

Ecological factors affecting mating of *Graellsia isabelae* (Graells, 1849) (Lepidoptera : Saturniidae)

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Summary

Weather parameters affecting mating of the saturniid moth *Graellsia isabelae* (Graells, 1849) have been analysed during an eight year field study. The study was carried out in one of the natural habitats of the species, a large area of Scots pine, *Pinus sylvestris* Linnaeus, located in the north of the province of Barcelona (in the NE of the Iberian Peninsula). With 194 nights of observation and a total of 426 attracted males detected, the authors realised the importance weather conditions have for successful mating of this nocturnal moth. Although males are able to detect calling females within a broad range of temperature and relative humidity, the best weather conditions are those when temperature is higher than 10°C and relative humidity lower than 80%. Also, the possible effect of cloudiness and wind speed on mating was evaluated.

Résumé

Au cours de recherches poursuivies pendant plus de huit ans sur le terrain, les auteurs ont étudié les paramètres climatiques qui influent sur l'accouplement du Saturnide *Graellsia isabelae* (Graells, 1849). Ces recherches ont été effectuées dans l'un des habitats naturels de cette espèce, soit une grande forêt de pins sylvestres, *Pinus sylvestris* Linnaeus, dans le nord de la province de Barcelone (NE de la péninsule ibérique). Au cours de 194 nuits d'observation, avec un total de 426 mâles attirés, les auteurs ont constaté l'importance des conditions météorologiques pour le succès de l'accouplement de ce Saturnide. Certes, les mâles sont capables de détecter les femelles qui appellent dans un large éventail de températures et d'humidité relative, mais les meilleures conditions sont une température supérieure à 10°C et une humidité relative inférieure à 80%. Ont été également évaluées l'influence possible d'un ciel nuageux et celle de la vitesse du vent sur l'accouplement.

Resumen

Durante un estudio realizado a lo largo de ocho años, se han considerado los parámetros ambientales supuestamente relacionados con el apareamiento del saturnido *Graellsia isabelae* (Graells, 1849). El estudio se llevó a cabo

en uno de los hábitats naturales de la especie, una amplia zona de pino negral, *Pinus sylvestris* Linnaeus, situada al norte de la provincia de Barcelona (en el NE de la Península Ibérica). Con un total de 194 noches de observación y 426 machos atraídos, los autores pudieron constatar la importancia que las condiciones ambientales tienen sobre el éxito del apareamiento de este lepidóptero nocturno. A pesar de que los machos son capaces de detectar hembras emisoras de feromonas dentro de un amplio margen de temperatura y humedad relativa, las mejores condiciones ambientales para el apareamiento se dan cuando la temperatura es superior a 10°C y la humedad relativa inferior al 80 %. Los posibles efectos del grado de cobertura nubosa y de la velocidad del viento también han sido evaluados.

Introduction

As is fairly well known, *Graellsia isabelae* (Graells, 1849) is a beautiful green saturniid with a very restricted distribution. In fact, it occurs only in certain areas of the Iberian Peninsula and also in a small area of the French Alps (for the Iberian distribution see Masó & Ylla, 1989 ; 1990).

The species was discovered by the Spanish physician Mariano de la Paz Graells who found, during the spring of 1849 at the locality of Pinares Llanos in the province of Avila, a female resting on a pine trunk. The first description was by Graells, in the French journal *Revue et Magazine de Zoologie*, as *Saturnia isabelae* (though wrongly translated from the original Spanish to French by Fairmaire and appeared as "*isabellae*"). No plates accompanied this original description. A year later (1850), in another paper appearing in the *Annales de la Société Entomologique de France*, Vol. VIII, one excellent colour plate of this species was published representing the female (the only sex known until then) displaying two postures as well as the larva, cocoon and pupa. The male remained undescribed until 1853.

Later, in 1922, it was also found at Bessée-sur-Durance, in the Department of Hautes-Alpes in France, and Oberthür considered it a new subspecies, naming it *galliaegloria*. However, we question the validity of this subspecies, and indeed other subspecies described from Spain. A different issue is whether the moth's occurrence in France is natural. On that point, certainly controversial, we tend to agree with Fernández-Vidal (1992) who strongly supports Agenjo's 1943 view (see Ceballos & Agenjo, 1943), that the moth was introduced into France by Oberthür himself. Fernández-Vidal brought new arguments, and urged that some kind of genetic research should be undertaken to clarify the issue.

