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Modelling populations of *Erigone atra* and *E. dentipalpis* (Araneae: Linyphiidae) across an agricultural gradient in Scotland

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Abstract

Linyphiid spiders are important generalist predators of insects in agricultural habitats. Their ability to rapidly disperse and colonise disturbed habitats makes them important as a natural form of pest control, often present before other predatory groups arrive. This paper examines the distribution of *Erigone atra* and *E. dentipalpis*, which are amongst the commonest linyphiid species to be found on agricultural land in Scotland. The habitat preferences of these species were assessed using abundance and proportion data from 71 independent sites sampled using pitfall traps over 2 years and a selection of repeat first-year sites sampled during the second year, incorporating a range of land-uses from extensive moorland, through grasslands to intensive arable fields. *E. atra* dominated in autumn sown crops, and *E. dentipalpis* dominated at the other end of the agricultural management spectrum in low-intensity grasslands. Both species were considered absent from upland and moorland habitats. Linear regression modelling was used to create a model which best estimated the variance in proportions of *E. atra* in the catch across the sites using a selection of vegetation, soil, management and landscape variables. This model was based on data from 58 sites where *Erigone* species were abundant and explained 66% of the variation in *E. atra*. The variables included were increasing vegetation biomass above 50 mm and increasing levels of mixed grazing (both positive), and a combination of increasing plant species richness and vegetation stem density (negative). The efficiency of the model was examined using data from 13 sites which were sampled in the subsequent year to assess the effects of no changes and changes in land-use on the proportions of the two species. Only two sites were considered inaccurate (more than 20% different from the model), suggesting a relatively high level of accuracy. Interaction between the two species was tested for and not found to explain the differences in proportion observed. Comparisons with other studies were carried out, showing similar trends in proportions and in some of the variables identified as important. The influence of specific variables on each species is described in light of possible allometric-type effects, and the importance of these species for conservation and pest control in agriculture is discussed.

Keywords: *Erigone atra*; *E. dentipalpis*; Agricultural land; Modelling; Scotland

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1. Introduction

Linyphiid spiders (Araneae: Linyphiidae) are the most species-rich family of spiders in Britain, and are important predators of insects in most terrestrial habitats (Sunderland et al., 1986). Their strong tendency towards aerial dispersal by ballooning within disturbed habitats, such as those typical of agriculture, often result in linyphiid spiders being the first predatory group to arrive in cultivated areas (Weyman et al., 1995), and in these situations they are thought to limit the increases of pest populations before the arrival of more specific predators (Reichart and Lockley, 1984; Sunderland et al., 1986). Many studies have commented on the general distribution, life-cycle and behaviour of species from this spider family (e.g. Duffey, 1956; De Keer and Maelfait, 1988; Topping and Sunderland, 1992), and often one particular genus (*Erigone* Audouin) accounts for the majority of individuals investigated. Adults of this genus can be found throughout Britain, some widespread, others only from particular habitats. In agricultural systems, they are primarily ground-dwelling species, building webs predominantly over small depressions in the ground, feeding on small prey items such as Collembola, aphids and thrips (Sunderland et al., 1986; Alderweireldt, 1994).

Ten species of *Erigone* are currently known in Britain. Four were found in this survey, of which, two are considered common and widespread; *E. dentipalpis* (Wider) and *E. atra* (Blackwall). *E. promiscua* (O.P.-Cambridge) is widespread, but appears to be less common by comparison (Roberts, 1987). *E. aletris* (Crosby & Bishop) has only recently been recorded from Britain (Snazell, 1980), and although it is confined to south-east Scotland, its range is expanding (Stewart, 1997). Other members of the genus tend to be rare (*E. capra* Simon, *E. welchi* Jackson) or restricted to particular habitat types (*E. longipalpis* (Sundevall), *E. arctica* (White)) or high altitude (*E. tirolensis* L. Koch, *E. psychrophila* Thorell), and were not found in the present survey.

Regression models were used to determine the management and environmental factors which best estimate the distribution using proportion data for adult specimens of two of the commonest species of *Erigone* found on agricultural land in Scotland; *E. dentipalpis* and *E. atra*. These species are nearly always found together as they have almost identical life cycles, niches and habits (De Keer and Maelfait, 1988; Hänggi et al., 1995). However, recent surveys suggested that the relative proportions of each species varies across the agricultural land-use gradient. A review of previous ecological studies concentrating on spiders in agricultural systems indicated that differences in proportionate abundance were most pronounced between sites which differ greatly in management intensity. For example, in high intensity arable fields, such as autumn sown wheat, *E. atra* was more abundant than *E. dentipalpis* (Sunderland et al., 1986; Topping and Sunderland, 1992; Thomas and Jepson, 1997; Feber et al., 1998), whereas the reverse was found in less intensive sites such as established grassland habitats (Rushton et al., 1987; Rushton, 1988).

