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POLLINATION ECOLOGY IN TRIBE DELPHINEAE (RANUNCULACEAE) IN W MEDITERRANEAN AREA: FLORAL VISITORS AND POLLINATOR BEHAVIOUR

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Abstract

The pollination ecology of W. Mediterranean species of the genera *Aconitum, Delphinium* and *Consolida* has been studied, mainly from the point of view of floral visitors and potential pollinators. Investigations about the foraging behaviour on the flower allowed us to differ between legal pollinators, nectar or pollen robbers, floral predators and accidentals. Field observations showed that the main pollinators are hymenoptera of the genus *Bombus,* principally in high mountain species (*Aconitum* and *D. montanum*), whereas the remaining species growing in lower habitats showed a wider taxonomic range of visitors, including other Hymenoptera, Lepidoptera and Diptera, some of which acted as pollinators. The plants studied have a complex floral morphology, closely adapted to insect-pollination. They produced a large amount of nectar in specialized structures hidden in a spur (in *Delphinium* and *Consolida*) or in a helmet (in *Aconitum*). Correlation between nectary length and insect tongue length has been studied. Analysis of corbiculae showed that the *Delphineae* species are the greatest pollen source, together with small amounts of other neighbouring plants in each population.

Introduction

The tribe *Delphineae* Warming (*Ranunculaceae* L.), consists of four genera: *Aconitum* L., *Delphinium* L., *Consolida* (DC.) Gray and *Aconitella* Spach, with near of 700 species (TAMURA, 1995). They are herbaceous perennials or annuals, mainly distributed in temperate zones of the northern hemisphere (JALAS & SUOMINEN, 1989; TAMURA, *l.c.*). In the Western Mediterranean area –taking the Alps and Tunisia as the oriental boundaries– there are 30 species belonging the first 3 genera, with a high degree of endemicity. If we consider the Himalayas as a primary centre of tribe speciation (BLANCHÉ, 1990), these species occupy the westernmost position in the Eurasian continent. These two facts, high endemicity and possible extreme area effect, suggest that these taxa could have undergone particular evolution processes, in which pollination ecology could play an important role.

Correlations between certain floral characteristics of plant species and the kind of animal pollen vectors that visit their flowers are well known. In many cases, a parallel evolution between plants and their pollinator vectors has been established (LØKEN, 1981). This adaptation, usually known as co-evolution (MACIOR, 1971, 1974; FAEGRI & PIJL, 1979; KEVAN & BAKER, 1983), has as a main result, to optimize the foraging process of pollen and/or nectar collection for vectors, and from the point of view of plants, to profit the insect mobility to ensure outcrossing. This great interdependence

and reciprocal adaptation has reached surprisingly high levels in certain taxa. What is the case in the *Delphineae*?

Flowers of *Delphineae* have a complex floral morphology, closely adapted to insect–pollination (MÜLLER, 1883). These taxa conform to a classical "bumblebee pollination syndrome" (MÜLLER, *l.c.*; KNUTH, 1906–09; BAKER & HURD, 1968; MACIOR, 1975; FAEGRI & PIJL, 1979; PESSON & LOUVEAUX, 1984; WASER & PRICE, 1990). Some American species, however, are also pollinated by hummingbirds (GRANT & GRANT, 1968; SCHLISING & TURPIN, 1971; GUERRANT, 1982a, 1982b; WASER, 1982; WASER & PRICE, 1990; INOUYE & al., 1991; KOTLIAR, 1992).

