evolution and conservation. *Eur J Entomol* 107:305–315
- Preston-Mafham K (2001) Resource defence mating system in two flies from Sulawesi: *Gymnonerius fuscus* Wiedemann and *Telostylinus* sp. near *duplicatus* Wiedemann (Diptera: Neriidae). *J Nat Hist* 35:149–156
- R Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: <http://www.R-project.org/>
- Rotheray GE (1991) Larval stages of 17 rare and poorly known British hoverflies (Diptera: Syrphidae). *J Nat Hist* 25:945–969
- Rotheray G (2001) Aspen, a vital resource for saproxylic flies. In: The biodiversity and management of aspen woodlands, proceedings from a one-day conference held in Kingussie, Scotland, on 25th May 2001, pp 29–31
- Rotheray EL (2012) The ecology and conservation of endangered saproxylic hoverflies (Diptera, Syrphidae) in Scotland. PhD thesis, University of Stirling
- Rotheray GE, MacGowan I (2000) Status and breeding sites of three presumed endangered Scottish saproxylic syrphids (Diptera, Syrphidae). *J Insect Conserv* 4:215–223
- Rotheray GE, Hancock G, Hewitt S, Horsfield D, MacGowan I, Robertson D, Watt K (2001) The biodiversity and conservation of saproxylic diptera in Scotland. *J Insect Conserv* 5:77–85
- Rotheray EL, MacGowan I, Rotheray GE, Sears J, Elliott A (2009) The conservation requirements of an endangered hoverfly, *Hammerschmidtia ferruginea* (Diptera, Syrphidae) in the British Isles. *J Insect Conserv* 13:569–574
- Sekar S (2011) A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? *J Anim Ecol* 8:174–184
- Speight MC (1989) Saproxylic invertebrates and their conservation. *Nature and environment series*, Council of Europe, Strasbourg, France
- Speight MCD, Monteil C, Castella E, Sarthou JP (2010) StN Database, In: Speight MCD, Castella E, Sarthou J-P, Monteil C (eds) Syrph the Net on CD:7 the database of European Syrphidae. ISSN 1649-1917 Syrph the Net Publications, Dublin
- Stevens VM, Trochet A, Van Dyck H, Clobert J, Baguette M (2012) How is dispersal integrated in life histories: a quantitative analysis using butterflies. *Ecol Lett* 15:74–86
- Thornhill R, Alcock J (1983) The evolution of insect mating systems. Harvard University Press, Cambridge
- Vinatier F, Tixier P, Duyck P-F, Lescouret F (2011) Factors and mechanisms explaining spatial heterogeneity: a review of methods for insect populations. *Methods Ecol Evol* 2:11–22
- Weisberg S, Fox J (2010) An R companion to applied regression. Sage Publications Inc., London
- Worrell R (1993) The location of aspen clones in Scotland. Unpublished report to Scottish Natural Heritage