Zeitschrift: Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society

Herausgeber: Schweizerische Entomologische Gesellschaft

Band: 73 (2000)

Heft: 3-4

Artikel: Analysis of the diurnal activity patterns of six species of Drosophila (Diptera, Drosophilidae) at Bordils (North East of Spain)

Autor: Argemí, Merce / Bächli, Gerhard / Mestres, Francesc

DOI: https://doi.org/10.5169/seals-402788

MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
73, 337 – 348, 2000

Analysis of the diurnal activity patterns of six species of *Drosophila* (Diptera, Drosophilidae) at Bordils (North East of Spain)

MERCE ARGEMÍ [1], GERHARD BÄCHLI [2], FRANCESC MESTRES [1] &
LUÍS SERRA [1,3]

The diurnal activity patterns of six species of *Drosophila* (*D. subobscura*, *D. simulans*, *D. melanogaster*, *D. immigrans*, *D. phalerata*, and *D. testacea*) collected at Bordils (North East of Spain) have been analysed. The analyses are based on daily samples of drosophilids taken during several months in two periods widely separated in time. The pattern of diurnal activity, measured by the adjusted abundance, does not in general differ significantly between species collected during the same day. Males and females of the same species usually have equivalent patterns of diurnal activity, the few exceptions being probably due to a particular behaviour of males. There is a quadratic relationship between the relative abundance of individuals collected at a particular hour and the solar angle, as a consequence of the bimodality of the diurnal activity patterns. Light intensity might trigger and set the boundaries of the diurnal behaviour of individuals, whereas additionally each species would have a particular adaptation to a given range of temperature and humidity, basically to prevent desiccation.

Keywords: Diurnal activity, solar angle, temperature, *Drosophila*.

INTRODUCTION

Despite the great amount of information available on the genetics of *Drosophila*, comparatively little is yet known about the ecology of the species which comprise the genus (CARSON, 1971; KRIMBAS, 1993; POWELL, 1997). With the extensive use of these organisms for studies of population genetics and speciation, ecological information becomes all the more important. Although some information is available on the diurnal periodicity of *Drosophila* very little is known about differences in activity between related species (PAVAN *et al.*, 1950; MITCHELL & EPLING, 1951; ISHIHARA *et al.*, 1953; DYSON-HUDSON, 1956; KANEKO, 1968; ROCHA PITÉ, 1978; ANĐELKOVIĆ *et al.*, 1985; NOOR, 1997) .

Temperature, humidity and light are the factors which have been considered as possibly having some limiting effects on the periods during which the flies visit the traps. These factors are interdependent but they differ in their daily range of variation, the reaction of the flies varying accordingly. They vary also from locality to locality because of various topographic, vegetation and climatic factors. Furthermore, the total number of flies which appear at the traps is determined by their abundance in a given season but the numbers that appear at different times of the day are determined by the factors which control the diurnal cycle.

[1] Departament de Genètica, Facultat de Biologia, Universitat de Barcelona. Diagonal, 654, 08071 Barcelona, Spain
[2] Zoologisches Museum, Universität Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland; e-mail: baechli@zoolmus.unizh.ch
[3] Corresponding author: Luís Serra; Phone: ++34934021499; Fax: ++34934110969; e-mail: lluis@bio.ub.es

The aim of the present study has been to analyse and compare the diurnal activity patterns of the most common *Drosophila* species collected at Bordils (North East of Spain), to find out whether there are significant differences between the daily activity patterns of species and also between males and females of each species, and to ascertain the influence of some environmental factors – temperature, humidity and solar angle – on these patterns.

MATERIAL AND METHODS.

Samples were taken from a plantation of *Populus nigra* and associated vegetation near Bordils (70 km North-east of Barcelona, Spain; 42° 3' N, 2° 54' E, altitude 42 m). The trees are arranged in rows and columns, separated from each other by a distance of approximately 5 m. There is a high degree of humidity in the hours of maximum activity and the whole area is a highly homogeneous habitat.

Flies were collected each month over fermenting banana baits (MONCLÚS, 1964) between September 1979 and August 1981 in the first period, and in October 1996 and in February, May and July 1997 in the second period. On each occasion 20 baits were set early in the morning on the ground. Collections were made by placing a net over the baits hourly until sunset. In December 1979 and in February, November and December 1980 it proved impossible to collect flies because of low temperature, rain or strong wind. For each collection, the temperature and humidity were recorded every hour (ARGEMÍ *et al.*, 1999). For the identification of the specimens we have used the keys given by BÄCHLI & BURLA (1985) and MONCLÚS (1964).

The monthly collections vary with regard to the number of individuals and the *Drosophila* species composition. In this study only the most frequent species have been considered: *D. subobscura*, *D. phalerata*, *D. melanogaster*, *D. simulans*, *D. immigrans*, and *D. testacea*. Furthermore, not all of them can be included in all the analyses because they have not been found in some hours of particular months. The winter collections, in which the dominant species was *D. subobscura* and only a few individuals of the other species were present, have not been included in the analyses.