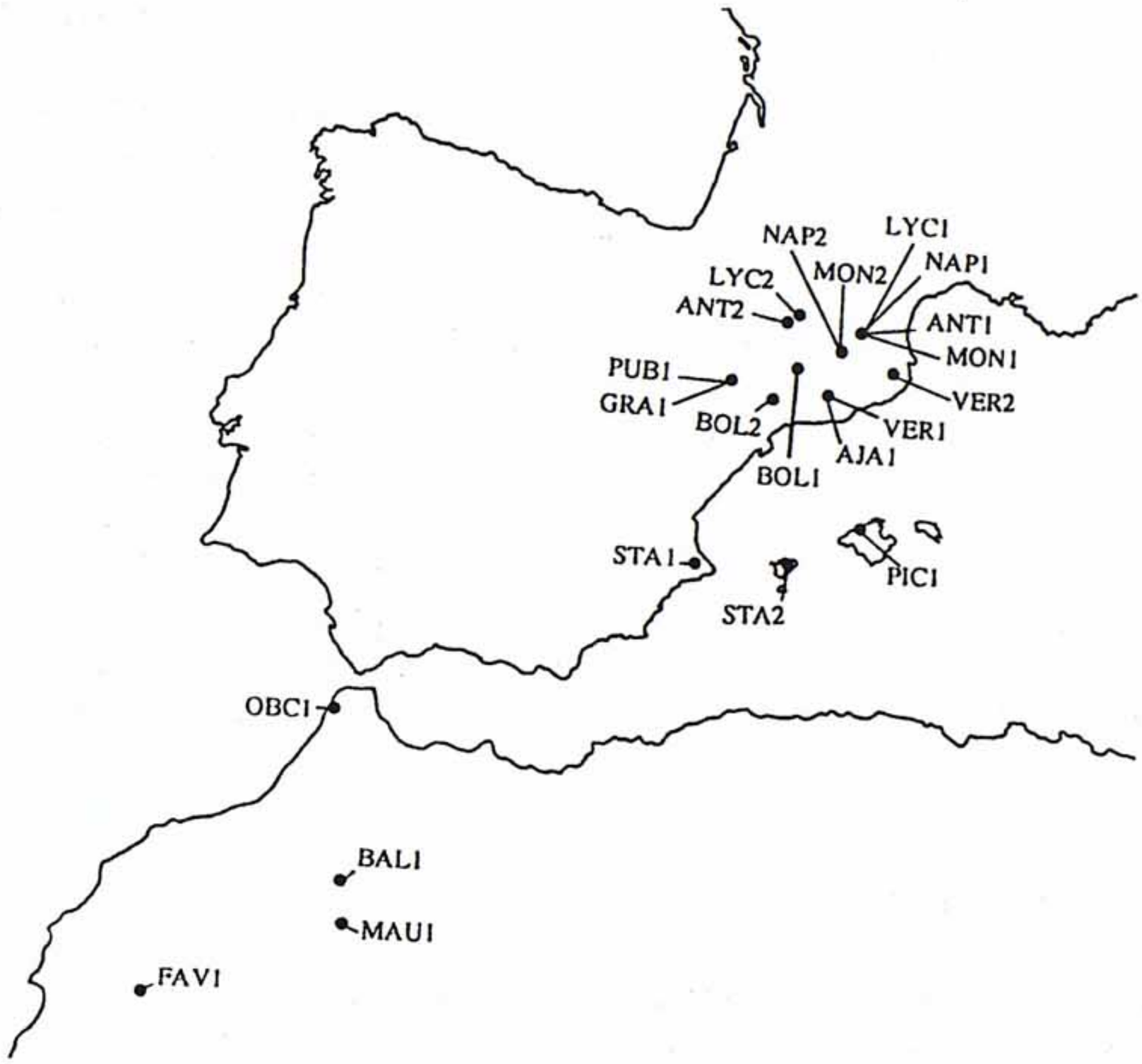
Given that the complex floral structure of these taxa suggests marked entomophily and dependence of insects, the purpose of this paper is to study the insect pollen vectors (at present unknown for the majority of the plant species investigated), their frequency, their behaviour on the flower, the degree of specialization through analysis of pollen loads and the relation between nectary and proboscis length, always from a comparative perspective, to assess the evolutionary trends within the tribe in the W. Mediterranean area and the functionalism of floral morphology, usually employed as a "good" discriminant taxonomic set of characters.

Material and Methods

Field work was carried out over four years (1992-1995), for a total of 217 h of censuses, –in which we counted 2876 insects– in 22 populations of the genera *Aconitum, Delphinium* and *Consolida* (3, 9 and 3 species, respectively), as indicated in Fig. 1. The *Delphineae* voucher specimens were deposited at the herbarium of the Facultat de Farmàcia de Barcelona (BCF). Other data such as population altitude, flowering time and life cycle appear in Table 1. The censuses were recorded at 15-30 min intervals, several times a day, allowing us to determine the frequency of each floral visitor. We observed their foraging behaviour on both flowers and inflorescences. To facilitate observations, insects were photographed and recorded with a domestic video–camera, following the procedures indicated by DAFNI (1992). Several specimens of each insect were captured, with ethylacetate, for further identification by specialists.

To determine the degree of correlation of pollinator tongue length and the nectary length, it should be remembered that the latter is difficult to estimate and that significant error could be introduced. In fact, we must consider the "total effective foraging length" (MACIOR, 1978). The length of the head and even a part of the thorax must be added to proboscis length, if the mouth of corolla is wide enough to accommodate the pollinators. On the other hand, the accumulation of nectar in the flower would notably reduce this distance (INOUYE, 1980b). However, to standardize the measurements for further comparisons, all the distances were taken in the same form. We measured only the proboscis (prementum + glossa) of 10-30 specimens. We considered only Hymenoptera and *Bombylius*, because the proboscis of Lepidoptera is too long in relation to nectary length, and they could distort the results, and small bees and

Fig. 1. Geographic situation of taxa studied.