The natural habitat of this species is mainly Scots pine (*Pinus sylvestris*) forest, the larvae feeding on needles of that pine. However, Scots pine is not the only pine species likely to be used as a foodplant in the wild, as it has been shown (Ceballos & Agenjo, 1943) that in the Sierras de Segura and Cazorla, in the province of Jaén, where Scots pine does not occur, it feeds successfully on *Pinus nigra* Arnold. In captivity, other coniferous foodplants have been tried, some of them being completely successful while others were not (Masó & Ylla, 1989; Nässig, 1991).

About the end of July, once they have finished feeding, the larvae leave the pine and spin a thick, brownish silk cocoon perfectly camouflaged among leaf litter. The pupae remain in the cocoon until the following spring when the imagines emerge; some of them though will wait another year before emerging. The first adults normally appear during the second half of April and emergences may last until the beginning of June. They live only about 6-8 days, during which time mating and oviposition must occur. Most larvae hatch during the last 10 days of May and the first 15 days of June. The complete life-cycle is shown in Fig. 1.

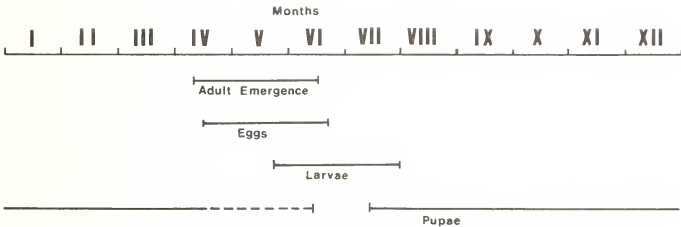


Fig. 1. Life cycle of *Graellsia isabelae* in the study area.

Adult activity, in both sexes, begins at dusk and lasts throughout the night, being especially intensive during the first 2 or 3 hours of darkness, when mating occurs. As in most *Heterocera* species, the females of *G. isabelae* produce and release pheromones to attract the males. However, while our research was in progress, we realised that mating success differed from one night to the other. In fact, on some nights, though the females were adopting the calling position extruding their pheromone gland, the males were not attracted at all. This phenomenon is not unique to *G. isabelae*, but widely spread amongst heterocerans. We

then considered that a possible reason for this lack of attendance by males might depend on certain weather conditions.

It is worth mentioning at this stage that while weather and physiological variables affecting sex pheromone release by females have received much attention (Han & Gatehouse, 1991; Bell & Cardé, 1983; Birch & Haynes, 1982; Turgeon *et al.*, 1983), there is a lack of studies focusing on how the weather variables affect female-attending behaviour by males. According to Sower (1980), nocturnal moths do not waste their energy trying to find each other for mating when ambient conditions are not favourable.

The aim of the present work was to find out which are the most suitable ambient conditions for the mating of *G. isabelae* as well as to determine whether these conditions have some influence on the degree of attraction males show for calling females. Previous observations involving *G. isabelae* are scarce and very general (Marten, 1955; Sanetra & Peuker, 1991) and sometimes the conclusions made are even wrong (Masó & Willien, 1989; Masó & Ylla, 1989; 1990).

This paper is about aspects of the ecology of *G. isabelae*. It does not consider aspects concerned with its nomenclature and systematics. However we can not avoid giving this species a name and including it in one or another genus. At this point, being fully aware of the recent controversy about its systematic position and about its specific name (with one "I" or two), we want to make our position clear.

About the spelling of the specific epithet, "*isabelae*" or "*isabellae*", we fully agree with the arguments brought by Agenjo (in Ceballos & Agenjo, 1943) and Fernández-Vidal (1992) that, according to the ICZN, only the name with one "I" should be used. We believe the controversy about the specific name would disappear if authors could have direct access to (and able to read) all papers by Graells. Agenjo and Fernández-Vidal, working separately, made a thorough search through all Graells' papers and summarised their work in two long and very well documented papers. We believe that all authors wanting to say anything about this affair should consider the arguments brought forth by these two Spanish authors. If this is not enough to stop the controversy, then it is the International Commission on Zoological Nomenclature who, taking into account all arguments, must decide. This is basically what De Prins proposed in his 1978 paper.

