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Original article

Faecal sampling along trails: a questionable standard for estimating red fox *Vulpes vulpes* abundance

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In most studies that estimate abundance of foxes from faeces counts, scanning is done along trails and roads or along linear features such as hedges, because it is supposed that foxes defecate mainly along these structures. As a consequence, only part (i.e. trails or linear features) of the total habitat is searched and results are possibly biased if usage by foxes of these searched features is subject to spatial or temporal variation. We therefore investigated three methods for counting red fox *Vulpes vulpes* faeces, that differ in the shape of the sampling units: trails and two alternatives; i.e. transects and squares. We searched for faeces using these three methods in two study areas (the Upper Rhine Valley and the Black Forest valleys) at 61 study plots and found a total of 257 fox faeces. Methods for estimating abundance should ideally have high accuracy and high precision. As actual fox densities in the areas were unknown, we were unable to assess the accuracy of our sampling methods and thus focused on method precision. We fit separate negative binomial regression models for each method with the number of faeces found as the dependent variable and a set of landscape variables as possible explanatory variables. The transect method detected significant differences in the number of faeces found between the study areas and was most precise. Even though we did find more faeces with the trail method, the precision of this method was lower than that of the transect method. For the methods trail and square, variance in the number of faeces found was large in comparison to their mean. Bias caused by methods that only sample part of the habitat is not limited to faecal counts and red fox studies, but can also occur with other species and methods.

Key words: Black Forest, faeces count, population estimate, red fox, road, trail, Vulpes vulpes

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Reliable, unbiased estimates of species abundance are often desirable in wildlife management. A wide variety of field methods are available to allow estimation of abundance, but if the species under investigation is elusive and the area of interest is large and densely forested, most of these methods are not effective. In this case, faeces counts are a cost-effective method and have a high correlation with abundance (Schauster et al. 2002). There is a vast amount of research on a wide range of species where faeces counts are used to either derive an index of abundance (e.g. Storch 2002, Acevedo et al. 2007, Jenkins & Manly 2008, Pita et al. 2009) or, with the help of additional information, estimate absolute abundance (e.g. de Boer et al. 2000, Lunt et al. 2007, Acevedo et al. 2010). There is great variety in the manner in which faeces counts are conducted. Faecal accumulation-rate techniques are based on an initial clearance of faeces, followed by a search after a fixed time period, whereas faecal standing-crop techniques measure overall abundance of faeces (Campbell et al. 2004). Counts have been conducted in quadratic or circular plots, transects or along linear features such as hedges, trails and roads.

For foxes and other canids, systematic surveys along trails, roads and other linear features are often used (e.g. Virgós et al. 2002, Harrison et al. 2004, Sadlier et al. 2004, Webbon et al. 2004, Virgós & Travaini 2005, Baker & Harris 2006, Beja et al. 2009, Mangas & Rodríguez-Estival 2010), because trails are easy for field workers to walk, visibility is normally good, foxes are assumed to prefer moving and defecating along these features (Macdonald 1980) and faecal accumulation-rate techniques can easily be applied. Searching along linear features for signs of foxes is presumed to be effective, because it is supposed that more faeces are found when searching in this way, resulting in more precise estimates. However, selectively searching only minor parts of the fox habitat, such as trails, may introduce severe bias if fox behaviour with regard to the searched parts differs across the study area or changes through time. De Boer et al. (2000) conducted elephant *Loxodonta africana* dung pile counts on transects and roads. In grass plains, mean dung pile density on transects was significantly higher than on roads, whereas in forests and woodlands, transects and roads had similar dung frequencies. Harmsen et al. (2010) suspected that for neotropical mammal species, there are differences in capture probability for camera traps placed on trails, depending on the surrounding vegetation. Further, Stanley & Bart (1991) showed that roadside habitat biased abundance estimates for red *Vulpes vulpes* and gray foxes *Urocyon cinereoargenteus* in Ohio, USA, based on a snow track survey of roads. To our knowledge, possible bias through the selective investigation of only certain habitat areas has not been investigated so far for counts of fox faeces. We hypothesised that foxes use trails, roads and linear features more often when the surrounding habitat is more difficult for them to walk in (i.e. in densely vegetated or steep terrain). This would introduce bias if the habitat varies across the study area.