CODE	TAXON	POPULATION
Aconitum		
LYC1	*A. lycoctonum* L.	Ga: Pyrénées Orientales, Vall d'Eina
LYC2	*A. lycoctonum* L.	Hs: Lleida, Vall del Nera
ANT1	*A. anthora* L.	Ga: Pyrénées Orientales, Vall d'Eina
ANT2	*A. anthora* L.	Hs: Lleida, Llauset
NAP1	*A. napellus* L.	Ga: Pyrénées Orientales, Vall d'Eina
NAP2	*A. napellus* L.	Hs: Barcelona, Serra del Cadí
Delphinium		
MON1	*D. montanum* DC. in Lam & DC.	Ga: Pyrénées Orientales, Vall d'Eina
MON2	*D. montanum* DC. in Lam & DC.	Hs: Barcelona, Serra del Cadí
BOL1	*D. bolosii* C. Blanché & Molero	Hs: Lledia, Rubió de Baix
BOL2	*D. bolosii* C. Blanché & Molero	Hs: Tarragona, Ulldemolins
STA1	*D. staphisagria* L.	Hs: Alacant, Pedreguer
STA2	*D. Staphisagria* L.	Bl: Eivissa, Benarràs
PIC1	*D. pictum* Willd.	Bl: Mallora, near Cala Tuent
VER1	*D. verdunense* Balb.	Hs: Barcelona, Sant Llorenç d'Hortons
VER2	*D. verdunense* Balb.	Hs: Girona, Canapost
GRA1	*D. gracile* DC.	Hs: Osca, Vedat de Fraga
BAL1	*D. balansae* Boiss. & Reut.	Ma: Meknès, Timahdit
OBC1	*D. obcordatum* DC.	Ma: Titt'aouen, Asilah
FAV1	*D. favargeri* C. Blanché, Molero & Simon P.	Ma: Agadir, near Tizin't Test Pass
Consolida		
MAU1	*C. mauritanica* (Coss.) Munz	Ma: Khénifra, Arbahlou to Ait-Mouli
PUB1	*C. pubescens* (DC.) Soó	Hs: Osca, Vedat de Fraga
AJA1	*C. ajacis* L.	Hs: Barcelona, Sant Llorenç, d'Hortons

INSECTS	*ACONITUM*						*DELPHINIUM*													*CONSOLIDA*		
	LYC1	LYC2	ANT1	ANT2	NAP1	NAP2	MON1	MON2	BOL1	BOL2	STA1	STA2	PIC1	VER1	VER2	GRA1	BAL1*	OBC1	FAV1	MAU1	PUB1	AJA1
HYMENOPTERA																						
Apidae																						
Bombus hortorum hortorum	8.6	21.6	46.4	45.9	72.8	18.5	49.3	51.1														
Bombus wurfleini pyrenaicus	31.5	59.8	5.7	13.5	0.5	30.5	18.1															
Bombus gerstaeckeri	22.8	6.3			8.0																	
Bombus terrestris terrestris									15.4	4.2			10.7		13.9			18.2		55.6		5.9
Bombus pasquorum rufocitrinus		0.5		1.3					1.0	1.5			6.5	1.4	9.7							
Bombus humilis quasimuscorum				9.5																		
Bombus mesomelas mesomelas			1.5	4.1	5.2																	
Bombus ruderarius ruderarius					1.6																	
Psithyrus sylvestris			3.1																			
Anthophoridae																						
Amegilla sp.												17.9		20.0	1.6		52.2	18.2	66.7		12.2	26.4
Anthophora dispar									1.8													
Xylocopa violacea									12.1				2.2			6.2						8.8
Megachilidae																						
Oplitis sp.												28.6										
Megachile rotunda												14.3										
Halictidae																						
Lassioglossum sp.									2.3	26.7	25.0			28.4	4.8	43.8	43.5			44.4	4.1	29.4
Halictus sp.										2.0				9.5	14.6							
Eumenidae																						
Alastor atropos									8.2	31.2				4.3		31.4					54.0	
LEPIDOPTERA																						
Macroglossum stellatarum							1.4		30.8	7.4	37.5	32.1	13.0	4.3	6.5		4.3	27.3				
Other	31.0	1.5					2.1		14.8	13.8				20.4	27.4	6.2		18.2	9.5		4.1	8.9
DIPTERA																						
Bombylius sp.									1.0	5.7					4.8	6.2		4.5			21.5	
Syrphidae	2.0		21.6	8.2	11.9	1.1	27.8	38.3	8.4	2.9	37.5	7.1	28.2	5.4	4.8				19.0			11.8

= robbers // (*) The only perennial species belonging to annual subgen. *Delphinium*.