There are many possible reasons for this variation. De Keer and Maelfait (1988) found small differences in habitat preferences of *E. dentipalpis* and *E. atra* in pastures. For example, webs of *E. dentipalpis* females are almost only found in short-grazed areas during spring and summer, but those of *E. atra* are usually higher in the vegetation. Although it has been shown that web location has little relation to prey capture (possibly, but not exclusively, they provide a base for active prey capture (Alderweireldt, 1994)), this (and probably other) differences in microhabitat choices might explain why these species can coexist. In addition it is thought that the increase in numbers during the life cycle in any given habitat is closely followed by the rapid dispersal of most specimens, thereby preventing competitive exclusion proceeding to its conclusion, and leaving only a small fraction to give rise to the next years' populations (De Keer and Maelfait, 1988). Small scale differences in response to management and environmental variables therefore seem the most likely cause for the change in dominance within the two species across the larger agricultural ecosystem, with the question remaining which factors are the most important.

This work stems from a broader study investigating spider species diversity in relation to agricultural land-use (Downie et al., 1998) and identifying management and environmental elements that influence overall spider diversity using predictive modelling (Downie et al., 1999). Biodiversity on farmland is an increasingly important issue, with loss of species a commonly accepted result of modern farming (McLaughlin and Mineau, 1995; Potter, 1997). The stability at genetic and population levels is just as important as overall species richness. This paper investigates the factors controlling the populations of two species of farmland spider, both regarded as useful generalist predators, with the aim of identifying activities that maintain more stable populations of each species in the farming landscape to enhance overall species diversity, richness and pest control potential.

2. Material and methods

2.1. Sampling areas

Seventy-one sites were sampled from nine localities throughout mainland Scotland during 1996 and 1997 covering an agricultural land-use gradient of arable crops, through intensive pasture and silage fields, to upland extensive sheep grazing and crofting. Examples of heather moorland and gorse pasture were also included, but forestry was excluded. Some restricted land-use types such as the machair areas (restricted to the islands and coastal areas of north-western Scotland) or organic farming were not included. Fig. 1 shows the principal areas where trapping occurred during both years. Table 1 summarises the location, principal land-use and number of trap sites for each area. This spread of sampling sites was designed to replicate the land-use gradient across a broad range of altitudes, latitudes and geo-climatic conditions prevailing in Scotland.

Fig. 1. Map showing location of principal sampling areas in Scotland during 1996 and 1997. See Table 1 for numbers of sites and land-use type in each area.

2.2. Methods

Ground-layer spiders were collected using nine pitfall traps (plastic cups; 75 mm diam) placed 2 m apart in a straight line at each site. The trapping fluid used was propylene glycol and each trap was covered by a wire mesh (15 mm diam aperture) to prevent capture of small mammals and to reduce trap interference from farm stock. In total, 450 pitfall traps were operated on

Table 1
Number of pitfall trap sites at each sampling location (with approximate national grid reference for the centre of the sampling location), the year sampled and the principal agricultural land-use of the study area

Location	UK national grid reference	1996	1997	Principal land-use
Auchincruive	NS 37 23	2	–	Intensive dairy (cattle grazing and silage fields)
Dalwhinnie	NN 63 86	3	–	Heather moorland (extensive heathland)
East Linton	NT 56 76	4	–	Intensive arable crops (primarily intensive arable fields)
Skerray	NC 66 62	10	–	Crofting (small-scale, sheep and arable in a heathland/semi-natural landscape)
Tain	NH 84 79	7	–	Mixed farming (cattle, sheep and arable fields)
Crianlarich	NN 35 30	9	4	Hill farming (mainly semi-natural grassland with some cattle, sheep and silage fields)
Crieff	NN 94 24	15	11	Mixed farming (heathland, semi-natural grassland, cattle, sheep, silage and arable)
Ae	NY 04 89	–	11	Mixed farming (semi-natural grassland, cattle, sheep and arable fields)
Glensaugh	NO 62 77	–	10	Mixed farming (heathland, semi-natural grassland, cattle, sheep and arable)

50 sites during 1996, and 324 traps on 36 sites during 1997. Fifteen of the 1996 sites from Crianlarich and Crieff areas (see Fig. 1) formed part of the 1997 survey as a selection of repeat sites of varying land-use including some management changes, giving a total of 71 independent and 15 repeat sites over the 2 years. The traps were serviced at roughly 4-week intervals for 4 months, beginning in May of both years, ending early September. The material from all nine traps at each site was collected and bulked before identification of all spider species captured.

The use of pitfall traps for between site comparisons within spider species poses well known problems of variations in trap efficiency between the different habitats (see Toft and Riedel (1995) for an extensive discussion). However, the members of the *Erigone* genus are very similar in their ecology and behaviour, particularly *E. dentipalpis* and *E. atra*, living close to the ground (Sunderland et al., 1986) and having similar powers of dispersal (Blandenier and Fürst, 1998). With this in mind, numerical comparisons based on proportions of each species within each site were considered acceptable: the primary aim was to study the relationships between the two most common species at each site across a broad management gradient. Topping and Sunderland (1992) found similar ratios of these species occurring in relation to each other from both density (3.09:1 *atra*:*dentipalpis* individuals ratio with D-Vac) and pitfall trap (3.14:1) samples from winter wheat fields suggesting that the sampling method is largely independent. Where between site comparisons of abundance of the two species were investigated, non-parametric methods of analysis were used (Spearman's rank correlation).