We fully disagree with the inclusion of *isabelae* in the genus *Actias*, as proposed recently by Nässig (1991). The arguments brought by Nässig to defend this change are few and weak. A thorough phylogenetic

analysis of these saturniids should clarify the situation and this will be the subject of another paper by us.

Material and methods

All the observations were carried out within the natural habitat of *G. isabellae*, in an area where both pine and moth are plentiful. These forests were located in the north of the province of Barcelona, in the NE of the Iberian Peninsula. The study lasted eight years (1983-1990).

Virgin females used as lures came from pupae obtained from eggs laid by the previous year's females. These pupae had been left in absolutely natural conditions, in order to assure female emergence being synchronous with that of wild individuals present in the area. After emergence, females were allowed to fly freely inside net cages (diameter 40 cm, length 60 cm). The cages were set in the forest along the perimeter of a circle with a radius of 15-20 metres and hung from tree branches two metres above the ground. According to Marten (1955), *G. isabellae* prefers the tree canopies for mating. This means that setting the cages only two metres above the ground might affect male attendance. However, from the results we obtained and knowledge concerning diffusion properties of lepidopterous pheromones, we do not believe this aspect to be very significant in the context of our study.

We assumed females released their pheromone as soon as they protruded the pheromone gland, which is easily observed (Sanders & Lucuik, 1972 ; Karandinos, 1974 ; Gorsuch et al., 1975). From that moment, all attracted males were recorded on arrival along with the most relevant ambient variables (see below). Females not protruding their glands were not counted.

Observations of female-attracted males started at dusk, and lasted until the completion of the first two hours. The temperature and relative humidity values were measured by a 24 hour thermo-hygrograph, set up where the observations took place. Sky cloudiness was stated at the beginning of each night, using the meteorological method of dividing the sky into 8 parts and looking at the number of parts with clouds (for instance 2/8, 4/8, 8/8, etc.) (Gómez & Arteaga, 1987). We used an anemometer and the Beaufort scale method to estimate wind speed (Roth, 1979).

Results

Total observation nights ($n = 194$) were spread over eight years (1983 to 1990). During this time we used 656 females and registered the attendance of 426 males.

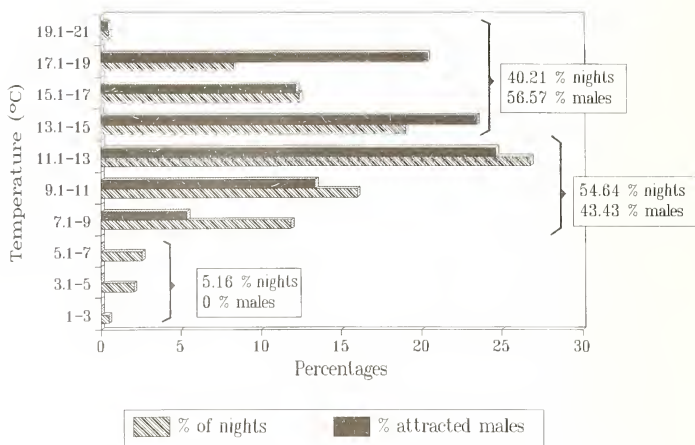


Fig. 2. Percentage of nights and female-attracted males for the different temperature intervals.

Effect of temperature and relative humidity

Fig. 2 shows the percentage of attracted males as a function of average temperatures (grouped in 2°C intervals) during the first two hours of darkness. Also shown is the percentage of nights in which the latter temperature intervals occurred. The effect of relative humidity (grouped in 10 unit intervals) is shown in the same way (Fig. 3).