ALTITUDE (in m a.s.l.)	1980	1600	1980	1750	1980	2350	1980	2350	290	600	150	160	100	196	50	300	1930	5	1300	1650	300	196
FLOWERING (in months)	7-8	7-8	8-9	8-9	7-8	7-8	7-8	7-8	6	6	5-6	5-6	6	7-8	7-8	7-8	6-7	6-7	6-7	6-7	5-6	6-7
LIFE CICLE	PERENNIALS										ANNUALS											

Table 1. Percentage of total visits corresponding to pollinators and robbers observed in each population.

Syrphidae only forage pollen. The length of the nectaries of each plant species was measured in 30 fresh flowers (internal nectariferous petals in *Delphinium* and *Consolida*, and length of nectary in *Aconitum*).

Pollen carried by floral visitors was removed from various body regions, mainly corbiculae. Many apidae (*Bombus, Apis*...) presented these structures on posterior tibias and they are a pollen mass agglutinated with insect saliva (JANDER, 1976; MICHENER & al., 1978; ROBERTS & VALLESPIR, 1978). The sample was disgregated with phosphate 0.1 M buffer, embedded into fuchsinate glycerogelatin and identified microscopically (if necessary, compared with the pollen reference collection kept in the Laboratori de Botànica, Facultat de Farmàcia Universitat de Barcelona).

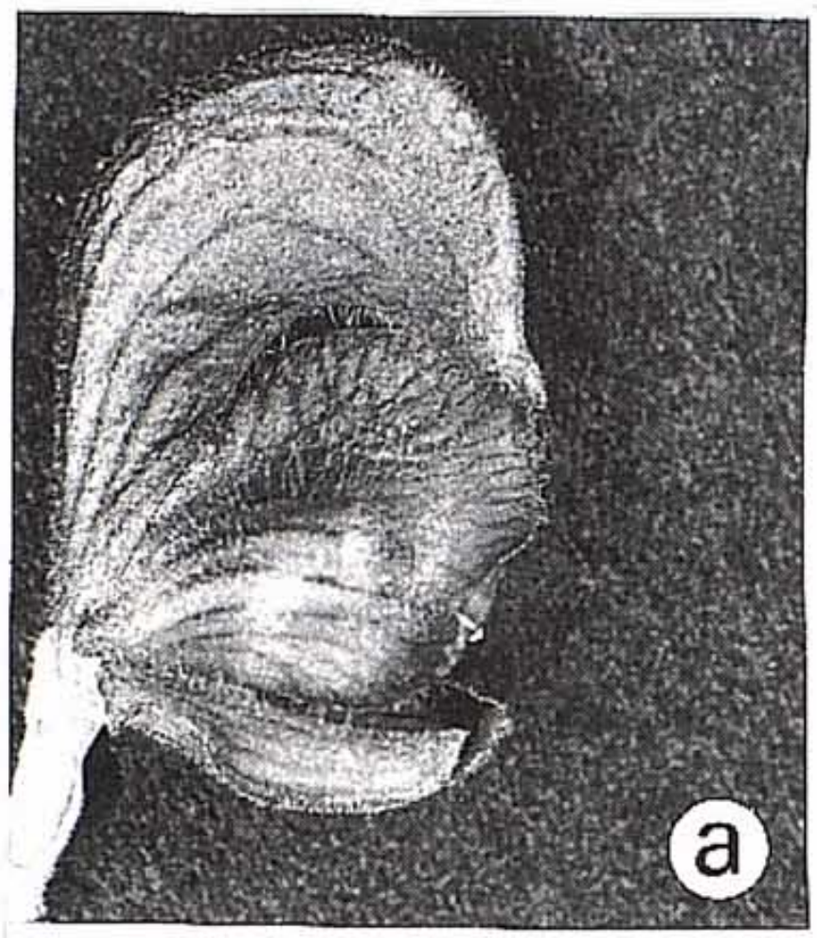
Results

Floral morphology and rewards

Flowers of tribe *Delphineae* show bright colours, mainly of the blue-purple range, and less frequently yellow or pink. They often present nectar guides. *Aconitum* (Fig. 2a-b) has five petaloid sepals, one of which is transformed into a helmet, that contain a couple of pedicellate nectaries (nectary length range in studied species is 15.2-18.8 mm), and 3 or 5 carpels. *Delphinium* (Fig. 2c-e), also has five petaloid sepals, one of which, in this case, is extended into a tubular sheath covering the nectariferous spurs (4.6-19.5 mm) of the two upper petals. Two additional lateral petals (with a great diversity of shapes, colours, dispositions, indument, depending on the species) are placed over the sexual organs, acting as a landing surface. The investigated species have 3 carpels, exceptionally 5. Floral morphology of *Consolida* (Fig. 2f) is quite similar to *Delphinium,* but the two nectariferous petals (12.5-18.9 mm) are coalesced in a single one and lateral petals disappeared. There is only one carpel in the *Consolida*. It seems that a trend towards simplification of floral structure can be recognized (see discussion chapter).