2.3. Environmental and landscape variables

Table 2 lists the vegetation, soil, land-use/management and wider environmental variables collected. Vegetation data (means) were collected three times during each season (June–August) at approximately monthly intervals from a permanent 10 m×10 m quadrat located adjacent to the pitfall traps. Soil and environmental variables were collected during early May (except soil penetrability which was averaged from five samples per season), and management information was obtained from the land owners at the end of each season. A composite management index was devised to provide a single measure of management intensity for each site based on eight management variables labelled in Table 2; soil disturbance, cutting, grazing, inorganic fertiliser, organic manure levels, pesticides, sward type and age. Each was assigned a score on a four-point scale, from 0 to 3 in ascending order of intensity (e.g. Soil disturbance — (1): only harrowed once in previous 3 years (2): ploughed once in previous 3 years (3): ploughed twice or more in previous 3 years. Cutting — (1): topping only (2): one complete cut and removal of vegetation (3): two or more complete cuts and removal of vegetation). From the summation of these scores, the cumulative Management Intensity Index (MII) was compiled (giving a possible range of 0–24) for each site.

An initial investigation into multi-collinearity within the variables was performed and, as expected, there were very high correlations between some variables. For example, soil organic and moisture contents were significantly correlated across all sites sampled (r=0.87, df=70, p>0.001) and those included in the analysis of the proportion data (r=0.88, df=57, p>0.001). As a result, soil organic content and biomass total (the latter highly correlated with biomass above 50 mm) were removed from the analyses. All remaining data were transformed where necessary.

2.4. Analysis of E. dentipalpis and E. atra relationships with variables

The main aim of the analyses was to model the proportional data of each species across the agricultural gradient. Before this, Spearman's rank correlation was used to identify variables of importance in determining the abundance of each species across all 71 sites. This non-parametric approach allowed for the caution required when analysing pitfall traps and was used only for identifying potentially important species:variable relationships. However, this analysis also highlighted any differences in direction and magnitude of response of the species to the different variables. Variation in the proportion data could result from both species having different directions of response to significant variables (for example, if *E. atra* responded positively to any variable, yet *E. dentipalpis* responded negatively, this would cause a change in proportion across the variable range). If however, they showed differences in magnitude of response to the variables in the same direction,

Table 2
Vegetation, soil, land-use/farming methods and wider landscape/environment variables recorded for each site

Variable	Data and source
Biomass	Three measures of dry weight (g) from 20 cm×20 cm quadrat (below 50 mm, above 50 mm, total).
Canopy height	Mean height (cm).
Stem density	Mean density per 10 cm×10 cm quadrat.
Bare ground	Percentage estimate from m^2 quadrat.
Litter cover	Percentage estimate from m^2 quadrat.
Bryophyte cover	Percentage estimate from m^2 quadrat.
Plant species richness	Mean number per m^2.
Sward type[a]	Determined in the field (0) natural/semi-natural (1) sown/improved, now reverted (2) grass mixture (3) ryegrass ley).
Available P	Soil core analysis (mg/g from Acetic acid extract).
Available K	Soil core analysis (mg/g from Acetic acid extract).
PH	Soil core analysis (Calcium Chloride solution).
Moisture content	Soil core analysis (percentage water content).
Organic content	Soil core analysis (percentage loss on ignition).
Soil impenetrability	Soil penetrometer (kg/m^2 pressure)
Age[a]	Time since cultivated, obtained from farm records ((0) uncultivated (1) >10 years (2) 5–10 years (3) <5 years).
Cutting[a]	Intensity from farm records ((0) no cutting (1) topping only (2) one complete cut (3) two or more complete cuts).
Soil disturbance[a]	Obtained from farm records ((0) no disturbance (1) only harrowed in last 3 years (2) ploughed once in last 3 years (3) ploughed twice or more in last 3 years).
Grazing[a]	Number of cattle and/or sheep grazing units per ha (lu/ha).
Inorganic input[a]	Inorganic fertiliser levels (N, P and K) applied from farm records ((0) none (1) <50 kg/ha (2) 51–100 kg/ha (3) >101 kg/ha).
Organic input[a]	Organic fertiliser levels applied from farm records ((0) none (1) slurry (2) light manure dressing (3) heavy manure dressing).
Pesticides[a]	Intensity from farm records ((0) none (1) fungicide only (2) one herbicide and fungicide if used (3) two or more herbicide and/or insecticide and/or glyphosate).
Altitude	m above sea level.
Habitat type	(1) autumn crop (2) spring crop (3) root crop (4) set aside (5) intensive grass (6) improved grass (7) upland grassland (8) mires and heathland.
Habitat change	(0) same Habitat type as last year (1) change to different Habitat type
Area of field/habitat	Up to a maximum of 100 ha from traps.

[a] Variables included in management intensity index (MII; see text). A combined grazing score was created for the MII based on four categories ((0)=none (1)=low (<0.8 livestock units (lu/ha)) (2)=moderate (0.8–1.14 lu/ha) (3)=high livestock density (>1.14 lu/ha).

then the changes in proportion would be due to an allometric-type response (in this sense differential rates of response by the two species), which would validate any relationships found during the modelling process.

The proportion of *E. atra* relative to *E. dentipalpis* at each of the independent sites was then analysed using the Generalised Linear Interactive Modelling package (GLIM, Royal Statistical Society, 1992) to develop multiple regression models relating the proportion of *E. atra* to the variables at each site. Thirteen sites where less than five specimens of both species combined were found were removed before the modelling process, leaving 58 sites included in the model. The appropriate error pattern, link function and overdispersion procedures were used (binomial, logit and Pearson χ^2 scale directive, respectively within GLIM).

