Temporal and spatial distribution patterns of *Scathophaga stercoraria* (Linnaeus, 1758) in a Mediterranean oak forest

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Abstract

From May 1987 to April 1988, 7260 specimens of the Yellow Dungfly, *Scathophaga stercoraria* (LINNAEUS, 1758), were trapped in a Mediterranean oak forest in the North West of Spain. The specimens were captured by pitfall traps baited with bovine dung.

The spatial and temporal activity patterns of *S. stercoraria* are studied. Yearly and daily flight activity are also considered. **Key words**: *S. stercoraria* daily flight, activity patterns, Mediterranean forest.

Résumé

De mai 1987 à avril 1988, 7.260 exemplaires appartenant à l'espèce *Scathophaga stercoraria* (LINNAEUS, 1758) ont été piégés dans une chênaie du nord-ouest de l'Espagne. Les exemplaires ont été capturés avec «pièges à fosse» appâtés de la bouse de vache.

On examine l'activité spatiale et temporelle, annuelle et journalière de cette espèce.

Mots clés: *Scathophaga stercoraria*, activité journalière de vol, modèle d'activité, forêt méditerranéenne.

Introduction

Decaying organic matter temporarily forms microhabitats capable of sheltering many organisms. Herbivorous droppings are an example of this kind of environment and dung from cattle is an important source of attraction for coprophilous insects (FINNE & DESIERE, 1971; GRAEF & DESIERE, 1984).

The first colonizers of faeces are Diptera. Among them, the Yellow Dungfly, *Scathophaga stercoraria* (LINNEAUS, 1758), is perhaps the most widespread fly in the world (GORODKOV, 1986). Adults of this species visit droppings, often in considerable amounts, and are depredators of many of the coprophilous Diptera living there (SEGUY, 1934; SYCHEVSKAYA & VTOROV, 1969; ROJO & MARCOS-GARCIA, 1991). Nevertheless, adults also show secretophagous habits (PAPP, 1985) and can be regarded as an intermediate link between both obligated and facultative hematophagous taxa (PRIDANTSEVA, 1967). The larval stages of this species develop in the dung with either a coprophagous diet (COTTERELL, 1920) or a zoophagous one (SEGUY, 1951; GORODKOV, 1986).

Animals living in this kind of habitat must adapt their life cycle to a rapid succession which finally turns into resource destruction (KOSKELA, 1979). These, species have to be well adapted to search other similar sites (SOUTHWOOD, 1977) and develop spatial-temporal behaviour strategies which maximize the resource usage (HANSKI, 1980a).

There are papers on the flying activity of some flies (NUORTEVA, 1965; HANSKI & NUORTEVA, 1975; GILBERT, 1985) and PARKER (1970, 1974) explains the spatial and temporal distribution of males of *Scathophaga stercoraria*, and the duration of their copulation, as results of selection towards equalized fitnesses of different types of behaviour. In this paper we investigate some factors which influence the diurnal activity patterns of *Scathophaga stercoraria* focusing on the following objectives: (1) to determine the spatial and temporal activity patterns of *S. stercoraria*, (2) to examine their interrelations, and (3) study their variations according to the population evolution during the year.

Materials and methods

EXPERIMENTAL SITE. The study was carried out in a pasture-grounded oak forest situated in Aldehuela de la Bóveda (Salamanca, Northwest of Spain) located at coordinates 40° 52' N., 6° 3' W (29TQF4926, U.T.M.), with an altitude of 803 meters above sea level. The forested ground is rather degraded by the clearing of the original vegetation, and presents a weak erosion with losses of depth and organic matter in the uppermost horizon. The studied area is placed in the Mediterranean-Iberoatlantic zone of the Iberian Peninsula, which is characterized by a cold winter, a hot dry summer, and rather scarce precipitation which is remarkable in springtime and autumn. The bioclimate is Mesomediterranean, varying arround the dry and sub-humid ombroclimates (RIVAS-MARTINEZ, 1987). The dominant vegetation is a Mediterranean oak forest basically composed of *Quercus rotundifolia* LAMARCK. Under human influence, it has formed a clear-felled savanna-like woodland denominated «dehesas» (GALANTE *et al.* 1991). The presence of irrigated cultivations close to the oak forest has to be stressed.