To compare the diurnal activity of the different species during the different hours of the same day, we have used an adjusted abundance parameter (NOOR, 1997) which is obtained for each species dividing the number of individuals collected at a particular hour by the maximum number of individuals collected at any hour of the day. In addition to temperature and humidity, other environmental factors have an influence on the diurnal activity patterns of *Drosophila* species (PAVAN *et al.*, 1950; MITCHELL & EPLING, 1951; ISHIHARA *et al.*, 1953; DYSON-HUDSON, 1956; KANEKO, 1968; SHORROCKS, 1977; ROCHA PITÉ, 1978; TODA, 1981; GOÑI *et al.*, 1997), in particular the light intensity. It can be measured by the solar angle of each solar time. The solar angle has a zero value at sunrise and sunset, and describes a parabola with a maximum at noon. In this work, the solar angle values have been calculated according to the expression given by NOOR (1997); the values of the apparent solar declination have been obtained from the astronomical almanac: "ALMANAQUE NÁUTICO DEL MINISTERIO DE DEFENSA" (1999).

The relationship between the number of individuals collected for each species and month with temperature and humidity has been analysed using the Spearman Rank correlation test (to avoid problems with lack of normality). For comparing the diurnal activity of the different species in a particular month we have car-

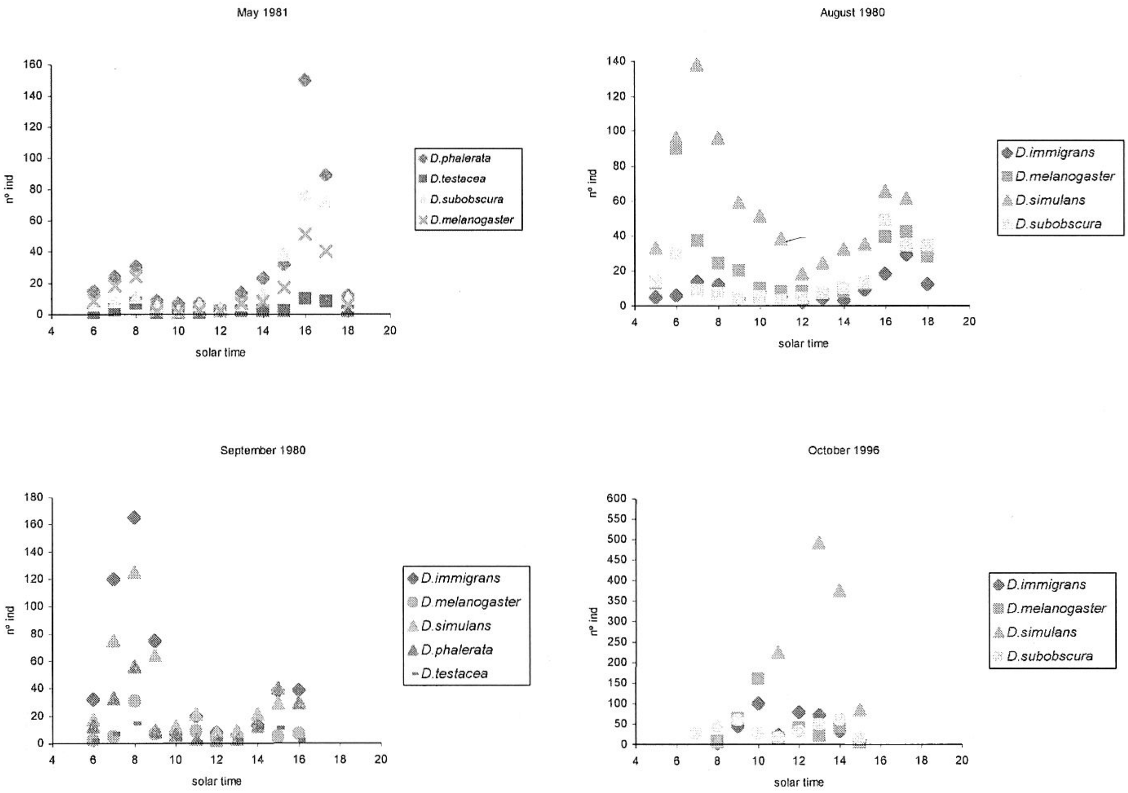

Fig. 1. Diurnal activity patterns of six species of *Drosophila* collected in Bordils (North East of Spain).

ried out an ANOVA analysis with the factor species and solar time as the block factor, using the new variable "adjusted abundance" (AA). This method can be used since there is homogeneity and the residual distribution fits the required conditions. Then, a multiple comparisons test (Tukey and Bonferroni methods) was done considering the factor species. For the months and species in which enough data were available, we have also compared the diurnal activity distributions of males and females of the same species. Using the AA variable for males and females, a t-paired test (the same hour of the day) has been done.

To study the relationship between the daily distribution of individuals and the solar angle we have defined two new AA variables: morning and evening and analysed the linear and quadratic regression between them, the R coefficient being estimated in each case.

RESULTS

The analysis has been carried out for those months in which data for practically each hour were available, and only for those species with a sufficient number of individuals. The distributions of the individuals of the different species against the solar time are shown in Fig. 1: in this figure only the most significant months within each season (not including winter time) have been chosen in the period 1979–81; in the period 1996–97 only the autumn collection has been selected. The observed distribution patterns are clearly bimodal, as a function of the solar time. The corresponding peaks of these curves for each species and in the same month, are located at approximately the same hour of collection, which indicates a similar behaviour of the different species analysed with regard to the environmental conditions.