This tribe presented flowers closely adapted to insect pollination because, in addition to the general floral morphology, many stamens (15-48 in number) allowed the feeding of floral visitors, and produced large amount of nectar (1-17 µl and 40- 60% of sugar concentration, Bosch *unpubl.* data) in specialized structures hidden deeply in the helmet (in *Aconitum*) or in the spur (in *Delphinium* and *Consolida*), which force insects to describe certain movements. Corolla shapes are illustrated in Fig. 2. Finally, both marked proterandry and marked herkogamy were also detected, which prevent, as far as possible, self-pollination.

Flowers of this kind, with a complex floral morphology, a greater deep effect, mechanically strong and reward concealed, are usually pollination-dependent of bumblebees, with a robust body that allowed them to separate floral pieces and a long proboscis that permitted nectar to be obtained. Bumblebees have been considered the ideal pollinators (MÜLLER, 1883; MACIOR, 1975; WASER, 1982; PESSON & LOUVEAUX, 1984).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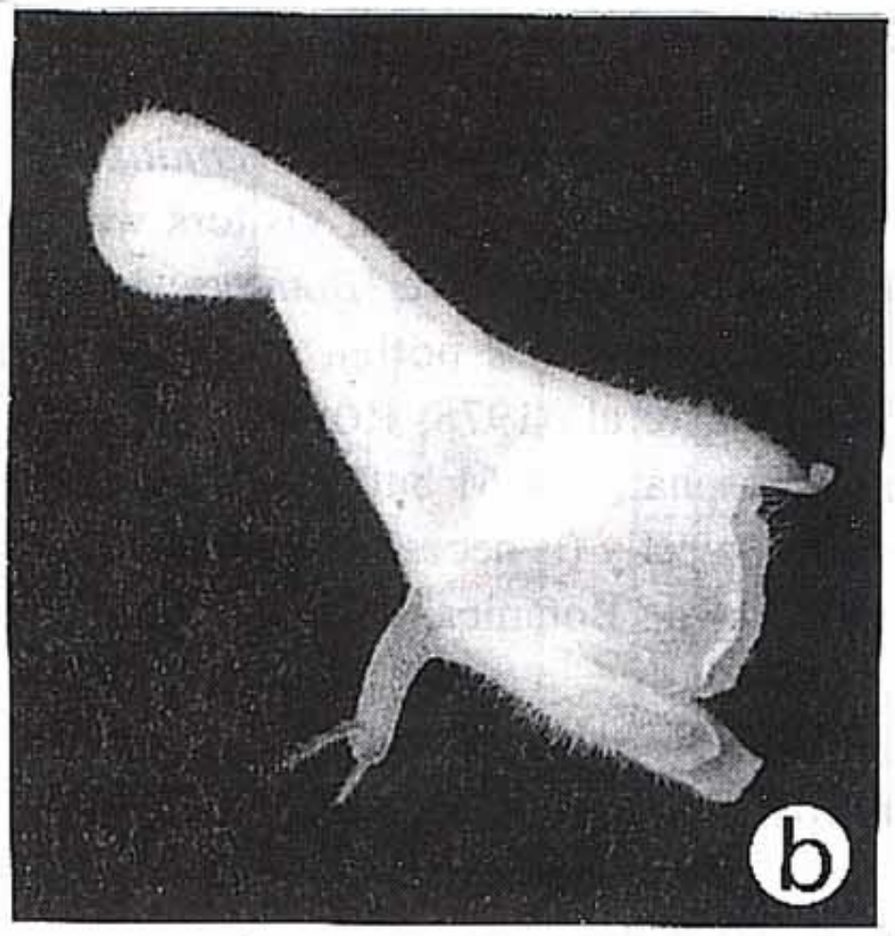
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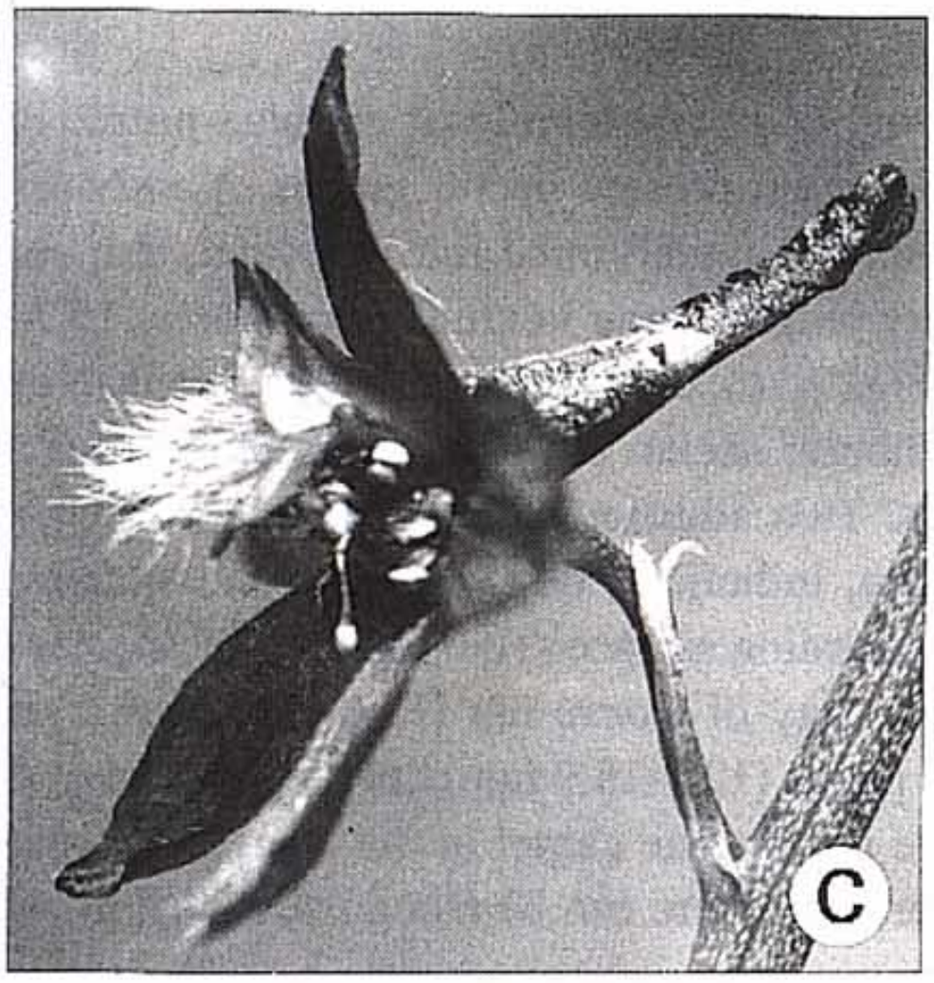
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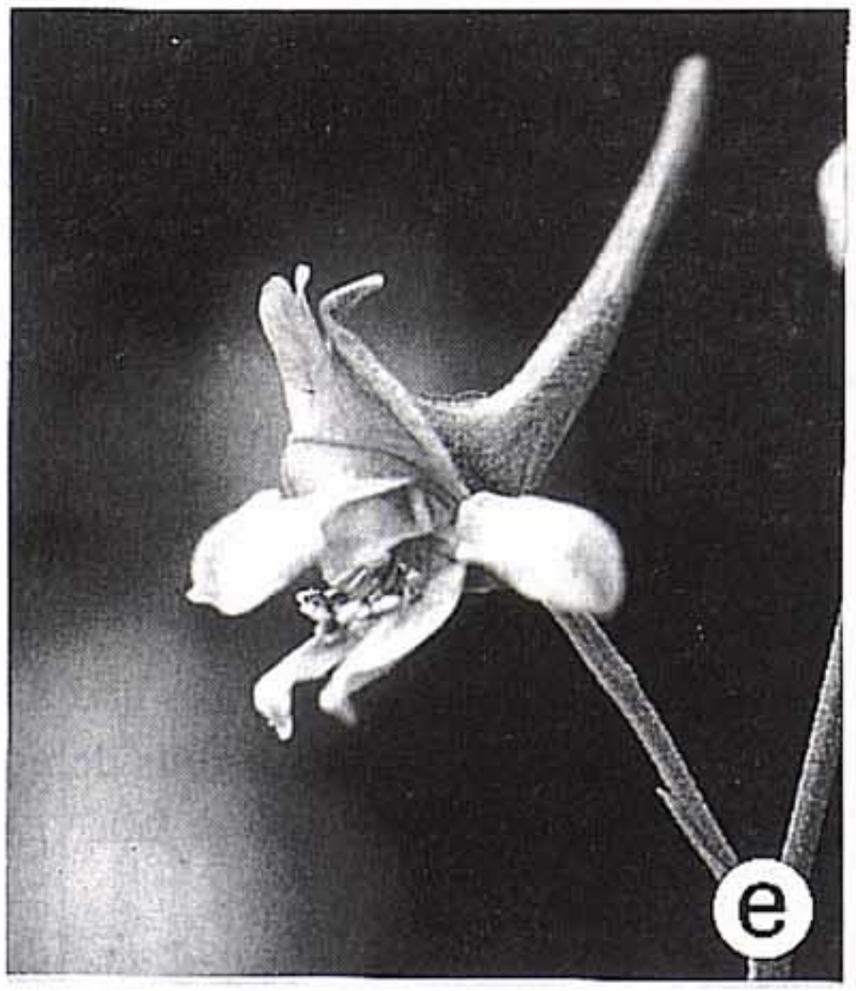
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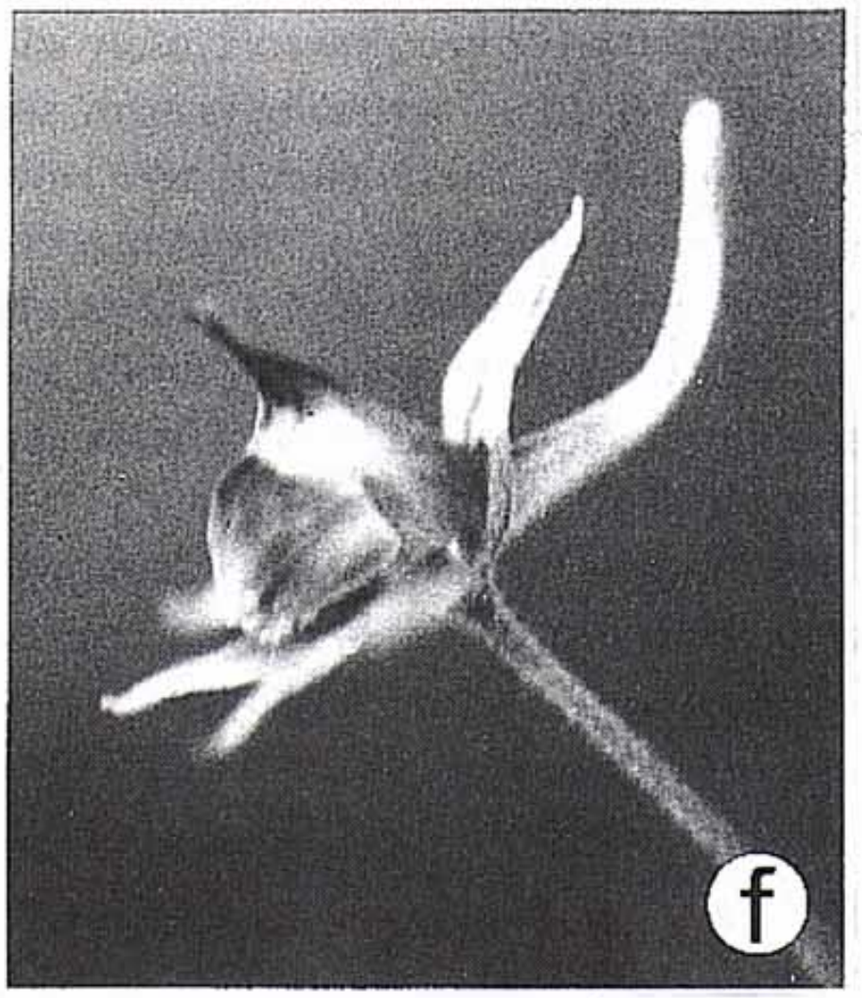
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Floral visitors