An analysis of Figs 2 and 3 gave the following results :

- 1) The two distributions are not random as they are significant to $\alpha < 0.001$ (Chi-square analysis). Thus, there is an influence of both temperature and relative humidity on the percentage of attracted males.
- 2) Males were attracted to the female sexual lure within a very wide range of temperatures (between 7.1°C and 21°C). Only nights with average temperatures lower than 7°C did not register any attracted male ; this only happened on 5.2 % of the nights.
- 3) Temperatures above 13°C seem to favour male attendance, since 56.6 % of attracted males came under these conditions, which only occurred on 40.2 % of the nights. Particularly noteworthy is the

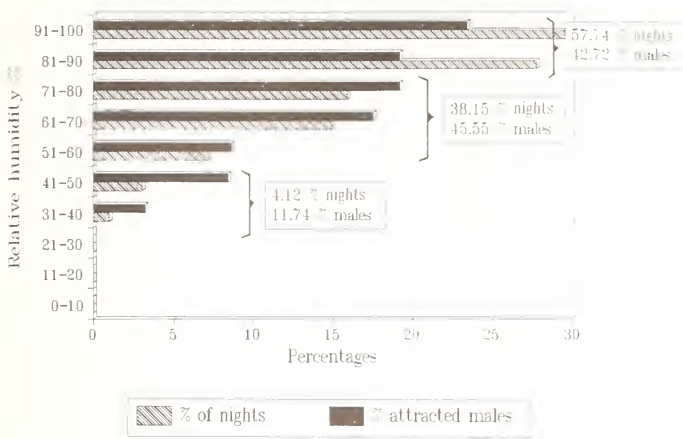


Fig. 3. Percentage of nights and female-attracted males for the different relative humidity intervals.

- 17.1-19°C interval, which despite its occurrence on only 8.3 % of the nights, accumulated 20.4 % of attracted males.
- 4) Females attracted males over the whole range of relative humidity levels recorded (31-100 %).
 - 5) Relative humidity below 50 % seems to favour male attendance, since 11.7 % of attracted males came under these conditions, which only occurred on 4.1 % of the nights.
 - 6) As the relative humidity levels rise, both percentages become closer. Thus 45.6 % of males were attracted throughout nights with relative humidity ranging between 51-80 % (which occurred on 38.2 % of the nights). When relative humidity was higher than 80 % (which occurred on 57.7 % of the nights) attracted males scored 42.7 %.

Fig. 4 shows the average temperature and relative humidity registered during the first two hours of darkness of the sampled nights (n = 194). Triangles inside the squares indicate those nights on which at least one male was attracted by the calling females (a total of 121 nights). This graph can be divided into four regions by tracing two lines at 80 % relative humidity and 10°C. This arrangement clearly shows that males are attracted to calling females under practically any thermo-hygrometric situation occurring within their habitat. Only when temperature is low (below 7°C), and hence relative humidity generally high,

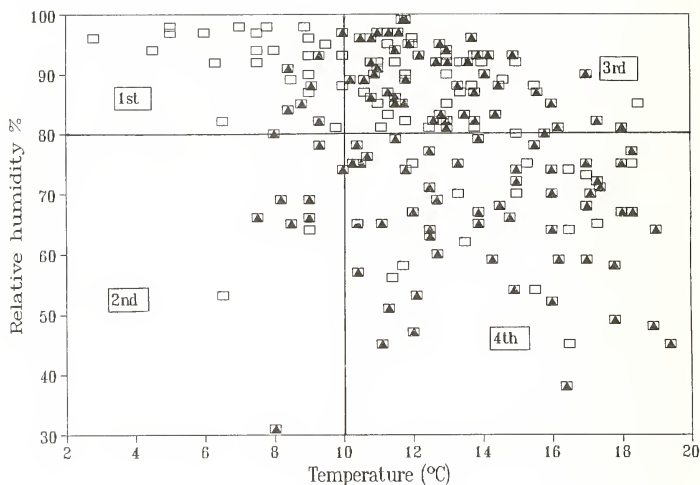


Fig. 4. Average temperature and relative humidity recorded during the first two hours of darkness of the 194 sampled nights (triangles inside the squares indicate nights with attracted males). For comparison purposes 4 relative humidity-temperature (RH-T) groups have been established (see text).

are males not attracted to calling females. This finding can be easily explained because when the temperature is so low, males are unable to take flight (Ylla & Sarto i Monteys, in preparation).