METHODS. For the capture of adults we used pit-fall traps (Fig. 1) according to the HANSKI model (1980b) which we have successfully used in other studies about coprophagous Diptera (LOBO *et al.* 1988; ROJO & MARCOS-GARCIA, 1990, 1991).

The traps were baited with fresh bovine cattle scum in amounts of approximately 950-1000 cc (1150 grams). Ethylene-glycol at 50% was used as preservation liquid.
For the daily activity study, the daily section was divided into three time periods (according to MENA *et al.* 1989):

period A: morning

period B: afternoon

period C: evening

The traps were not withdrawn during the night but no adult activity was ever detected during this period. Since the durability of these periods is not constant during the year, hours of collection were fixed depending on the season (Table I).

- At the end of each period the captured specimens were removed and the bait was changed for fresh faeces.

The study was carried out during the period between May, 1987 and April, 1988 with monthly samples taken during 48 hour periods. 8 traps were disposed (4+4) in two parallel lines from the wooded oak forest area. Each trap was situated 20 meters away from the following one, in this way a gradient was created according to the vegetal cover from the dense wooded area (T-1 trap) to the part where the vegetation was totally lacking (Fig 1).

- The fact of putting 2 parallel lines results from the aim pursued of reducing possible changes of the environment that the researcher cannot control.

- 7,260 specimens of *S. stercoraria* were captured and they are now deposited in the entomology collection of the Departamento de Ciencias Ambientales y Recursos Naturales of the Universidad de Alicante (Spain).

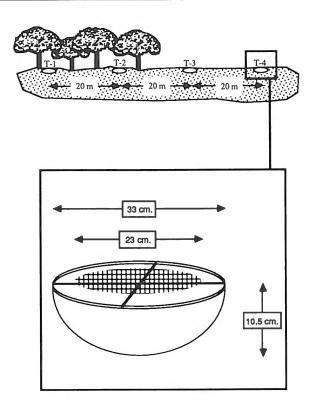


Fig. 1 – Location of the traps in the studied area traps T-1 and T-2 in the wooded area; traps T-3 and T-4 in the open pasture. Figure of pit-fall trap builtaccording to HANSKI, 1980b.

DATA ELABORATION. In order to estimate the degree of adult activity, the number of individuals obtained in each sample was divided by the number of hours of the time period when they were captured. In the period A, moreover, the first 90 minutes were eliminated because no kind of adult activity was detected during the whole year.

The study of the spatial-temporal distribution has been carried out at two levels:

a) First an individualized analysis of both environments (oak forest and pasture area) was done to check out if the two traps placed in each environment could be considered as replicates.

	A period ^(*)	B period ^(*)	C period ^(*)
Spring	5.30-10.30 h.	10.30-16.30 h.	16.30-19.30 h.
Summer	5.00-11.00 h.	11.00-17.00 h.	17.00-20.00 h.
Autumn / Winter	7.00-12.00 h.	12.00-16.00 h.	16.00-18.00 h.
(*) Solar time	La		L]

Table 1 - Duration of selected periods through the year.

b) A joint analysis of both environments was carried out. In order to detect if significant differences between the spatial-temporal adult activity of each period exist -in traps or environments according to the analysis level-, the statistical test of variance analysis was used (ANOVA). This kind of test allows us to contrast the equality between two or more population means using independent samples.

An ANOVA was used with two interaction factors. One of the results of the two days of sampling was considered as a replicate. In this way we have taken into consideration the time period factor with the following levels: A, B, C and the environment factor with levels T-1 and T-2 or T-3 and T-4 -according to the environment- for the individualized analysis or with oak forest and pasture area levels, for the joint analysis.