Tab. 1. Spearman rank correlation tests.

Species	April 81	May 81	June 80	July 80	Aug 80	Sep 80	Oct 80	Feb 97	May 97	July 97	Oct 96
D. subobscura	ns	ns	+H	ns	-T +H	ns	ns	-T +H	+H	ns	ns
D. phalerata	-T	-T	-T +H	-T +H	ns	-T +H	ns				
D. testacea		ns		-T +H	ns	ns					
D. immigrans			-T +H	-T +H	ns	-T +H	ns	ns	ns	-T +H	-T +H
D. simulans					ns	-T +H	ns		ns	-T +H	-T +H
D. melanogaster		-T +H			-T +H	ns	ns	ns	ns	-T +H	-T +H

-T = significant negative correlation with temperature
+H = significant positive correlation with humidity
ns = non significant correlation

All species show an increase early in the morning reaching a peak; then a decrease during the central hours of the day is observed followed by an evening increase, reaching a second peak followed by a rapid decrease during the last collections (Fig. 1). This behaviour is similar to that found in other studies (PAVAN *et al.*, 1950; ISHIHARA *et al.*, 1953; DYSON-HUDSON, 1956; KANEKO, 1968; ROCHA PITÉ, 1978; TODA, 1981; NOOR, 1997). These bimodal curves vary according to the month, showing a maximum distance between peaks in June (maximum variation of the solar angle) and becoming practically unimodal in winter months (minimum variation of the solar angle). The solar angle plays a significant role in the daily activity of the *Drosophila* species studied. During May and June, the evening decrease takes place with a solar angle of approximately 5 degrees; in July and August, the value of the angle is practically 2 degrees (of course, the other environmental conditions as temperature and humidity must be taken into account, mainly the temperature which is high late in the evening and shows a low gradient of decrease). In April, September and October the evening decrease takes place at approximately 10 degrees. In summary, within permissive ranges of temperature and humidity the species set their daily activity clock according to the solar angle.

The temperature ranges in which the six species have been collected are shown in Tab. 5, together with the the corresponding humidity values, solar time and month of collection. To analyse the influence of temperature and humidity on the distribution of the number of individuals of each species collected every month, we have used a Spearman rank correlation test to avoid lack of normality. The results are given in Tab. 1. Only those cases for which the test is significant are shown. Out of 43 cases analysed, 18 show a significant negative correlation with temperature ($p < 0.05$) and two have a p value between 0.05 and 0.1. For humidity the results are similar, with 17 cases showing a significant positive correlation ($p < 0.05$) and two with a p value between 0.05 and 0.1. In summary, all species analysed show in general a significant negative correlation with temperature and a positive significant correlation with humidity, as also observed by other authors (MITCHELL & EPLING, 1951; DYSON-HUDSON, 1956).

To compare the daily distribution pattern of the different species within the same month, we have carried out an ANOVA with the factor species and considering the different hours of the day as a block. On applying this method the adjusted abundance parameter (AA) has been used. The distribution of AA is approximately normal with equality of variances which justifies the use of the method. The ANOVA analysis has also been done only for those species and months for which a sufficient number of individuals was available. The diurnal activity patterns of the