Fig. 5 shows again the average temperature and relative humidity registered during the first two hours of darkness, but in this case including only the 121 nights in which at least one male was attracted by the calling females. As in Fig. 4, this graph can be divided into four regions (designated RH-T groups) by tracing two lines at 80 % relative humidity and 10°C. Attracted males ($n = 426$) fell into these four RH-T regions as follows :

2.58 % when temperature $< 10^{\circ}\text{C}$ and relative humidity $> 80\%$ (1st RH-T group)

4.46 % when temperature $< 10^{\circ}\text{C}$ and relative humidity $< 80\%$ (2nd RH-T group)

41.08 % when temperature $> 10^{\circ}\text{C}$ and relative humidity $> 80\%$ (3rd RH-T group)

51.88 % when temperature $> 10^{\circ}\text{C}$ and relative humidity $< 80\%$ (4th RH-T group)

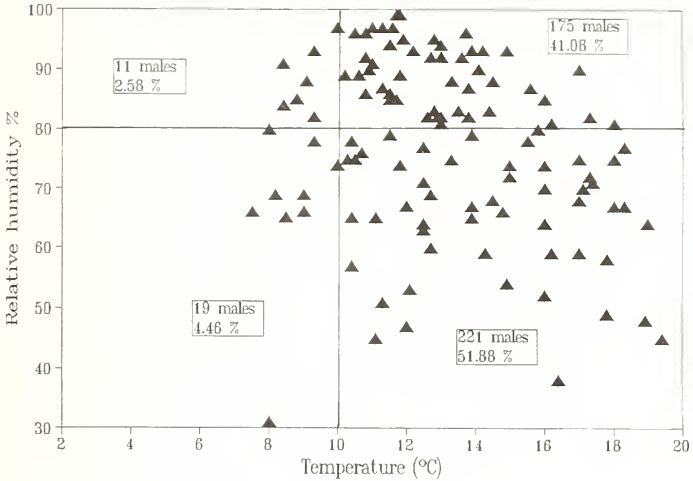


Fig. 5. Appearance of female-attracted males, detected over the whole period, split into the 4 RH-T groups, as in Fig. 4.

Fig. 6 shows the percentages of attracted males within each RH-T region together with the percentages of sampled nights ($n = 194$) in which such RH-T conditions occurred. In order to properly assess these results, a “success index” (percentage of attracted males / percentage of nights) was determined for each RH-T group: 1st RH-T group = $2.58 / 15.46 = 0.165$; 2nd RH-T group = $4.46 / 4.64 = 0.961$; 3rd RH-T group = $41.08 / 43.18 = 0.938$; 4th RH-T group = $51.88 / 36.08 = 1.438$. If these two weather factors (Relative humidity and Temperature) had no effect on male attendance at all, then values of 1 for each RH-T group in Fig. 6 should be expected.

Two RH-T groups give “success index” values very close to 1, which would indicate that these conditions have little affect on male attendance. However the other two RH-T groups give values far from 1. In the 1st RH-T group, the very low value of 0.165 would clearly indicate that its conditions do not suit male attendance. On the other hand, the high value of 1.438 given by the 4th RH-T group, would indicate that its conditions do favour male attendance. In summary, low temperatures ($< 10^{\circ}\text{C}$) combined with high relative humidities ($> 80\%$)

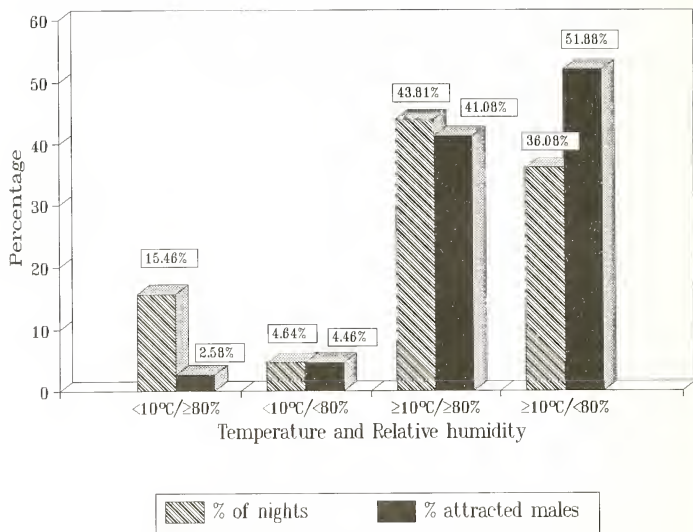


Fig. 6. Percentage of nights and attracted males for the different RH-T groups.

negatively affects male attendance while high temperatures ($> 10^{\circ}\text{C}$) and low relative humidities ($< 80\%$) would favour it.