The fact of studying the interaction between both agents is very important in the study of the spatial-temporal distribution since one agent levels do not have to act in a similar way to the other's levels. For this reason if the ANOVA detected an interaction existing between both factors it was decided to study it by carrying out the necessary contrasts between each of the affected levels. TUKEY test was used for the comparison between contrasts.

The variance analysis is a statistical test which needs the started populations to have normal distribution and to have homogeneity of variances. These hypotheses were verified by using the DAVID test and the BARTLLET test respectively. Data were transformed by the expression ln(n+1) in order to get the homogeneity of variances.

Results and discussion

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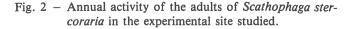
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The annual activity and several data about the biology of this species have already been the objective of a



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previous study (ROJO & MARCOS-GARCIA, 1991). In this paper a seasonal model of activity between September and June was given. At the same time the activity of the adults drastically decreases in summer (Fig. 2).

The period of the presence of the adults embraced three seasons. We have analysed in an isolated way the activity model of the adults between seasons, assuming in each of them that the climatological conditions are not homogeneous during the year.

I. - Spatial-temporal activity during autumn

The adults of S. stercoraria gradually appear during autumn after the summer diapause period. The number of captured adults during this period of the year is scarce (4% of all the captures) and it is greatly influenced by the variability of the external climatological conditions. Thus, in years with winters characterized by extremely cold temperatures (e.g.: a range between -8C and 10C, average of 5C) and little humidity, the rate of population increase during the winter does not correspond with that of the autumn. For this reason, in years with winters without such extreme temperatures and humid autumns the total number of individuals in both seasons will increase according to the cold and dry years, as it corresponds to our data (ROJO & MARCOS-GARCIA, 1991). The low number of specimens obtained in this season does not allow the realization of an exhautive statistical analysis of the data, so we will analize the spatialtemporal dimension of the S. stercoraria in this period of the year in a percentage form.

The analysis of the spatial distribution indicates a clear preference of the species for the open pasture area (72.43%). This general behaviour can be clearly seen in the formation of an increasing abundance from the traps arranged in the thick oak forest area (T-1 and T-2) to the pasture without vegetation (T-3 and T-4) (Fig. 3).

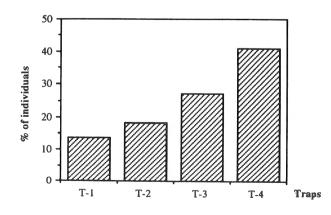


Fig. 3 – Increasing number of captures from traps displayed in the oak forest area (T-1, T-2) to those in the pasture without vegetation (T-3,T-4), during autumn.

Through the above mentioned selection it avoids the highest extreme temperatures as it spends most of the time under the effects of solar radiation. This tendency is general in autumn but it becomes more pronounced when winter comes.

With regard to the daily activity, the situation is not so uniform and an attempt to explain it thoroughly can lead us to wrong conclusions, since there are notable differences between the activity of the adults from the beginning to the end of the season. Thus, the largest number of specimens were captured during the beginning of autumn, when the daily mean temperature was still relatively high. Due to this, most of the individuals occupied the period C. On the other hand, the rest of the specimens belonging to the samples of the end of the season have been captured nearly totally during the period B, when they could profit from the warmer hours of the day and counteract the progressive decrease in temperature (Fig. 4).

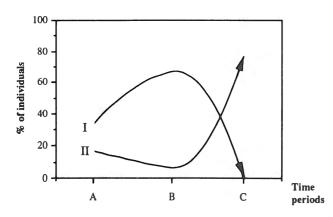


Fig. 4 – Daily activity (in three time periods) of *S. stercoraria* at beginning (II) and end (I) of the autumn.