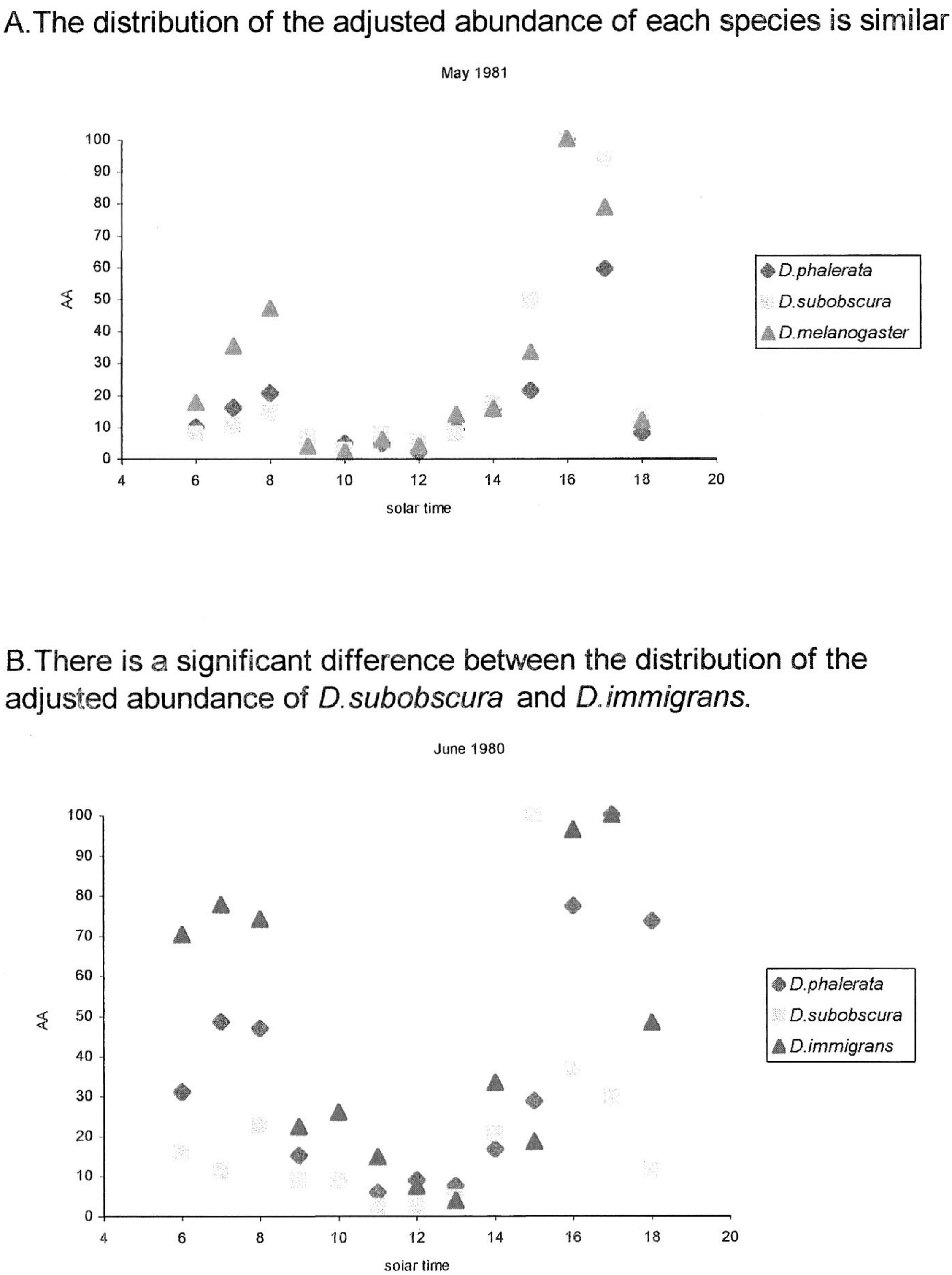

Fig. 2. Adjusted abundance of each species as a function of solar time.

species are in general equivalent, as shown in Fig. 2 for the case of the May 1981 collection. Significant differences between the patterns have only been found in two cases (June 80 and October 96 samples). As shown by a subsequent multiple comparison test (Tab. 2), the significance is due to the difference between *D. subobscura* and *D. immigrans* for the sample of June 80 (Fig. 2) and between *D. subob-*

Tab. 2. Similarities between the diurnal activity patterns of species of *Drosophila*, as revealed by multiple comparison tests of the ANOVA analysis.

Species		May 81	June 80	July 80	Aug 80	Sep 80	Oct 80	July 97	Oct 96
D. subobscura	D. phalerata	ns	ns	ns					
	D. immigrans		*		ns		ns	ns	ns
	D. simulans				ns		ns	ns	ns
	D. melanogaster	ns			ns			ns	*
D. phalerata	D. immigrans		ns			ns			
	D. simulans					ns			
	D. melanogaster	ns							
D. immigrans	D. simulans				ns	ns	ns	ns	ns
	D. melanogaster				ns			ns	ns
D. simulans	D. melanogaster				ns			ns	ns

ns = non significant differences
* = significant at the 0.05 level (p-value<0.05)

scura and *D. melanogaste*r for the sample of October 96. In the period 1996–97 we have not been able to compare the distribution of *D. phalerata* because this species was not collected in July 97 and October 96. As expected, in all these ANOVA analyses a great component of variability is due to the block factor (solar time). In summary there are in general no significant differences between the daily distribution of the adjusted abundance of the different species analysed which shows that their daily activity patterns are similar.

Thus, a close relationship between the solar angle and the number of individuals collected every hour must exist. If we divide the collections into two groups: morning collections (solar time ≤ 12) and evening collections (solar time > 12), a quadratic regression of the number of individuals against the solar angle would be expected (a parabola with a maximum). As the behaviour of the different species is similar in the analysed months (as shown by the results given in Tab. 2, with the only exceptions of the samples collected in June 80 and October 96), we have grouped the number of individuals of the analysed species for each hour and defined a new AA variable (AA*) for the morning and evening periods, respectively. In the case of the sample obtained in October 96, in which a different behaviour between species was detected, we have grouped only the data corresponding to *D. simulans*, *D. immigrans* and *D. melanogaster*, which are the species for which no significant differences have been observed using the multiple comparison test. Then, the linear and quadratic relationship between this new variable (AA*) and the solar angle has been studied. The results are shown in Tab. 3. The quadratic model is significant for all months ($p < 0.05$) and for those cases in which the linear model is significant, the R coefficient is always greater in the quadratic model than in the linear model, so the quadratic adjust is very good, as expected.

Tab. 3. Regression model analysis of *Drosophila* diurnal activity on solar angle.