In our study, we investigated three methods for counting red fox faeces that differ in the shape of their sampling units: trails and two alternatives; i.e. transects and squares. We conducted fieldwork in two different physiographic areas of southwestern Germany. We aimed to assess the precision of the three methods, as it is linked to the ability of identifying possible differences between the areas and factors that might influence fox abundance.

Methods

Study area

Our study was conducted around Freiburg, in

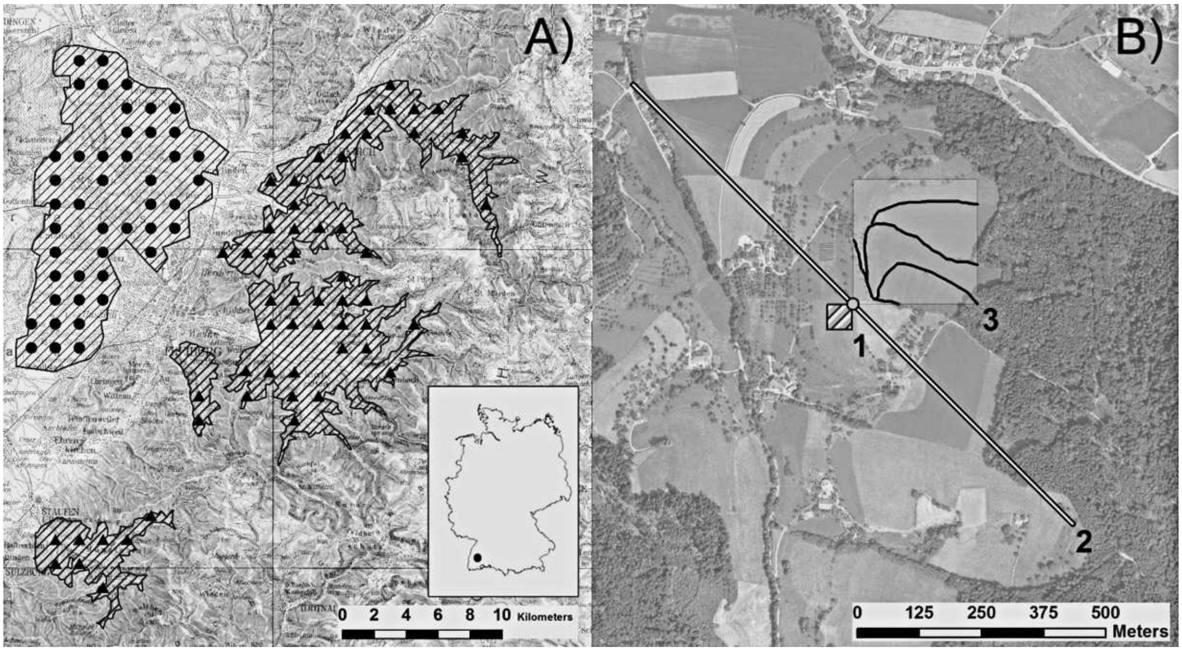

Figure 1. Study plots within the two study areas: Upper Rhine Valley (●) and Black Forest valleys (▲), A), and layout of the three sampling units at a study plot: (1) squares, (2) transects and (3) trails, B).

southwestern Germany (Fig. 1A). The area is characterised by steep geographic and climatic gradients. At the time of our study, information on fox densities was not available for the Freiburg area. In general, red fox home-range sizes and population densities in southern Germany appear to vary with the availability of natural and anthropogenic food resources and shelter (Vos 1995, Kaphegyi 2002, Janko 2003). We selected the following two study areas that were different with regard to elevation, relief, climate and landscape pattern to test the methods in different settings: the Upper Rhine Valley and the Black Forest valleys. The Upper Rhine Valley is located west of Freiburg, with a maximum altitude of 220 m a.s.l., an average annual temperature of about 10°C and an average annual precipitation of about 750 mm. A majority of the landscape is used as farmland, with arable fields, meadows and some pastures. Within this matrix, some mixed deciduous woodlots are present. The Black Forest valley study areas are east of Freiburg, within an altitudinal range of 300-600 m a.s.l. The average annual temperature is around 8°C with the average annual precipitation at around 1,250 mm. Pastures dominate the valley floors, which are often only a few hundred metres wide and surrounded by steep slopes covered mainly by mixed-species forests.