S. stercoraria manifests, during the autumnal period a clear tendency to occupy the faeces of the cattle which are sited in the open pasture area (Fig. 5). This tendency is less obvious at the begining of the season when the period C is the one which presents a degree of higher activity. This could be on one hand because the daily temperatures are still relatively high for the optimum of the species in this period (ROJO & MARCOS-GARCIA, 1991); on the other hand because of competition which exists with other species of coprophilous flies which have their high activity during the periods A and B (ROJO & MARCOS-GARCIA, forthcoming). At the end of autumn when the temperature gets lower, most of the adults tend to occupy the faeces deposited in the pasture, profiting from the central hours of the day when the influence of the sun is greater (period B).

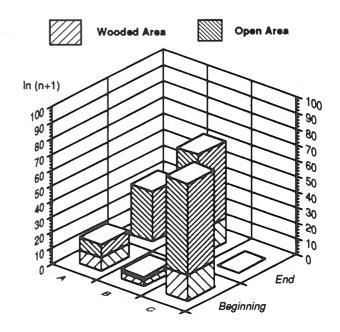


Fig. 5 – Spatial-temporal activity of *S. stercoraria* adults during autumn.

II. - Spatial-temporal activity in winter

Scathophaga stercoraria, is one of the few coprophilous flies adapted to resist the hard climatological conditions of this season -it is practically the only coprophilous fly present- and if temperatures are not too low it develops normally and reaches a considerably high number of individuals.

The activity of adult *Scathophaga stercoraria* in the wooded area (34.87%) is clearly lower than in the pasture area. Moreover the hourly distribution of the adults changes markedly in both areas. Thus, in the oak forest

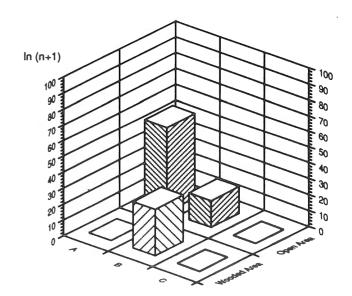


Fig. 6 – Temporal and spatial distribution pattern of S. stercoraria during wintertime.

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		T-2 vs. T-3	6.107	*
*		Г-2 vs. Т-4	6.662	**
*		Γ-3 vs. T-4	0.563	
-	*		* T-3 vs. T-4	* T-3 vs. T-4 0.563

Table 2 - Comparison between traps during winter.

all the individuals are concentrated in the period B (as much in the T-1 trap as in the T-2 one). Notwithstanding, the behaviour in the open area is slightly different since 100% of the activity of the adult concentrates during the periods A and B (Fig. 6).

If we compare the set of captures done with each trap (table 1, appendix), significant differences can be detected among them. Nevertheless, the contrasts between each one indicate that these differences only exist when we compare the traps of the oak forest with the ones in the pasture area (table 2).

Since the activity of the adults in the oak forest is concentrated in one time period both traps situated in the oak forest can be considered as replicates. Nevertheless specimens have been captured in the open area during both the periods A and B. An ANOVA has been carried out to observe if an interaction between the trap factor and the time period factor exists. The results of this analysis (table 2, appendix) indicate that significant differences (p = 0.0133) exist between the levels of the period factor.

Comparison:	t Exp.:	Tukey t:
A-Wooded vs. A-Open	17.544	**
B-Wooded vs. B-Open	3.208	
A-Wooded vs. B-Wooded	14.084	**
A-Open vs. B-Open	6.667	**
t (4,4) : 0.01 = 6.48 *	* Significant	at 99%
0.05 = 4.07	* Significant	at 95%

Table 3 – Comparison between periods and habitats during winter.

As we have not detected significant differences, neither between the traps situated in the oak forest nor between the ones in the pasture area, we can do a joint ANOVA for both environments. The results (table 3, appendix), show that significant differences exist both in the habitat factor and in the time factor, but moreover a strong interaction effect between both of them is detected (p = 0.0001). The study of this interaction can be observed in table 3.