		April 81	May 81	July 80	Aug 80	Sep 80	Oct 80	July 97	Oct 96
Linear model	F	5.9	3.44	2.87	7.17	0.12	18.53	1.58	30.65
	p-value	0.035	0.09	0.112	0.02	0.736	0.001	0.23	0.0001
	R	0.609	0.597	0.412	0.577	0.579	0.766	0.318	0.838
Quadratic model	F	19.42	5.28	6.88	13.79	5.63	9.65	7.82	17.02
	p-value	0.0005	0.027	0.009	0.001	0.021	0.003	0.006	0.0003
	R	0.901	0.902	0.717	0.859	0.764	0.785	0.739	0.859

Tab. 4. Similarity between the diurnal activity patterns of males and females of the same species (paired-samples t tests).

Species	May 81	June 80	July 80	Aug 80	Sep 80	Oct 80	July 97	Oct 96
D. subobscura	ns		*	ns		ns	ns	ns
D. phalerata	*	ns	ns		ns			
D. immigrans		ns			*	ns		ns
D. simulans				ns	*	ns	ns	ns
D. melanogaster				ns				ns

ns = non significant differences
* = significant at the 0.05 level (p-value<0.05)

For the months and species in which enough data are available, a comparison of the diurnal activity between males and females of the same species has been carried out. We have used the adjusted abundance variable (AA) for males and females separately and applied a paired-samples t test (Tab. 4). Out of 21 possible comparisons, 17 show no significant differences between the diurnal distribution of AA of males and females. One of these cases (*D. phalerata*) is shown in Fig. 3. In four cases significant differences have been found: *D. immigrans* and *D. simulans* collected in September 80, *D. phalerata* collected in May 81 and *D. subobscura* collected in July 80 (Fig. 4). In all these cases the AA of males is significantly lower than the AA of females. A possible explanation of this situation would be that males present a flush during a determined hour in which the environmental conditions are optimal for them. On the other hand, the distribution of females, although having the maximum at the same hour as that of males, is more regular all day long: the difference among the number of females collected every hour is not so conspicuous.

DISCUSSION

In this work we have found a clear bimodal diurnal pattern of activity for the 6 most abundant species (*D. subobscura*, *D. immigrans*, *D. simulans*, *D. melano-*

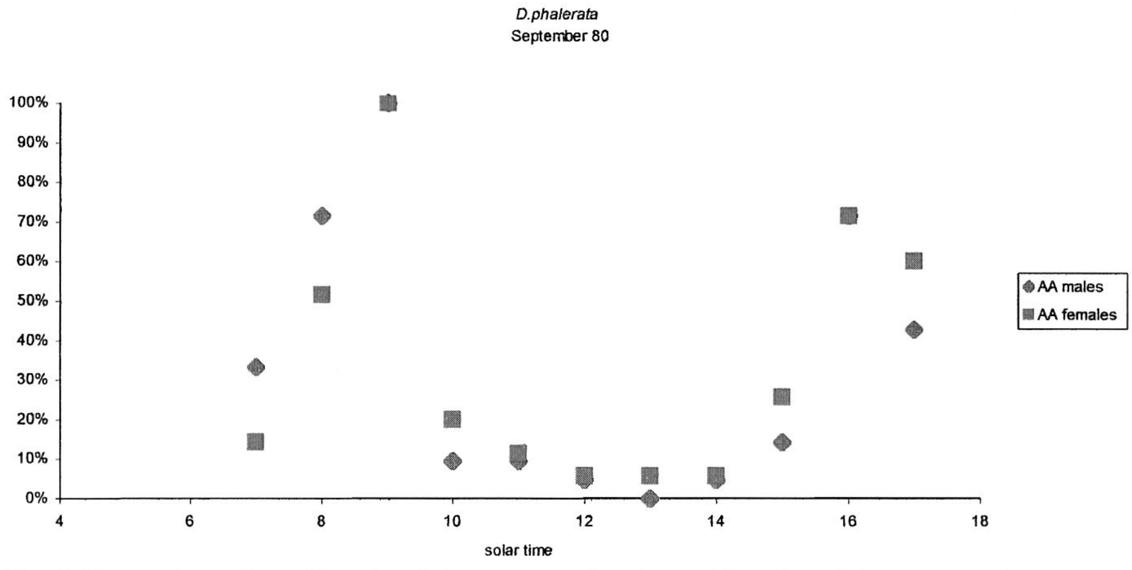

Fig. 3. Comparison of the diurnal activity patterns of males and females of the same species.