All variables in the data set were first considered independently to indicate which had the greatest influence on the model. Significance was assessed using the χ^2 approximation and *t*-tests on coefficients (Crawley, 1993). These variables were used as seeds for regression model development. Considerable care was taken in the interpretation of the results, especially when the parameters were marginally significant (*p* values between 0.05 and 0.01) or when they explained a small fraction of the variation, as the χ^2 might be misleading (more relevant in analyses involving 30 or less samples; Crawley, 1993). The effects of these variables were then considered when used in combination (and through interaction) with each other and the remaining variables. A minimum adequate model was then constructed (using both insertion techniques which added random variables to the initial best-fit variable, and deletion techniques which removed random variables from the maximal model) which explained the maximum significant fit with as few variables as possible.

The model was applied to the repeat sites to compare predicted *E. atr*a proportions with those actually recorded during 1997. Although these sites were not spatially independent, they nevertheless provide information on the effects of both no changes and changes in land-use and management on the *Erigone* proportions. The land-use at these sites during 1997 included low, medium and high intensity grassland and spring crops (autumn sown crops were not sown on the repeat sites so none were available for testing).

Finally, the abundance data for each species was modelled individually using GLIM (Poisson error, log link and Pearson χ^2 scale directive) to test for interaction between the species. The residuals of the maximal model (all variables) related to each species were obtained and correlated. If a positive relationship was found between the species after all variables were extracted, then this would indicate that some variation was still unaccounted for through an unmeasured variable, or that if some level of interaction exists between the species, it does not explain the differences in proportion observed. A negative relationship would suggest that there was an interaction influencing the results, and no relationship would suggest that all variables included in the maximal models fully explained the variation.

3. Results

A total of 30,546 *Erigone* specimens was collected from the 71 independent sites over the 2 years, with a further 6594 taken from the 15 repeat sites sampled during 1997 (see Table 3). *E. dentipalpis* and *E. atra* comprised 63.5 and 34.4% of the combined total, respectively. The only other species of *Erigone* found were *E. promiscua* and *E. aletris*, which represented only 1.7 and 0.4% of the total catch, respectively.

Table 4 shows the results of the Spearman's rank correlations relating the different variables with the abundance of both *E. atra* and *E. dentipalpis* at all sites. The most important environmental variables indicated for *E. dentipalpis* were cattle grazing levels, soil pH and impenetrability (all positive). The most important variables for *E. atra* included plant species richness, bryophyte cover, soil moisture (all negative) and soil pH, available P (both positive). In addition, habitat type and MII were important, both indicating that, as general management increases, be it on the MII scale or by the broad land-use categories included in Table 2, *E. atra* populations increased. These results are constrained by the problems with pitfall trapping and should be treated with caution, hence the non-parametric approach.

Table 4 also shows that both species respond to each variable of importance in the same direction, or where there is a difference in direction, then one of the scores is non-significant, as in the case of stem density. This suggests that both species are responding in the same direction to each variable measured, and it is the differences in magnitude of response (or importance of the variables) which is influencing the differences in proportions found (an allometric-type response). These differences include lower amounts of litter cover, higher stem density and greater soil impenetrability which were more associated with *E. dentipalpis* numbers than *E. atra*. In contrast, *E. atra* was more associated with low plant species richness, low biomass below 50 mm, higher levels of available P and lower altitudes.

Sites with small numbers of *E. dentipalpis* and *E. atra* tended to be heather dominated or wet upland grassland, and these were removed from the binomial model analysis. Fig. 2 shows the remaining 58 sites classified into five main land-use groups (autumn and spring crops and three grassland groups based on management intensity) and the proportion of *E. atra* taken at each site. Autumn sown crops had the highest proportion of *E. atra* present, followed by spring-sown crops and then grassland ($F_{4,53}$=18.5, p<0.001). There was little difference among the three grassland categories, although the results suggest that *E. atra* increases in proportion as intensity increases. These findings equate well with the results from the Spearman's correlations, with *E. dentipalpis* preferring the more compacted and established grassland areas and *E. atra* crop situations.

Table 5 shows the importance and significance of each individual variable included in the binomial

Table 3
Land-use, management intensity index (MII) and numbers of *E. atra* and *E. dentipalpis* found at each site during 1996 and 1997