Survey design

First, we superimposed a grid over a map of our study area, with grid lines spaced 1.5 km apart. Grid points that fell within one of our two study areas were used as the midpoint of a study plot (see Fig. 1A). At each study plot, we used three different methods to search for fox faeces: squares, transects and trails. The square method consisted of systematically scanning a 50 × 50 m square for faeces, and the transect method of scanning a 1,250 × 2 m strip. The approximate amount of time needed to search a square or transect was one hour. For the trail method, all dirt roads and trails within a 250 × 250 m square were scanned systematically. If the total distance of trails within the square was insufficient, adjoining trails were also searched, as long as the total search time amounted to one hour. Hence, systematic scanning of one sampling unit took about one hour with each method, making the comparison of precision realistic. The three methods (sampling units) were arranged at each study plot as shown in Fig. 1B, with the orientation being assigned randomly.

Data collection

All fieldwork was conducted by one person, which precluded observer bias. We alternated between study areas daily. Within each study area, we chose study plots randomly. We investigated the three sampling units at one study plot on the same day. We quantified faecal standing crop, i.e. the total amount of faeces at the 61 study plots with all three methods (resulting in 183 sampling units), between 14 November 2008 and 13 March 2009. We chose this sampling period because of the good visibility due to sparse ground vegetation. Of the 61 study plots, 30 were in the study area Upper Rhine Valley and 31 in the Black Forest valleys.

We identified fox faeces according to their size, shape, odour and content (Bang et al. 2005). As stated above, we hypothesised that the surrounding habitat will affect trail use by foxes. To consider the effects of the close surroundings, we determined mean slope (Slope) and the percentage of the two non-forest land cover types, arable fields (Arable Field) and grasslands (Grassland), for each sampling unit. Further, we described the surrounding landscape, in a 1.5-km radius circle around the midpoint of each study plot, using the percentage of arable fields (SPArable Field), grasslands (SPGrassland), forest (SPForest) and settlements (SPSettlement) as well as an index of landscape heterogeneity (SPShannon). We calculated landscape heterogeneity using the Shannon Index (Shannon 1948) with the proportions of the four land cover types: settlements, forest, grassland and arable fields. We used the German Authoritative Topographic Cartographic Information System (ATKIS) to extract the landscape data with the geographical information system (GIS) program ArcGIS 9.2 (ESRI, Environmental Systems Research Institute, Inc., Redlands, California, USA).

Data analysis

A sound method for estimating abundance has both high accuracy (i.e. no bias) and high precision (i.e. low variation of the estimate). Actual fox densities were unknown, and there was no reference available to assess accuracy of our sampling methods. We therefore focussed on the precision of the methods. We fitted separate generalised linear regression models (GLM) for each method, with the number of faeces per sampling unit as the dependent variable and the variables mentioned above as independent variables. For each of these models, we performed model selection based on Akaike's Information

Criterion (AIC; Akaike 1973), with a correction for small sample size (AIC_c), to identify the model with the best fit (i.e. minimal AIC_c) out of all possible models. For the GLMs, we used the negative binomial family. Hence, we assumed that the number of faeces followed a negative binomial distribution: $Y_i \sim NB(\mu_i, k)$ with $E(Y_i) = \mu_i$ and $var(Y_i) = \mu_i + \alpha \mu_i^2$, where $\alpha = 1/k$.

We evaluated the precision of each method by comparing the heterogeneity parameter, α, from the negative binomial models. The variance of the negative binomial is comprised of two terms, μ_i and $\alpha \mu_i^2$, where μ_i relates to the Poisson variance and $\alpha\mu_i^2$ to the extra variance; the larger the α, the more extra variance is added to the model and $\alpha = 0$ yields the Poisson model (Hilbe 2011).

Each study plot was searched using the three above mentioned methods. If the methods are unbiased, precise and not driven by small-scale differences, their results should have high correlation. Hence, we compared methods across study plots. We calculated rank correlation between the results from the methods, using Kendall's tau. Moreover, counts from one method should have explanatory value for counts from the other two methods. We constructed two models with the trail data and the square data as the outcome and the transect data as the regressor. To these models we added the covariates mentioned above. We calculated relative importance and full model averaged coefficients for the covariates, based on all models with delta $AIC_c < 2$ (Burnham & Anderson 2002). If two methods measure the same, there should be no further regressors in the regression of the results of one method on the results of the other method. Therefore, the analysis enabled us to look at the relationship between the methods. We used a $\log_{10}(x+1)$ transformation on the transect counts.