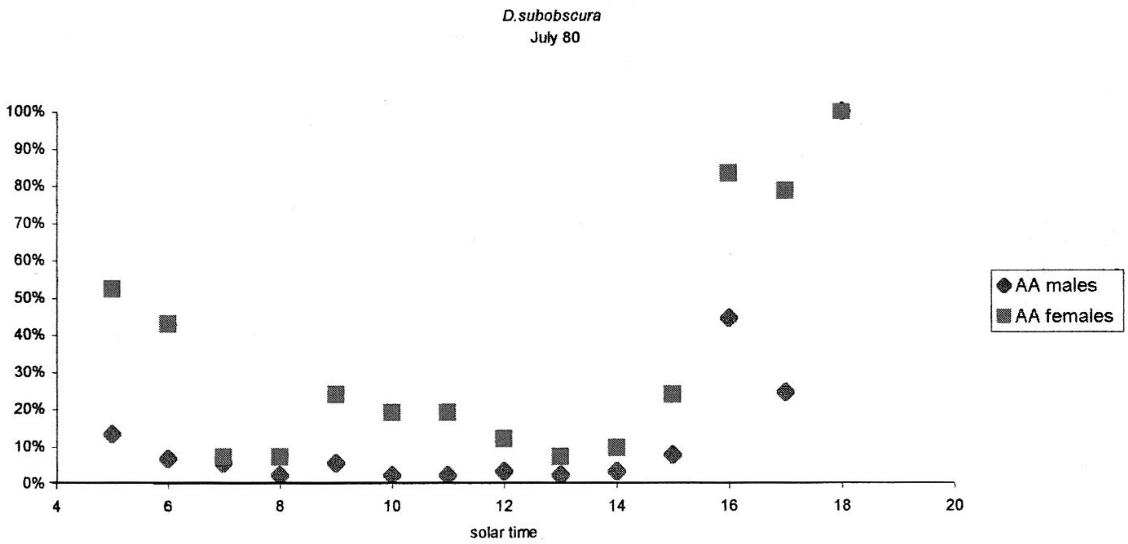

Fig. 4. Comparison of the diurnal activity patterns of males and females of the same species.

gaster, *D. phalerata*, *D. testacea*). However this pattern can be modified according to the season: it is most conspicuous from April to October and the bimodal pattern disappears in the collections of colder months, in which a unimodal or uniform pattern is found. In this case it is somewhat similar to the pattern observed on cloudy days by some authors according to the particular climate conditions (PAVAN *et al.*,1950; MITCHELL & EPLING, 1951; ROCHA PITÉ, 1978). This bimodal pattern of activity has also been found by the majority of authors and for many different species of *Drosophila* (DOBZHANSKY & EPLING, 1944; PAVAN *et al.*, 1950; HADORN *et al.*, 1952). The U-shaped model found in some occasions (NOOR, 1997) could be rather an effect of not sampling in a sufficiently wide hourly range during the day due perhaps to the limiting climatic conditions of the particular locality.The diurnal periodicity of the behaviour of these species is evidently adaptive. The flies wander, procuring food chiefly in the morning and before sunset, when relative humidity is highest and temperature lowest during the light hours, they are practically inactive during the middle of the day when the danger of desiccation is greatest.

The pattern of diurnal activity, measured by the adjusted abundance, does not in general differ significantly between species collected during the same day. Only in two cases, out of a total of 31 comparisons (Tab. 2), a significant difference between the daily activity patterns of the species has been found, having probably a random origin. Furthermore, the test is quite sensitive, because rather small differences in the adjusted abundances of the species being compared can lead to a rejection of the null hypothesis.

In general males and females of the same species have equivalent patterns of diurnal activity, as shown by the fact that, out of 21 possible comparisons, only in 4 cases significant differences have been detected (Tab. 4). These differences can be explained by a specific behaviour of males: they are quite abundant in some hours of the day. Females, instead, have a more uniform distribution, although both sexes have the peak of abundance at the same hour of the day. This is the reason that explains why the values of the adjusted abundance significantly differ between sexes. To give an example, *D. subobscura* (Fig. 4) has an abundance peak at 18 hours (solar time) with 90 males and 42 females; at 17 hours, 33 females and 22 males were collected. Thus, the adjusted abundance values for males will be much

Tab. 5. Minimum and maximum temperatures in which the corresponding species have been collected.

			temperature	humidity	solar time	month
D. subobscura						
	min.temp.	males	8	93 %	15	January 80
		females	10	68 %	14	January 80
	max.temp.	males	32	40 %	16	June 81
		females	32	40 %	16	June 81
D. simulans						
	min.temp.	males	9.5	93 %	10	November 79
		females	9.5	93 %	10	November 79
	max.temp.	males	28.5	48 %	13	August 81
		females	28.5	48 %	13	August 81
D. immigrans						
	min.temp.	males	9.5	93 %	10	November 79
		females	9.5	93 %	10	November 79
	max.temp.	males	33	40 %	14	June 81
		females	32	40 %	16	June 81
D. melanogaster						
	min.temp.	males	13	95 %	6	September 79
		females	13	95 %	6	September 79
	max.temp.	males	33	40 %	14	June 81
		females	33	40 %	14	June 81
D. phalerata						
	min.temp.	males	9.5	93 %	10	November 79
		females	9.5	93 %	10	November 79
	max.temp.	males	33	40 %	14	June 81
		females	33	40 %	14	June 81
D. testacea						
	min.temp.	males	10	95 %	15	November 79
		females	11	95 %	11	November 79
	max.temp.	males	28.5	63 %	9	June 81
		females	28.5	48 %	13	August 81

lower than those for females. The situation is much the same for the other hours of the day. This shows that, for this species, the differences between the diurnal distribution patterns of males and females could be explained by the fact that males are particularly active during some hours in which they have an abundance flush. This is in agreement with the results obtained in a study on the capacity of dispersal of this species carried out in the same locality (SERRA *et al.*, 1987), in which a greater activity and capacity of dispersal of males was detected.