Area	Site	1996 Land-use	MII	*E. atra*	*E. dentipalpis*	1997 Land-use	MII	*E. atra*	*E. dentipalpis*
Auchincruive	AU1	Silage and cattle grazing	15	305	618				
	AU2	Cattle grazing	12	376	618				
Dalwhinnie	CM1	Young heather	3	0	0				
	CM2	Old heather	1	0	0				
	CM3	Recently burnt heather	7	1	0				
East Linton	MM1	Winter barley	20	115	2				
	MM2	Winter wheat	18	142	2				
	MM3	Spring oil seed rape	17	79	14				
	MM4	Winter oil seed rape	17	12	1				
Skerray	SK1	Hay meadow	5	15	517				
	SK2	Rough grazing	3	1	4				
	SK3	Sheep grazing	11	31	324				
	SK4	Wet rough grazing	4	0	0				
	SK5	Sheep grazing	4	22	223				
	SK6	Extensive grass	2	1	405				
	SK7	Heather	2	0	0				
	SK8	Turnips	10	3	2				
	SK9	Forage rape	9	12	37				
	SK10	Swedes	13	16	33				
Tain	RH1	Cattle grazing	9	340	609				
	RH2	Spring barley	16	302	287				
	RH3	Setaside	8	450	657				
	RH4	Silage and sheep grazing	12	138	396				
	RH5	Winter wheat	17	159	31				
	RH6	Winter barley	17	173	58				
	RH7	Winter oats	16	233	87				
Crianlarich	KHUS1	Heather	1	0	0				
	KPLS1	Extensive grass	1	4	8	Extensive grass	1	0	7
	KPLS3	Improved mixed grazing	4	7	348	Mixed grazing	2	9	707
	KPLS4	Extensive grass	1	0	4				
	KPLS5	Extensive grass	4	1	217				
	KPUS1	Extensive grass	1	0	0	Extensive grass	1	0	0
	KPUS3	Extensive grass	4	0	0				
	KPVF2	Silage and sheep grazing	12	427	518	Silage and sheep grazing	11	711	473
	KPVF3	Extensive grass	4	0	0				
Crieff	SALS2	Spring oil seed rape	15	74	76	Spring barley	16	297	169
	SAMS1	Spring barley	17	196	237				
	SAVF1	Spring barley	17	189	210	Spring oil seed rape	16	206	211
	SAVF2	Setaside	9	23	5	Setaside	7	70	33
	SGUF1	Gorse scrub grassland	1	0	6	Gorse scrub grassland	1	3	35
	SHUF1	Heather	1	1	0	Heather	1	0	0
	SHUF2	Recently burnt heath	4	11	18	Heather	2	15	39
	SPMS1	Silage and mixed grazing	13	175	558	Silage and mixed grazing	11	165	690
	SPMS2	Spring barley	15	187	323	Spring barley	14	348	499
	SPMS3	Cattle grazing	10	100	364	Cattle grazing	7	176	887
	SPUF1	Sheep grazing	4	321	474	Sheep grazing	1	30	192
	SPUS2	Sheep grazing	10	165	665				
	SPVF1	Mixed grazing	5	217	152	Mixed grazing	12	191	264
	SPVF2	Mixed grazing	6	382	878				
	SSLS2	Winter barley	15	250	283				
Glensaugh	GS1					Heather	1	0	0
	GS2					Extensive grass	7	41	722
	GS3					Heather	1	1	0

Table 3 (*Continued*)

Area	Site	1996 Land-use	MII	*E. atra*	*E. dentipalpis*	1997 Land-use	MII	*E. atra*	*E. dentipalpis*
	GS4					Silage and sheep grazing	15	305	1358
	GS5					Gorse scrub grassland	1	4	13
	MK1					Winter barley	16	162	91
	MK2					Cattle grazing	12	171	612
	WP1					Hay meadow	12	529	345
	WP2					Spring barley	16	244	288
	WP3					Spring oil seed rape	16	279	250
Ae	BC1					Extensive grass	1	57	321
	BC2					Sheep grazing	5	86	617
	BC3					Cattle grass	5	62	266
	BC4					Extensive grass	1	15	16
	DF1					Cattle grazing	8	161	293
	DF2					Silage and cattle grazing	16	346	394
	DF3					Spring barley	19	262	659
	DF4					Winter wheat	17	754	448
	DF5					Cattle grazing	16	268	459
	DF6					Setaside	12	753	1056
	DF7					Fodder Beet	16	390	904

analysis. Because of the large number of variables available for testing and the necessary caution required in identifying marginally significant variables, significance was taken at $p<0.01$. Habitat type proved to be the predictor which explained the most variation in the proportion data, followed by five variables associated with vegetation structure. These variables were used as the starting points for further GLIM analyses. The large number of variables which represent a significant proportion of the variance (see Table 5) is probably an artefact of the multi-collinearity of many of the variables, i.e. they explain similar proportions of model variance. The next step was to find the variables which among them represented the maximum significant variation in *E. atra* proportions.

Table 4
Significant Spearman's rank correlations between variables and *E. dentipalpis* and *E. atra* abundance*

Variable	*E. dentipalpis*	*E. atra*
Plant species richness	−0.19	−0.58*
Litter cover	−0.35*	−0.12
Bryophyte cover	−0.39*	−0.53*
Stem density	0.39*	−0.04
Biomass below 50 mm	−0.07	−0.39*
Cattle (lu/ha)	0.59*	0.48*
Soil pH	0.43*	0.60*
Available P	0.31	0.55*
Moisture	−0.35*	−0.56*
Soil impenetrability	0.52*	0.29
MII	0.37*	0.68*
Altitude	−0.21	−0.38*
Field/site area	−0.34*	−0.46*
Habitat type	−0.30	−0.62*
Change in habitat	0.31*	0.48*

* Significance taken at $p<0.01$, variables which were not-significant against both species are not shown.