In view of this, the spatial-temporal distribution of the adults of *S. stercoraria* in winter is determined by the fact that it is a dominant species at this period of the year and for this reason it has not competitive problems for the selection of the habitat or time period. Therefore, this species will have to adapt its behaviour just to climatological conditions to reach its physiological optimum. During the first hours of the day (Period A) most of the adults of *S. stercoraria* will choose the faeces which are situated in the open area, since in this area the influence of the solar radiation will be a little higher than in the wooded area. During period B, temperature increases in a gradual way until it reaches its top value and *S. stercoraria* will occupy both environments without significant differences.

Nevertheless, the larger number of individuals found in the oak forest area can be related to the hygrophilous behaviour of this species (SEGUY, 1951; SYCHEVSKAYA & VTOROV, 1969), since in the oak forest a considerable proportion of the relative humidity of the air is maintained. During the last time period the thermic levels are too low for the adults to be active even in the pasture area (Fig.-6).

III. - Spatial-temporal activity in spring

The population increase of *Scathophaga stercoraria*, started at the beginning of autumn and maintained during the whole winter, will grow up in an exponential way during the spring. The maximum of the population is approximately reached at the beginning of april (Fig. 2); from that moment, the number of individuals will slowly decrease until summer, when no adult activity is detected. When analysing the spatial-temporal distribution during

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Table 4 – Comparison between periods in wooded and open area during the spring peak.

this period of the year, we have considered it convenient to divide the work into two sections: the behaviour of the adults during the population peak and during the period immediately before the summer diapause. The study of these two "stages" of *S. stercoraria* activity is justified on one hand by the typical heterogeneity of the climatological conditions of this season in the studied area, and on the other by the great fluctuation in the number of individuals that are observed during this season.

A. Spatial-temporal distribution during the peak of the population

During autumn and winter the largest number of adults were found in the traps situated in areas without trees but during the spring maximum, prefer *S. stercoraria* largely the oak forest area (77.75%). With regard to the daily activity set, the largest number of specimens were captured both in oak forest and in pasture areas during period C, this tendency being more marked in traps situated in pasture areas (Fig. 7).

To determine if the traps situated in each environment can be considered as replicates the significance of the existent differences between the number of captured individuals in each trap and in each time period was studied. Tables 4 and 5 of the Appendix show the results of the ANOVA used for the individualized analysis of habitats. In both environments the test does not detect significant differences between captures done by each trap situated in each environment, although highly significant differences (p < 0.05) exist between the three time periods. The results of the contrasts between the levels of the period factor (table 4) show that both in the wooded area and in the pasture area the greater degree of adult activity is produced during period C and the minimum during periods A and B, without detecting significant differences between them.

Since we do not detect differences in the adult activity degree between the traps of each studied environment we can consider them as replicates and study the differences observed among the different time periods of both environments jointly. The results obtained from this analysis (table 6, appendix) show highly significant differences (p=0.001) in the period factor and in the habitat factor. An interaction effect between both periods (p=0.016) is also detected but as the respective contrasts show (table 5), it is not a difference of behaviour in each environment but the major individual abundance in the oak forest area present in front of the pasture area.

Comparison:	t Exp.:	Tukey t:	Comparison:	t Exp.:	Tukey t:
A-Wooded vs. A-Open	15.898	**	B-Wooded vs. C-Wooded	7.654	**
B-Wooded vs. B-Open	12.760	**	A-Open vs. B-Open	0.290	
C-Wooded vs. C-Open	14.966	**	A-Open vs. C-Open	14.094	**
A-Wooded vs. B-Wooded	2.847		B-Open vs. C-Open	13.811	**
A-Wooded vs. C-Wooded	4.807	*			
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Table 5 - Comparison between periods and habitats during the peak spring.