In all models, we standardised the covariates (by subtracting the mean and dividing by the standard deviation), as the regression estimates from standardised covariates reflect effect size. Proportion of forest was not included, because it is a linear combination of proportion of arable fields, grasslands and settlements. In all models for the trail method, different lengths of trails searched were adjusted for by adding the log transformed length as an offset in the model. We used the Kruskal-Wallis test to check for differences between the methods in the number of faeces found. We carried out calculations using the statistical software package R (R Development Core Team 2011) using the MASS-glm.nb, MuMin-dredge and MuMin-model.avg functions.

Genetic identification

Another source of bias in estimates of abundance using signs, such as faeces counts, is false identification of these signs (Davison et al. 2002). We used restriction fragment length polymorphism (RFLP) analysis to genetically decipher if the faeces found really were from foxes. We estimated the rate of misidentification based on a random sample of 80 out of the 257 faeces collected. DNA was extracted using the QIAGEN stool kit. A 436 base-pair fragment of the cytochrome b gen was amplified and the polymerase chain reaction (PCR) product digested using restricted enzymes Eco47I and KspAI to obtain a species specific restriction pattern for red fox.

Results

Only 42 of the 80 randomly selected faecal samples for genetic identification could be sequenced due to low DNA quality and quantity. Of these 42 samples, 40 were from foxes and two could not be positively identified, although one was most likely from a dog. Hence, we assumed a misidentification rate of two out of 42, which corresponds to 4.8% (95%-confidence interval: 0.06; 0.16).

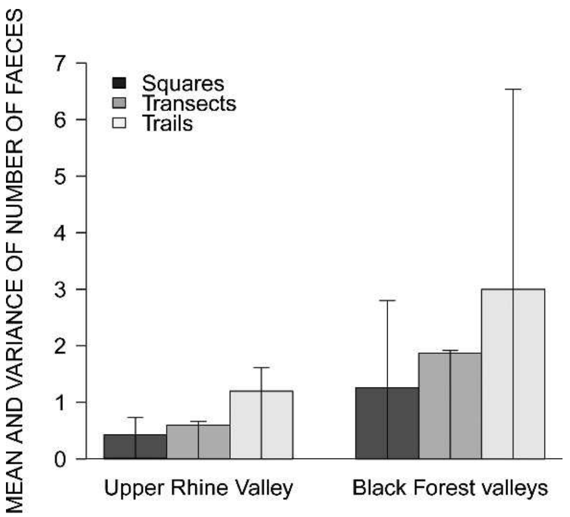

Figure 2. Mean (bars) and variance (T) of the number of faeces found per sampling unit within the two study areas for the three sampling methods.

Table 1. Estimated effect size (β), standard deviation (sd) and p-values (P) of the covariates in the best negative binomial model to estimate precision for the methods: transects, trails and squares.

Variable	Transects			Trails			Squares		
	β	sd	P	β	sd	P	β	sd	P
Black Forest valleys	0.41	0.15	0.008		-			-	
Grassland	0.33	0.12	0.007		-		0.70	0.20	< 0.001
Arable field		-		0.35	0.13	0.006	0.46	0.23	0.048
SPSettlement		-			-		0.31	0.18	0.080
SPGrassland		-		0.30	0.11	0.006			
Slope		-		0.58	0.12	< 0.001	0.62	0.21	0.003

We found a total of 257 red fox faeces. In both study areas the trail method yielded the highest number of faeces and the square method the lowest (Fig. 2). Differences in the number of faeces between the three methods were significant at the 5% level. Between study areas, we found that the mean number of faeces in the Upper Rhine Valley was lower than in the Black Forest valleys. Variances for the methods trails and squares were larger than their means and in the Black Forest valleys they were even double their means (see Fig. 2). Variance was equal to the mean (as expected for Poisson distributed data) only for the transects method.

Table 1 shows the models used to evaluate precision, after variable selection was performed. The transects model included the fewest covariates: study area and grassland. The trails and squares models both included arable fields and slope, with the squares model additionally including grassland and SPSettlement, and the trails model SPGrassland. The transects model was the only model with significant differences between the two study areas. Approximately twice as many faeces were found in the Black Forest valleys as in the Upper Rhine Valley.

Table 2. Relative variable importance (RI) and full model averaged coefficients (averaged β) of the negative binomial models, with the trail data and the square data as the outcome and the transect data as the regressor.