Each variable was added to the different starting variables in turn, and subtracted from the maximal model, including interaction variables. Table 6 shows the final results (minimum adequate model) of the GLIM analysis, which explains 66.2% of the variation in proportion of *E. atra* relative to *E. dentipalpis*. Increasing vegetation biomass above 50 mm accounted for the largest variation, positively explaining 41.5%. The addition of decreasing plant species richness further altered the explained variation by 14.8%, and low stem density another 2.8%, although when considered alone, stem density was not significant. However, when both plant *S* and density were combined through interaction, this altered the explained variation by 20.3%, additional to the biomass above 50 mm model, which had a significant and negative effect on the *E. atra* proportion. Neither sheep nor cattle grazing intensity added to the percentage explained when considered individually: however the product of cattle and sheep grazing added a further 4.5% to the explained variance, a significant effect, in-

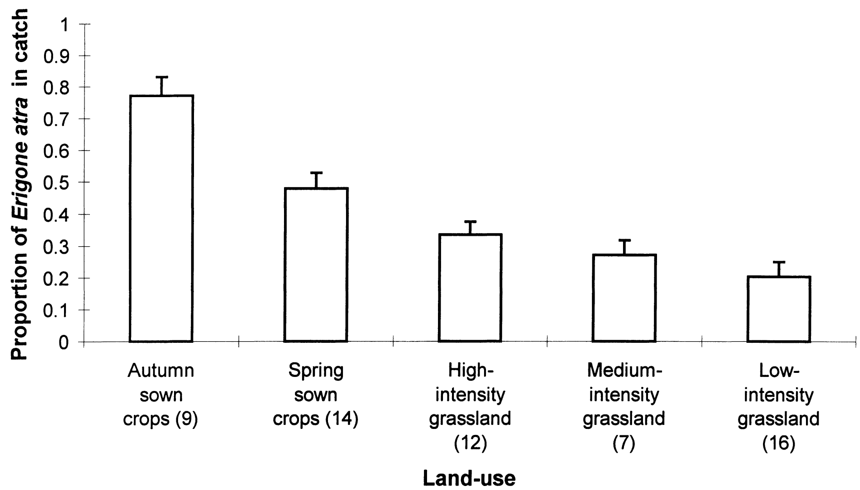

Fig. 2. Mean proportion (±s.e.) of *E. atra* relative to *E. dentipalpis* taken in the catch at each main land-use. Grassland has been classified into three groups based on their Management Intensity Index scores which ranged between 1 and 16 (low: 0–5, medium: 6–10, high: 11–16). Numbers in parenthesis indicate number of sites in each land-use category.

Table 5
Percentage variance accounted for (in decreasing importance) by considering each environmental variable independently using GLIM, against the proportion of *E. atra* taken across the sites

Variable	Significant	Variable	Not significant
Habitat type	53.0	Field/site area	8.0
Biomass above 50 mm	41.5	Bryophyte cover	6.4
Stem density	40.8	Available P in soil	7.6
Canopy height	40.5	Cattle (lu/ha)	0.2
Plant species richness	36.3	Organic input	0.02
Biomass below 50 mm	31.5	Available K in soil	0.01
Soil disturbance	30.9		
Pesticides	27.8		
Sward type	26.3		
MII (see text)	24.4		
Age	21.4		
Inorganic input	21.0		
Cutting intensity	20.7		
Bare ground	20.5		
Altitude	20.1		
Soil moisture content	17.7		
Soil impenetrability	17.2		
Sheep (lu/ha)	16.2		
Litter cover	15.4		
Habitat change	12.8		
Soil pH	11.6		

dicating that when grazing levels were high from both types of livestock, *E. atra* proportions increased. Although the categorical variable habitat type explained the greatest variation of all initial variables, the value of 53% deviance accounted for could not be improved with additional single or interactive variables without loss of significance of parameters. Thus, using the necessary transformations, the proportion of *E. atra* in the combined species catch is best represented by:

$$\frac{1}{1+(1/\exp(-a+(\text{Biomass}\times b))-((\text{Plant } S \times\text{Density})\times c)+((\text{Cattle}\times\text{Sheep})\times d))}$$

where a, b, c and d represent the coefficient estimates shown in Table 6 and where × indicates interaction with.

The predictive efficiency of this model was examined further using the repeat sites sampled in 1997. Only 13 of the 15 sites were used for predictive testing as two sites recorded less than five individuals of either species (during 1996 and 1997). Table 7 shows the expected proportions of *E. atra* at each site using the above model compared with the actual proportion found. Eight of the sites (60%) were closely predicted (within 15% of the actual found), including SHUF2, an area of recently burnt heather with a high grass content. Only two sites predicted were more than 20% different. These latter sites were a silage/grazing field at Crianlarich (KPVF2:

Table 6
Amount of variation in proportion of *Erigone atra* accounted for by considering vegetation biomass above 50 mm, vascular plant species richness, vegetation stem density, cattle and sheep grazing (in lu/ha) together in the GLIM analysis in the null model[a]

Source	Deviance accounted for	Change in d.f.	Percentage explained
Biomass above 50 mm	26.54	1	41.5
Plant (*S*) × Stem density	12.96	1	20.3
Cattle × Sheep	2.86	1	4.5
Model deviance	42.36		66.2
Residual deviance	21.63	54	
Coefficient estimate[b]	**SE**	**Parameter**	***t*-value**
−0.6255 (*a*)	0.1999	1	
0.0236 (*b*)	0.0075	Biomass (>50 mm)	3.15***
−0.0004 (*c*)	0.0001	Plant (*S*) × Stem density	3.20***
0.4021 (*d*)	0.2348	Cattle × Sheep	1.71*

[a] Total deviance=63.99; d.f.=57; Probability distribution=Binomial; Link function=Logit; Scale parameter=77.10; × indicates interaction with.
[b] *a* to *d* relate to the model present in the text.