It would seem likely that when there are more calling females, the higher pheromone levels in the air would increase the probability of the females being detected by males. The number of calling females present in each RH-T group and the corresponding number of attracted males is considered in Fig. 7. We can also determine here an “attraction efficacy index,, (number of available calling females / number of attracted males) for each RH-T group: 1st RH-T group = $73 / 11 = 6.64$; 2nd RH-T group = $18 / 19 = 0.95$; 3rd RH-T group = $315 / 175 = 1.80$; 4th RH-T group = $250 / 221 = 1.13$. Again it becomes clear that conditions within the 1st RH-T group are not favourable for attracting males, yielding a ratio of 1 male attracted by 6.64 calling females.

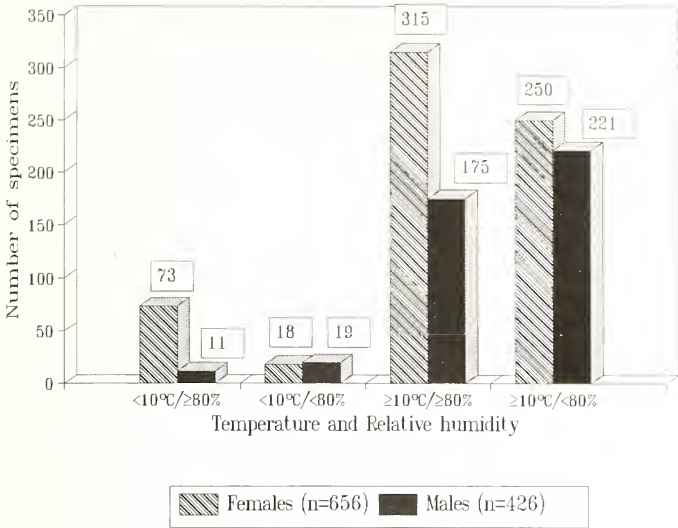


Fig. 7. Total number of calling females and female-attracted males, over all the sampled nights, for the four RH-T groups.

Effect of cloudiness (Fig. 8)

Though it is obvious that males were attracted in any situation, the distribution is not random (Chi-square significant to $\alpha < 0.001$). Male attendance seemed to be less favoured on completely cloudy nights, which occurred on 26.3 % of all nights. Under these conditions only 16.7 % of males were attracted (71 males instead of the 112 expected if they had been attracted at random). Of the cloudy nights, 26 (13.4 %) were rainy, yet 38 males were attracted (8.9 %).

Effect of wind speed (Figs 9, 10)

Again this distribution is not random (Chi-Square significant to $\alpha < 0.001$). Though the majority of males (65.5 %) were being attracted when wind speed was between 0-0.2 m/s, this probably only reflects the large number of nights on which such conditions occurred (75.3 %). Possibly a wind speed a little higher, e.g. 0.3-1.5 m/s, is more

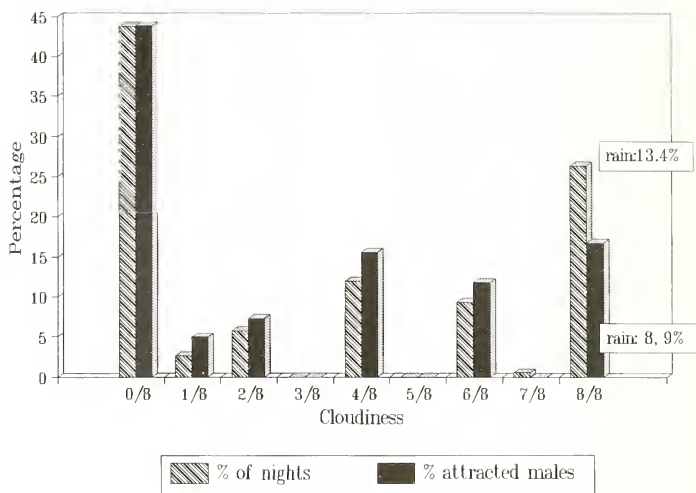


Fig. 8. Effect of cloudiness on male attendance as shown by percent attracted males and nights for the different degrees of cloudiness.

favourable as in this situation 120 males were attracted (28.2 %). In fact, from the values of "Relative Percentage of Success" (Fig. 10) it would appear that relative male attendance increases with wind speed. However, as the sample sizes at wind speeds higher than 1.5 m/s are small, more data are required to validate these findings.