As has been observed in different studies, three main environmental factors can determine the daily distribution of the species: temperature, humidity and light intensity. Light intensity might trigger and set the boundaries of the diurnal behaviour of individuals and, additionally, each species would have a particular adaptation to a given range of temperature and humidity, basically to prevent desiccation (LILLELAND, 1938). Different measures of light intensity have been used by authors (MITCHELL & EPLING, 1951; DYSON-HUDSON, 1956). We have used the variable "solar angle" (NOOR, 1997) as a measure of this environmental factor which, in spite of having some drawbacks, is a more accurate and comparable measure. One of the drawbacks is described by the "clear sky" condition during the collecting times: the influence of the factor "solar angle" may be modified by clouds. Although we have not monitored this parameter systematically in our analysis the data obtained in October 96 (Fig. 1) show that the general pattern is preserved on cloudy and rainy days. This is reinforced by the observation of the maintenance of the bimodal pattern of the number of *D. subobscura* individuals caught in a suction trap both on fine and dull days (TAYLOR & KALMUS, 1954). Our results show that there is a quadratic relationship between the relative abundance of the individuals collected at a particular hour and the corresponding solar angle. Furthermore the diurnal activity of the flies would start and finish at a given threshold value of the solar angle, equivalent to the threshold values of the light intensity found by DYSON-HUDSON (1956) for *D. subobscura* and by MITCHELL & EPLING (1951) for other species. The quadratic relationship with the solar angle is just a consequence of the bimodality of the patterns of diurnal activity. Were the pattern U-shaped, which is not the case in our study, then a linear relationship with the solar angle would be expected.

There is no doubt that light is a key factor for the diurnal activity behaviour of these *Drosophila* species, but the highly correlated factors temperature and humidity should also be taken into account. During the warmest season it is possible to collect individuals with a solar angle less than 4°, although with a very high relative humidity and a fairly high temperature (lower than that of the central hours of the day). There is a negative significant relationship between the number of collected individuals and temperature and a positive significant relationship with humidity (Tab. 1). In the case of *D. subobscura*, fly activity has been noticed at temperatures as low as 4.4 °C (BASDEN, 1953). The higher upper limit varies significantly according to the locality. There is probably a gradient, geneticallly determined, for these thresholds in the North-South direction (KRIMBAS, 1993). The threshold value of the solar angle is higher during the cold season (10 °) because the low temperatures have an important effect (below 10 °C). In this season the activity appears to be primarily dependent on temperature and light has only a subsidiary influence.

In Bordils *D. subobscura* can be collected all year long. It is the dominant species in winter months, having a flush when temperature increases during the winter-spring transition (in March). In January some specimens have been collected at 8 °C (93 % humidity) at 15 hours (solar time) with a solar angle of approximately 10 ° (Table 5). In summer the species is found in lower numbers, although it can still be collected during the central hours of the day. Apparently it can withstand extreme temperatures although its activity is markedly reduced, as observed by DYSON-HUDSON (1956) for temperatures below 10 °C. The diurnal activity pattern of the *D. subobscura* populations that have recently colonized the New World (NOOR, 1997) is similar to that observed in this study for the population of Bordils. In this locality, *D. subobscura* is the most representative and permanent species. The results obtained in this study let us conclude that, within permissive ranges of temperature and humidity, these species set their diurnal activity clock according to the solar angle. In general there are neither significant differences between the diurnal distribution of the adjusted abundance of the different species nor significant differences between the diurnal activity of males and females. *D. phalerata* has been collected from March to November with a maximum in summer months, probably in relation with fungi. The presence of the species over this broad range indicates that it is adapted to rather extreme temperatures: it has been collected within a temperature range of 9.5–33 °C (Tab. 5). SHORROCKS (1977) has also collected the species at rather low temperatures; its fair abundance in Bordils is also in agreement with the data obtained by ROCHA PITÉ (1978) in Portugal, in spite of the climatic differences between the two localities (Atlantic and Mediterranean climates). On the other hand *D. testacea* is collected during the warmest months, within a narrower range of temperatures (10–28.5 °C). It is also collected in smaller numbers than the other five species, so it might be more sensitive to the particular environmental conditions. *D. simulans* is found mainly from August to October, showing a flush in August, when it is collected in very large numbers. It is very rarely found in November; its seasonal activity period in Bordils coincides with the description given by ROCHA PITÉ (1978) in other studies. The minimum temperature at which it has been collected in Bordils is 9.5 °C, in agreement with the observations of GOÑI (1997) in American populations in spite of the habitat and climatic differences. However the species is not found at high temperatures (maximum 28.5 °C). *D. melanogaster* shows a wider tolerance to more extreme physical environments (PARSONS & STANLEY, 1981), specially temperature and desiccation. As it has been collected only from May to October, the minimum temperature at which it has been found is higher (13 °C) than that of *D. simulans*. *D. immigrans* has also been found within a fairly wide range of temperatures; as it has been collected in November, the minimum temperature at which it has been found in Bordils (9.5 °C) is lower than that of *D. melanogaster*. *D. simulans* and *D. immigrans* have a flush in August-September; this similar seasonal behaviour is in agreement with the observations made by ROCHA PITÉ (1978) at Sintra-Colares (Portugal).