Variable	Trails		Squares	
	RI	Averaged β	RI	Averaged β
Log(transect data)	1.00	0.42	1.00	0.88
Slope	1.00	0.69	0.58	0.23
Arable field	1.00	0.35	0.37	0.15
SPGrassland	0.60	0.14	0.24	-0.07
Black Forest valleys Valleys	0.54	-0.23	0.00	-
SPShannon	0.10	-0.01	0.21	-0.07
Grassland	0.00	-	0.48	0.18
SPArable	0.00	-	0.17	0.05
SPSettlement	0.00	-	0.30	0.08

The heterogeneity parameter α, as a measure of precision, was smallest for the method transects (< 0.001), intermediate for the method trails (0.1) and largest for the method squares (0.3).

Rank correlation between the transect method and the trail method was 0.45 ($P < 0.001$, $N = 61$) and between the transect method and the square method it was 0.48 ($P < 0.001$), whereas correlation between the trail method and the square method was only 0.22 ($P = 0.038$).

In the regression of the transect data on the trail data, we used the five best models ($\Delta AIC_c < 2$; Table 1 in Appendix I) for full model averaging. The transect data, slope and arable fields were included in all of these five models. Slope had the largest averaged effect size (averaged $\beta = 0.69$; Table 2), followed by the transect data (averaged $\beta = 0.42$) and arable fields (averaged $\beta = 0.35$). In the regression of the transect data on the squares data, 22 models were ranked best (Table 2 in Appendix I). AIC_c values of all these models were very similar. The model with the lowest AIC_c included only the transect data, which was the only variable that was included in all of these models (RI = 1) and had the largest averaged effect size (averaged $\beta = 0.88$; see Table 2). Slope and grassland had medium relative importance of 0.58 and 0.48, respectively, but averaged effect size was only 0.23 for slope and 0.18 for grassland (see Table 2).

Discussion

Our study indicated that transects may be better suited in detecting differences in red fox faeces density than other sampling designs. Sampling along trails and linear features, which is commonly considered the best method in fox faeces counts (Webbon et al. 2004), was clearly less effective. Although more faeces were found using the trail method (see Fig. 2), the method transects had the highest precision and hence most power in detecting differences in relative faeces abundance.

Sampling of squares had the lowest precision, with the model for estimating precision seeming to be driven by the small scale preference of foxes for habitats of high food availability (large and intermediate effect sizes of arable fields and grassland, respectively). This was not surprising as the distribution of faeces is often clumped (Lunt et al. 2007) and therefore square plots are likely to have extreme counts (either zeros or high numbers), which result in lower precision. Long rectangular plots of the same area, such as transects, allow for the surveying of a cross sectional area, which increases variation within the sampling units and reduces variation between them, thereby increasing precision (Thompson 2002).

At each study plot, we searched using the three methods. If methods are unbiased and precise, their results should be highly correlated. We found high correlations between the method transects and the other two methods (at least high for estimates of relative abundance; compare Acevedo et al. 2010). In contrast, correlation between squares and trails was much lower. The results of the regression of the transect data on the trail and the square data showed that even though the correlation between transects and trails and transects and squares was of similar magnitude and the models for estimating precision included similar variables, they did not measure the same. No further regressors remained in the best regression model of the transect data on the square data. However, in the model for the trails method, many additional variables remained, of which slope had the largest effect size, and not the transect data. The analysis showed that the trails method measured something different from what the transects or square methods measured. Unfortunately, we could not show that these differences were due to bias through slope in the method trails, because no information was available to determine which method was the closest to the true abundance. Serious errors could be made, if the factor that introduces bias changes between the units of comparison (e.g. years or sites). For example, if sampling on trails is biased by slope, then comparison between sites with different magnitudes of slope can result in differences between sites when in fact they are the same or *vice versa*. Sampling based on non-random selection of sample units, such as trail counts, will probably provide more biased estimates compared to those obtained through random design.

The fact that the percentage of grassland in the sampling unit had a positive effect in the transects and squares model, but was not included in the trails model, might indicate that in grassland it is easier for foxes to walk through the vegetation so that trails are less utilised in this habitat. On the other hand, this could also have been caused by better visibility in grassland and/or higher faeces prevalence, as foxes have been reported to prefer grassland for feeding (Storch et al. 2005). Another indication that there might be differences across habitats in fox trail usage was that arable fields had a positive effect in the trails model. For the squares model, we hypothesised that a positive effect of arable fields indicated higher small-scale usage of this habitat due to increased food availability. The trails model should not be affected as much by such small-scale differences, though, and this could therefore be an indicator that, when in arable fields, foxes prefer using trails.