Finally, as at least three of the factors considered were correlated with the number of attracted males, a multiple regression analysis was undertaken in order to determine their joint effect on male attendance. After trying diverse combinations among the three variables, the best multiple regression was as follows :

number of attracted males = $2.286 + 0.155 T - 0.041 H + 0.374 F$
 where T = Temperature (C°), H = % Relative humidity, F = number of available calling females.

This equation has a $r^2 = 0.25$, i.e. the prediction value of this model is only 25 %. This suggests that other factors which have not been considered are determinant to male attendance. Some of these could be a) female age (in female Lepidoptera, pheromone production depends on age), b) male age and c) location of available males (under

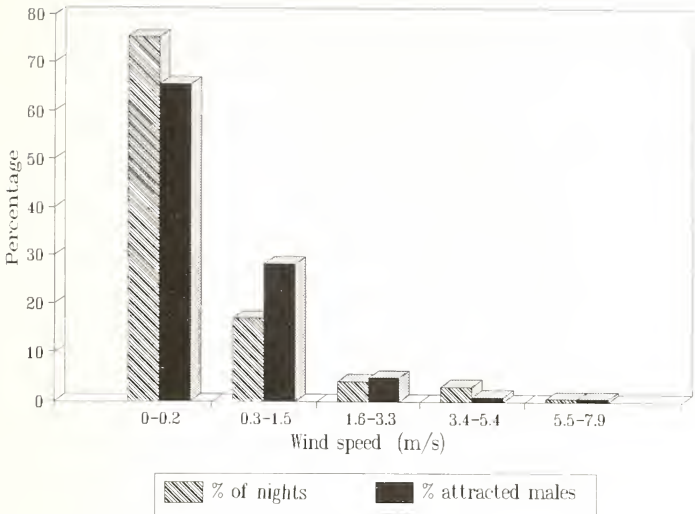


Fig. 9. Effect of wind speed on male attendance as shown by percent attracted males and nights for the different wind speeds.

unfavourable weather conditions only males resting in trees near the calling female would be attracted ; favourable conditions would determine a much wider range).

Discussion and conclusions

Many authors have pointed out the important effect that temperature has on female pheromone-releasing behaviour. Birch & Haynes (1982) found that females of the noctuid moth *Trichoplusia ni* (Hübner) do not call when temperature is below 12°C. Sower *et al.* (1971) consider that the female only releases pheromone when the temperature falls into a favourable male perception temperature region, while others say that temperature does not affect the pheromone releasing behaviour at all (Sanders & Lucuik, 1972 ; Daterman, 1980). In the latter case, the temperature would only affect the diffusion of the pheromone in the air : the higher the temperature, the higher will be the pheromone diffusion rate. In the case of *G. isabellae*, our data seem to support the second alternative, as females apparently release pheromone under

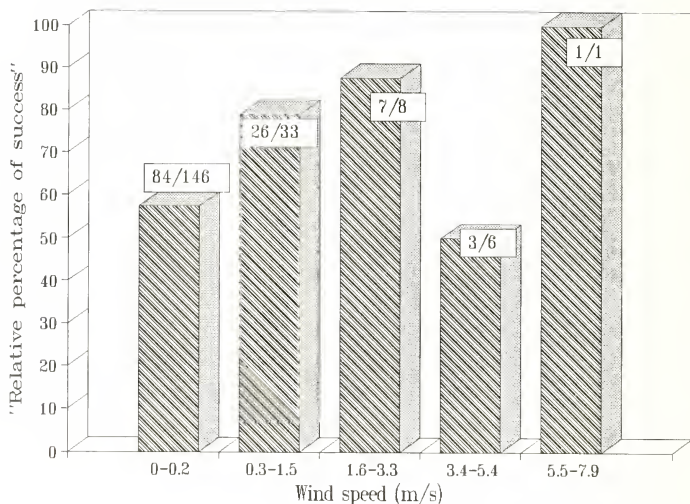


Fig. 10. "Relative Percentage of Success" for the different wind speed intervals (= number of nights with attracted males at a particular wind speed X 100 / number of nights with this particular wind speed).

any of the recorded temperatures (though no males came when temperature was below 7°C).