ACKNOWLEDGMENTS

We thank Dr. M. MONCLUS and Dr. G. PEGUEROLES for their participation in collecting the specimens of the first period. We also thank Dr. M. MONCLÚS for identifying these specimens.

REFERENCES

ALMANAQUE NAUTICO DEL MINISTERIO DE DEFENSA. 1999. Real Inst. y Observatorio de la Armada de San Fernando. Ministerio de Defensa. Spain.

ANĐELKOVIĆ, M., STAMENKOVIĆ-RADAK, M., & SEKULIĆ, M. 1985. The daily activity rhythm of *D. subobscura* COLLIN (Dipt., Drosophilidae) at Ravnište (Jastrebac) locality, Yugoslavia. *Acta ent. jugosl. 21*: 109–118.

ARGEMÍ, M., MONCLÚS, M., MESTRES, F., & SERRA, L. 1999. Comparative analysis of a community of Drosophilids (Drosophilidae; Diptera) sampled in two periods widely separated in time. *J. Zool. Syst. Evol. Res. 37*: 203–210.

BÄCHLI, G. & BURLA, H. 1985. *Drosophilidae*. Insecta Helvetica. Fauna. Vol. 7. Diptera. Entomolog. Institut der ETH. Zürich. 116 pp.

BASDEN, E.B. 1953. The autumn flush of *Drosophila* (Diptera). *Nature 172*: 1155–1156.

CARSON, H.L. 1971. *The ecology of Drosophila breeding sites*. Harold L. Lyon Arboretum Lecture Number 2, pp. 1-28, University of Hawai, Honolulu.

DOBZHANSKY, T. & EPLING, C. 1944. Contributions to the genetics, taxonomy and ecology of *Drosophila pseudoobscura* and its relatives. *Publ. Carnegie Inst. Washington 554*: 1–183.

DYSON-HUDSON, V.R.D. 1956. The daily activity rhythm of *Drosophila subobscura* and *D. obscura*. *Ecology 37*: 562–567

GOÑI, B., MARTINEZ, M.E. & DAGUER, P. 1997. Studies of two *Drosophila* (Diptera, Drosophilidae) communities from urban Montevideo, Uruguay. *Revta. Bras. Ent. 41*: 89–93

HADORN, E., BURLA, H., GLOOR, H. & ERNST, F. 1952. Beitrag zur Kenntnis der Drosophila-Fauna von Südwest-Europa. *Z. indukt. Abstamm.- u. VererbLehre 84*: 133–163.

ISHIHARA, T., MOMMA, E. & MAKINO, S. 1953. Diurnal activity of some *Drosophila* species. *D.I.S. 27*:95

KANEKO, A. 1968. *Drosophila* Survey of Hokkaido, XXV. Some Observations on Summer Diurnal Activity of Drosophilid Flies in two Localities of Southwestern Hokkaido. *J. Fac. Sci. Hokkaido Univ., 16 (Ser.6, Zool.)*: 537–541.

KRIMBAS, C.B. 1993. *D. subobscura: Biology, genetics and inversion polymorphism*. Verlag Dr. Kovac. Hamburg. 395 pp.

LILLELAND, O. 1938. Duration of life without food in *Drosophila pseudoobscura*. *Biol. Bull., Wood's Hole 74*: 314–318.

MITCHELL, D.F. & EPLING, C. 1951. The diurnal periodicity of *Drosophila pseudoobscura* in Southern California. *Ecology 32*: 696–708.

MONCLÚS, M. 1964. Distribución y Ecologia de Drosofilidos en España (I). *Genét. ibér. 16*: 143–165.

NOOR, M. 1997. Diurnal activity patterns of *Drosophila subobscura* and *D. pseudoobscura* in sympatric populations. *Am. Midl. Nat. 140*: 34–41.

PARSONS, P.A. & STANLEY, M.S. 1981. Domesticated and widespread species. *In*: ASHBURNER, M., CARSON, H.L., & THOMPSON, J.N. Jr. (eds), *The Genetics and Biology of Drosophila*, vol. 3a, pp. 349–385. London, Academic Press.

PAVAN, C., DOBZHANSKY, Th., & BURLA, H. 1950. Diurnal behavior of some neotropical species of *Drosophila*. *Ecology 31*: 36–43.

ROCHA PITÉ, M.T. 1978. Rythmes d'activité journalière des populations naturelles des Drosophilidae dans la région de Sintra-Colares (Portugal). *Bolm Soc. Port. Ciênc. Nat. 18*: 69–90.

SERRA, L., PEGUEROLES, G., & MESTRES, F. 1987. Capacity of dispersal of a colonizing species: *Drosophila subobscura*. *Genetica 73*: 223–235.

SHORROCKS, B. 1977. An ecological classification of European *Drosophila* species. *Oecologia 26*: 335–345.

TAYLOR, L.R. & KALMUS, H. 1954. Dawn and dusk flight of *Drosophila subobscura* COLLIN. *Nature 174*: 221–222.

TODA, M.J., 1981. Daily Activity of Drosophilid Flies in the Arctic Summer. *Low Temp. Sci., 39 (Ser.B, Biol. Sci.)*: 41–44.

(received September 26, 2000; accepted October 31, 2000)