The sampling period (mid-November - mid-March) was longer than in most studies and included two quite different periods with regard to red fox behaviour: the end of the dispersal period (around October through February; Kaphegyi 2002) and the mating period (December through March; Macdonald & Reynolds 2004). There may be differences in the use of trails between these periods, as dispersers might use trails more frequently (compare Cavallini 1996, Soulsbury et al. 2011). Further, Goszczynski (1990) found decreased defecation rates during the mating period, due to lower food availability. Such seasonal differences could have influenced our abundance estimates, but we did not find indications for temporal autocorrelation or bias in the residuals of the three regression models.

The actual fox densities were unknown, making it impossible to assess the accuracy of the methods or determine the bias of the trails method conclusively. All selective behaviour of the species under investigation that is linked to the survey method can cause bias in methods that sample only particular parts of that species' habitat. For example, foxes might use trails less in areas that are high in human disturbance or hunting pressure. Ideally, methodological studies should be carried out at locations where species population size is known, to identify and quantify sources of bias; however, for foxes this is rarely possible. Our study showed that although sampling on trails produced the greatest mean number of faeces found, transect sampling had the highest precision. In general, transect sampling is more likely to cover a representative sample than other methods with similar effort. We suggest researchers choose methods that sample representative parts of all habitat types (such as transects), if selective behaviour of the species under investigation cannot be precluded and the habitat changes across the study area. Further, more research should be addressed at investigating sources of bias in counts along trails, roads and/or linear features, not only for foxes but also for other species where counts of signs are used to derive estimates of abundance.

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Appendix I

Table 1. Best ranked models ($\Delta AIC_c < 2$) of the negative binomial regression, with the trail data as the outcome and the transect data as the regressor.

Variables included	AIC_c	ΔAIC_c	Weight
Log(transect data) + Slope + Arable field + Black Forest valleys + SPGrassland	206.6	0	0.204
Log(transect data) + Slope + Arable field	206.9	0.29	0.177
Log(transect data) + Slope + Arable field + SPGrassland	207.1	0.46	0.162
Log(transect data) + Slope + Arable field + Black Forest valleys	207.8	1.17	0.114
Log(transect data) + Slope + Arable field + Black Forest valleys + SPGrassland + SPShannon	208.6	1.96	0.076

Table 2. Best ranked models ($\Delta AIC_c < 2$) of the negative binomial regression, with the square data as the outcome and the transect data as the regressor.

Variables included	AIC_c	ΔAIC_c	Weight
Log(transect data)	135.2	0	0.081
Log(transect data) + Slope + Arable field + Grassland + SPGrassland	135.4	0.19	0.073
Log(transect data) + Slope + Arable field + Grassland	136	0.8	0.054
Log(transect data) + SPSettlement + SPShannon	136	0.81	0.054
Log(transect data) + SPSettlement	136.1	0.94	0.05
Log(transect data) + Slope + Grassland + SPGrassland	136.3	1.16	0.045
Log(transect data) + Slope + Arable field + Grassland + SPSettlement + SPShannon	136.4	1.22	0.044
Log(transect data) + Slope	136.5	1.3	0.042
Log(transect data) + SPGrassland	136.6	1.42	0.04
Log(transect data) + Slope + Arable field + Grassland + SPSettlement	136.7	1.52	0.038
Log(transect data) + Slope + Grassland + SPArable + SPShannon	136.7	1.53	0.038
Log(transect data) + SPShannon	136.7	1.55	0.037
Log(transect data) + Slope + Grassland + SPGrassland + SPArable	136.8	1.65	0.035
Log(transect data) + Slope + Grassland + SPGrassland	136.8	1.65	0.035
Log(transect data) + Arable field	136.9	1.76	0.033
Log(transect data) + SPArable	136.9	1.76	0.033
Log(transect data) + Slope + Arable field + Grassland + SPGrassland + SPSettlement	136.9	1.77	0.033
Log(transect data) + Slope + Arable field + Grassland + SPShannon	137.1	1.93	0.031
Log(transect data) + Grassland + SPSettlement + SPShannon	137.1	1.95	0.03
Log(transect data) + Grassland	137.1	1.96	0.03
Log(transect data) + Slope +SPSettlement	137.1	1.96	0.03
Log(transect data) + Slope + Arable field	137.1	1.97	0.03