Roelofs *et al.* (1982) have shown that the female of the geometrid moth *Operophtera brumata* (Linnaeus) releases a pheromone which is active at low temperatures. Such a pheromone works from 4°C upwards, showing maximum activity between 7°C and 15°C. According to these authors, such a property is unique among tested lepidopterous pheromones as, even though lepidopterans are able to keep rather high body temperatures and flying activity at low air temperatures, the minimum thermal threshold for pheromone perception lies normally between 15°C and 17°C. *G. isabelae* produces a pheromone which is active at temperatures well below the 15°C-17°C threshold (the lowest value registered for an attracted male was at 7.1°C) which is a clear adaptation to the prevailing weather conditions (temperatures often below 15°C-17°C).

Several other aspects related to sexual attraction via pheromones depend on temperature ; e.g. the rhythmic exposure of the pheromone

gland in arctiid moths (Conner *et al.*, 1985), the degree of male sensitivity when recognising different proportions of pheromonal components and modifications of the latent period (McNeil, 1991). These aspects, however, have not been considered here.

The effect of relative humidity on male attendance is poorly known and literature on it controversial. Comeau *et al.* (1976), with the tortricid *Argyrotaenia velutinana* (Walker), did not find any significant effect of this factor on male attendance. Miller & McDougall (1973), with *Choristoneura fumiferana* (Clem.), found a negative correlation between male catches and relative humidity. On the contrary, Webster & Cardé (1982) and Royer & McNeil (1991), with *Ostrinia nubilalis* (Hübner), and McNeil (1991), with *Lymantria dispar* (Linnaeus), found that a high relative humidity favours male attendance.

Daterman (1980) states that high relative humidity and rain result in a reduction of the efficacy for male attraction, which seems to agree with our results, suggesting that such conditions act in decreasing the pheromone releasing rate. There is also the possibility that high relative humidity interferes in some way with male antennae chemoreception. To solve those questions, the pheromone should be isolated and its chemical structure analysed and then perhaps the possible mechanism of interference could be determined.

More information has been published on the wind speed, as it affects directly pheromone air diffusion and propagation (Shorey, 1976 ; Karandinos, 1974 ; Kennedy, 1981 ; Linn & Gaston, 1981 ; David *et al.*, 1982 ; Willis *et al.*, 1991). *Trichoplusia ni* females will display the calling behaviour for longer periods when wind speed falls between 0.3 and 1 m/s ; wind speeds lower or higher will determine shorter periods for calling (Birch & Haynes, 1982). According to these authors, during windy nights, *Trichoplusia ni* females either move to the lowest parts of plants for calling or simply do not call at all.

In our case, female calling behaviour and female detection by males in *G. isabelae* does not seem to be greatly affected by the registered wind speeds (always below 8 m/s). However, should wind speed attain high levels it could act as a real physical barrier preventing males reaching the females. In our area and during the study period, we have never noted wind speeds higher than 8 m/s and those registered would not have prevented males from approaching females. It is worth pointing out that *G. isabelae* males are perfectly capable of finding calling females during completely windless nights, which is not the case with all lepidopterans (Kaae & Shorey, 1972).

We conclude that, in spite of all the details given above, male attendance takes place under the most diverse weather conditions : high or low temperature and relative humidity, windy or windless, rainy or rainless, cloudy or cloudless nights. Marten (1955), pioneer in the study of the biology of *G. isabelae*, had already stated that mating takes place under any weather conditions and at temperatures between 9°C and 14°C ; Sanetra & Peuker (1991) state that the best conditions for mating are 15°C, a slight wind and no rain. Obviously, *G. isabelae* is well adapted to the prevailing conditions in its particular ecological niche.

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