In conclusion, during the period of maximum population *S. stercoraria* move in large majority to the wooded area. This change in the behaviour, in relation to autumn and winter, is basically due to the temperature increase which is produced during this period of the year, so to get as close as possible to their optimum rank they must take refuge in areas where they less show this increase: the wooded area.

The maximum of daily activity is produced during period C, both in the oak forest area and in the pasture area (Fig. 7). In the same way in the spatial distribution this preference is related to the fact that in this period there is an average temperature lower than the temperatures during the rest of the day. In the pasture area these differences between periods are already more pronounced. In this habitat no differences between periods A and B have been detected regarding the daily activity.

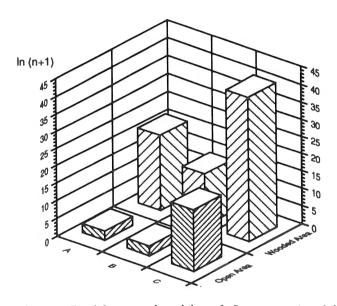


Fig. 7 – Spatial-temporal activity of S. stercoraria adult population at its top spring level.

Despite there is a mean temperature during period A similar to the period C, the greatest activity is evident during this last period. This happens because the temperature of the first hours of the period A is not high enough for the adults to be active and in the last hours of this period it exceeds the optimum level for the species; nevertheless, during period C these differences are not so extreme.

The hydric needs of *S. stercoraria* are also satisfied by this spatial-temporal distribution, so in the oak forest area and during the period C the greatest levels of air relative humidity are produced.

B. Spatial-temporal distribution in the rest of the spring As we have mentioned above the number of S. stercoraria individuals slowly decreases after the peak of the population at the end of May. This decrease is due to the climatic changes which are produced. After that, these changes also influence in a decisive way the spatial-temporal distribution of this species.

As the number of specimens after the population maximum is not so high we have not analysed separately the captures made in each trap, but the pasture and the oak forest areas were analysed jointly.

In the middle of spring majority of the Scathophaga stercoraria individuals continue to live largely in the oak forest area (64.98%) but at the end of the season the relative proportions between both environments do not show significant differences between them (47.7%, wooded area and 52.3% open area). Regarding daily activity, most of it is concentrated during periods A and C, the activity is reduced during the central hours of the day (Fig. 8).

While studying the spatial-temporal activity of *S. ster-coraria* in the middle of spring we have found significant differences between adult behaviour according to the environment, time period and interaction (table 7, appendix). The suitable contrasts between the levels of each factor (table 6) show significant differences between the

Comparison:	t Exp.:	Tukey t:	Comparison:	t Exp.:	Tukey t:
A-Wooded vs. A-Open	8.16	**	B-Wooded vs. C-Wooded	7.44	**
B-Wooded vs. B-Open	1.46		A-Open vs. B-Open	0	
C-Wooded vs. C-Open	1.87		A-Open vs. C-Open	10.76	**
A-Wooded vs. B-Wooded	8.16	**	B-Open vs. C-Open	10.76	**
A-Wooded vs. C-Wooded	0.72				
	•	nt at 99% nt at 95%			

Table 6 – Comparison between periods and habitats during the middle spring.

Comparison:	t Exp.	Tukey t:
Period A vs. Period B	6.729	**
Period A vs. Period C	0.310	
Period B vs. Period C	6.418	**
* Significant at 95% ** Significant at 99%		

Table 7 – Comparison between periods and habitats in the later spring.

number of specimens captured in the oak forest area and in the pasture area during the period A, most of the individuals preferring the wooded area. In this area the individuals concentrate during periods A and C without significant differences between them, whereas in the open area the adult activity is largely localized during period C.

At the end of spring, no significant differences have been detected between the number of specimens present in the oak forest and pasture but between the different time periods (table 8, appendix). The suitable contrasts (table 7) determine that the adult activity is largely concentrated during periods A and C without significant differences between them.