32%) and a set aside field at Crieff (SAVF2: 33%). Both sites were underestimated, suggesting that there was perhaps some landscape or management variable not measured influencing the proportion variation.

Testing for interaction between the species, the maximal models produced using GLIM using abundance data (natural log) explained 80% (*E. atra*) and 78% (*E. dentipalpis*) of the variation. The residuals produced from the analysis of each species were obtained and compared, and a significant and positive relationship was found (r=0.58, df=70, p<0.001). These results confirm that there may still be some variation within the environment or management which has not been sampled influencing both species, or that if some level of interaction exists between the species, it does not explain the differences in proportion observed.

Similar patterns in the relative proportions of *E. atra* have been found in many other studies, using a variety of sampling methods, in the UK and Ireland. Table 8 provides a comparison of the mean values of *E. atra* found in each of the main land-use categories (presented in Fig. 2). Comparable, but highly variable results are obvious. Autumn sown crops are high in *E. atra*. Spring crops are also high, but lower than autumn

Table 7
Predictive testing of the binomial model showing expected values of *Erigone atra* proportions compared to actual values found during 1997

Site	Land-use in 1997	Expected proportion (%)	Actual proportion (%)	Percentage difference (%)
KPLS1	Wet grassland	18.5	0.0	18.5
KPLS3	Improved pasture	6.8	1.3	5.5
KPVF2	Grazing and silage	28.3	60.1	31.8
SALS2	Spring barley	43.8	63.7	19.9
SAVF1	Spring oil seed rape	43.0	49.4	6.4
SAVF2	Setaside	35.2	68.0	32.8
SGUF1	Scrubby grassland	10.9	7.9	3.0
SHUF2	Recently burnt heather	31.2	27.8	3.4
SPMS1	Grazing and silage	35.2	19.3	15.9
SPMS2	Spring barley	55.2	41.1	14.1
SPMS3	Grazing	25.6	16.6	9.0
SPUF1	Grazing (*Juncus* grassland)	28.5	13.5	15.0
SPVF1	Grazing	37.4	42.0	4.6

Table 8
Comparison of proportion of *E. atra* relative to *E. dentipalpis* in catch with literature data

Landuse	This survey mean (±s.e.)	Literature value	Source	Trapping method
Autumn sown crops	0.77 (±0.06)	0.91	2 sites: Sunderland et al. (1986)	Hand search
		0.76	2 sites: Topping and Sunderland (1992)	Suction+Pitfall
		0.80	4 sites: Thomas and Jepson (1997)	Suction
		0.85	3 conventional farmed: Feber et al. (1998)	Pitfall
		0.91	3 organically farmed: Feber et al. (1998)	Pitfall
		0.83	Combined data from six autumn+two spring-sown sites: White and Hassall (1994)	Pitfall
Spring sown crops	0.48 (±0.05)	0.61	2 sites: Duffey (1978)	Emergence
High-intensity grassland	0.33 (±0.04)	0.84	3 sites: Thomas and Jepson (1997)	Suction
		0.49	2 sites: Topping and Lövei (1997)	Pitfall
Medium-intensity grassland	0.27 (±0.05)	0.24	7 sites: Luff and Rushton (1989)	Pitfall
		0.14	3 sites: Downie et al. (1996)	Pitfall
Low-intensity grassland	0.20 (±0.05)	0.07	2 sites: Luff and Rushton (1989)	Pitfall
		0.00	9 sites: McFerran et al. (1994)	Pitfall

sown crops, and grasslands show a gradual decrease as management intensity decreases. The values for autumn sown crops are in general higher (76–91% *E. atra*) than those found during this survey (77%). Also, the high-intensity grasslands were considerably higher (49–84% compared to only 33%). Despite these differences within land-use type, the overall trend of autumn sown crops being dominated by *E. atra* relative to *E. dentipalpis*, and the reverse for low-intensity grasslands, is clear and apparently independent of sampling method.

4. Discussion

The binomial modelling process identified three variables (or combinations of variables) which best reflect these differences; vegetation biomass above 50 mm, plant species richness and structural density combined, and levels of mixed cattle and sheep grazing. Autumn-sown crops represent the sites sampled with highest levels of plant biomass above 50 mm throughout the year, as by June, when the first vegetation measurements were taken, these sites already had a high canopy compared with the spring-sown crops. This aspect of vegetation present throughout the winter may be important for *E. atra* populations. Both species are successful colonisers of recently disturbed habitats (Weyman et al., 1995), shown by the almost equal proportions of both species in spring-sown crops. However, it appears that *E. atra* is more successful if there is a stable canopy cover over the winter, just after disturbance events such as ploughing and crop sowing which allow colonisation. Dispersal of these species relies on specific climatic conditions (Duffey, 1956) but is usually motivated by stress on the populations such as food shortage (Weyman et al., 1995) or harvesting (Blandenier and Fürst, 1998). A combination of these factors results in maximal dispersal events of both species occurring during October and November (De Keer and Maelfait, 1988; Blandenier and Fürst, 1998), although ballooning can occur in any month. Ironically, neither biomass above 50 mm nor canopy height were correlated with log abundance of either species (Table 4), strengthening the argument that it is timing of the disturbances and subsequent succession that influences the data most (also suggested by Duffey, 1978).