We can conclude that because of the progressive increase of the temperature of the environment during this season the adults of S. stercoraria tend to concentrate their

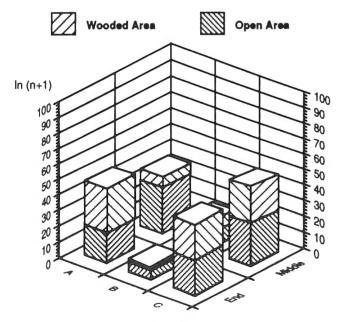


Fig. 8 – Temporal and spatial distribution pattern of S. stercoraria in mid and late spring.

activity during daily [section] periods when the temperature of the environment is less high and as a consequence there is a great level of air relative humidity, these periods are A and C (Fig. 8). This event can be clearly observed, in the wooded area in the middle season. The sun radiation acts directly in the open area but not in the oak forest area. So after the explosion of the population maximum the individuals are chiefly concentrated in the period C, nevertheless at the end of the season the activity is concentrated during the periods A and C. The differences between these periods with respect to the central hours of the day (Period B) are clearly more accentuated than in the wooded area.

In the last part of spring no differences are detected with regard to the number of individuals in both environments. This happens because of the low number of existent specimens and because activity is concentrated in the periods A and C, the differences between the pasture area and the oak forest area are not so significant as in the central hours of the day.

Acknowledgements

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APPENDIX Analysis of Variance Tables:

Table1: One Factor ANOVA X = Traps during the winter

Source:	df:	Sum Squares:	Mean Square:	F-test:
Between groups	3	1.118	.373	24.909
Within groups	4	.06	.015	p = .0048
Total	7	1.177		

Table2: 2-factor ANOVA of imaginal activity of S. stercoraria in the Open Area during the winter

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Open Area (a)	1	2.312E-3	2.312E-3	.048	.8366
Period (b)	1	.855	.855	17.921	.0133
ab	1	.15	.15	3.134	.1514
Error	4	.191	.048		

Table3: 2-factor ANOVA of Spatio-Temporal distribution of S. stercoraria during the winter

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Habitat (a)	1	2.465	2.465	101.508	.0005
Period (b)	1	.66	.66	27.165	.0065
ab	1	5.167	5.167	212.784	.0001
Error	4	.097	.024		

Table 4: 2-factor ANOVA of distribution of S. stercoraria in Wooded during spring top

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Wooded Area (a)	1	1.696E-3	1.696E-3	.021	.8899
Period (b)	2	2.17	1.085	13.334	.0062
ab	2	.025	.012	.151	.8627
Егтог	6	.488	.081		

Table 5: 2-factor ANOVA of distribution of <u>S. stercoraria</u> in the Open Area during spring peak

Open Area (a)	1	.021	.021	.226	.6511
Period (b)	2	8.923	4.462	48.276	2.0E-4
ab	2	.158	.079	.855	.4715
Error	6	.555	.092		

Table6: 2-factor ANOVA of Spatio-Temporal distribution of <u>S. stercoraria</u> during the spring peak

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Habitat (a)	1	7.462	7.462	417.892	.0001
Period (b)	2	4.946	2.473	138.486	.0001
ab	2	.804	.402	22.523	.0016
Error	6	.107	.018		

Table7: 2-factor ANOVA of Spatio-Temporal distribution of S. stercoraria during the middle spring

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Habitat (a)	1	.257	.257	29.878	.0016
Period (b)	2	1.496	.748	86.94	.0001
ab	2	.629	.315	36.55	.0004
Error	6	.052	.009		

Table8: 2-factor ANOVA of Spatio-Temporal distribution of S. stercoraria during the later spring

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Habitat (a)	1	4.8133E-4	4.8133E-4	.033	.861
Period (b)	2	.809	.404	28.083	9.0E-4
ab	2	.053	.026	1.831	.2395
Егтог	6	.086	.014		

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