High numbers of plant species and high stem density were not favourable situations for high proportions of *E. atra*. Crops were both species poor and had a less complex structural component in comparison with grassland habitats, which correlated with lower proportions of *E. atra*. Edwards et al. (1976) also found a strong negative relationship (r=−0.61) between *E. atra* and increasing plant richness, and commented on *E. atra* increasing in numbers in high yield–low species grasslands.

Grazing by either cattle or sheep had no significant influence on the model. However, in combination they represented an increase in *E. atra*. Ironically, grazing tends to reduce the vegetation biomass and frequently diversifies the sward, which would suggest fewer *E. atra* specimens. It is possible therefore that it is the actual physical intensity of mixed grazing which provides a habitat which *E. atra* is able to colonise successfully. Cattle and sheep grazing combine to make a sward that is both uniform and closely cropped, different from the sward resulting from either just cattle or sheep (Nolan and Connolly, 1977; Vallentine, 1990), where some degree of structural heterogeneity usually persists. Under normal conditions (i.e. not over-grazed) swards grazed by sheep tend to develop tussocks through selective grazing (Grant et al., 1985; Frame, 1992), and swards stocked with cattle develop distinct dung-heap areas which are not grazed (Forbes and Hodgeson, 1985). Although the variables described above represent the maximum variance for describing *E. atra*, the opposite effects must influence *E. dentipalpis* in a similar fashion. This may explain the effect of grazing on the proportions found. As mixed grazing increases, it may have a more detrimental effect on *E. dentipalpis* populations than *E. atra*, thus *E. dentipalpis* abundance decreases more rapidly than *E. atra* giving the latter a higher proportion in the catch (the allometric-type effect again). This may be evident for several variables, but only important for those included in the model.

Interaction between the two species of spider was excluded as contributing to the habitat preferences and proportions found. Although they have almost identical life cycles, niches and habits in pasture areas in Belgium, De Keer and Maelfait (1988) concluded that they probably coexist without exclusion of one another through dispersal processes. However, in this broader land-use situation in Scotland, clear preferences for particular habitats, and the factors probably influencing this distribution are evident.

The residual variation not explained in the model is most likely a combination of landscape structure and some specific management technique (or timing of) not recognised in this survey. Linyphiid dispersal is greatly influenced by land-use type, with higher levels of dispersal activity occurring in cereal fields compared with perennial grass fields (Thomas and Jepson, 1999). This is probably because of a variety of factors associated with a gradual deterioration of habitat quality with time, such as unfavourable changes in microclimate (Geiger et al., 1995) or shortages in food resources (Weyman et al., 1994). These observations may have important consequences for conservation and pest control in intensively managed agricultural landscapes. Maintaining populations or metapopulations of each species in the environment is probably self-regulating if the landscape consists of a patchwork of varying land-use, all acting as sources and sinks of dispersal and colonisation (Thomas and Jepson, 1999). The variation and rotation in the mixed farming situation means that populations of either species will never be excessively low during periods of the year, with dispersal behaviour refounding local extinctions (Gilpin and Hanski, 1991). However, large fields within an intensive arable landscape will result in lower proportions of *E. dentipalpis*, as well as lower densities of linyphiid spiders in general (Halley et al., 1996), especially if the trend in the area is for autumn-sown crops.

The allometric-type response pattern has strong implications for habitats managed for the conservation of specific species. The apparent spectacular differences in proportions between the different habitats sampled here may in reality be the result of small differences in response to variables that are otherwise very similar. Even if species have similar ecology (which is usually measured in crude terms like positive or negative responses to environmental variables), the actual effects of habitat manipulations, for farming or conservation purposes, can produce extremely dissimilar results between species. Hence, in situations where specific biodiversity programmes target single or few species by habitat conservation management, an awareness must be made of the possible detrimental effects on the other species within the same niche. After all, overall biodiversity is just as important as individual species within the environment.

Maintaining both species of *Erigone* within the local environment through landscape diversity has distinct advantages for agriculture. It allows a pool of predatory spider species to exist in the agricultural ecosystem (Sunderland et al., 1986) which will adapt to differential responses to changes in management or the environment, maintaining a greater degree of pest control.

The binomial modelling process used in this analysis was not intended to identify the specific relationships between the variables and each species (other authors have highlighted specific relationships not discussed here, e.g. positive correlations between soil P and K and both *E. atra* and *E. dentipalpis* have been shown by Edwards et al., 1976), rather it aimed to present an indication of how best to estimate the relative proportions of each species in the catch. Although only 66% of the variation was explained by the minimal model, the results nevertheless suggest that relatively accurate predictions of *E. atra* and *E. dentipalpis* presence can be made across the Scottish agricultural gradient examined here. This approach has formed a useful first step in estimating the numbers of these agriculturally important species. Further sampling from a wider range of sites or from other existing datasets would facilitate more accurate testing of the model.

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