Fig. 3a shows, in percentages, the frequency of the main insect orders that visited the flowers of tribe *Delphineae* studied in this area. There was a broad spectrum of floral visitors, wider in the genus *Delphinium*. Hymenoptera is the most frequent group of visitors of the 3 genera, followed by Diptera in *Aconitum, D. montanum* and *Consolida*, and by Lepidoptera in *Delphinium*. Heteroptera and Coleoptera were scarce, clearly accidental and occasionally predators. Fig. 3b represents, in percentages, the visits of only the legal pollinators, also arranged by insect order. Hymenoptera are still the most habitually recorded pollinators, although in some *Delphinium* Lepidoptera were more abundant visitors; their pollen-carrying capacity being much lower. They should be considered as much less effective pollinators (HERRERA, 1987; DAFNI & O'TOOLE, 1994).

Table 1 summarizes the main pollinators and robbers in each population examined. There was a greater diversity of *Bombus* species in alpine and high mountain *Delphineae* species (*Aconitum* and *D. montanum*), which decreased markedly in

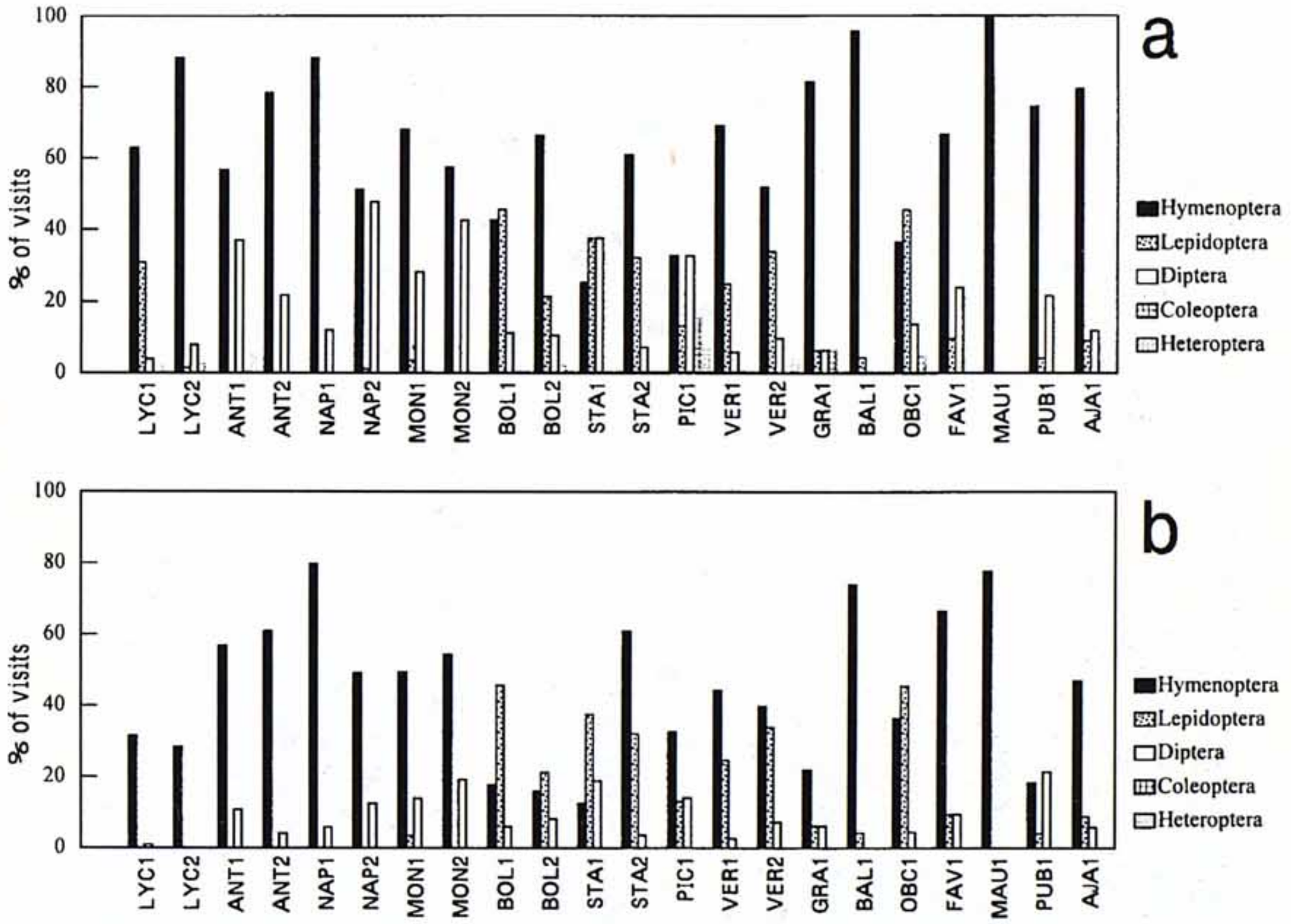


Fig. 3. Percentage of visits arranged in insect order. a, Total recorded visits; b, Legal visits (excluding visitors not pollinating and nectar robbers).

Fig. 2. Corollas of W. Mediterranean representatives of tribe *Delphineae*. a, *A. napellus* (blue flowers); b, *A. lycoctonum* (yellow flowers); c, *D. bolosii* (blue-lilac flowers); d, *D. staphisagria* (blue-purple flowers); e, *D. gracile* (pale blue flowers); f, *C. pubescens* (pale purple flowers)

montane and lowerland localities. In fact, there was a clear correlation between altitude and percentage of *Bombus* that visit each taxon: y=20.765x+428.614 r=0.756 p<<0.001 (see Fig. 4). In annual taxa (belonging to the genera *Consolida* and *Delphinium*), the species of *Amegilla* are the most recorded, notably in North-African populations. Population altitude and nectary length, although there is a large variety of taxa, are also significantly correlated, but to a lesser extent: y=97.055x–407.104 r=0.488 p=0.021; there was a slight but non significant correlation (p>0.05) between rate of visits by *Bombus* and nectary length: y=0.54x+14.432 r=0.391 p=0.072 (see also Fig. 4).

Pollinator behaviour

During floral development, the stamens move. When the flower blooms, stamens are situated at the floral base. Progressively, they mature and dehisce, ascending and to become strategically placed (see Fig. 2 and Fig. 8) above lateral petals (in *Delphinium*) or protected by sepals (in *Aconitum*) or by lateral lobes of upper petals (in *Consolida*). In this way, when the vector comes into the flower to reach the nectar, pollen adheres to its ventral part, which is known as a sternotribic behaviour (FAEGRI & PIJL, 1979).

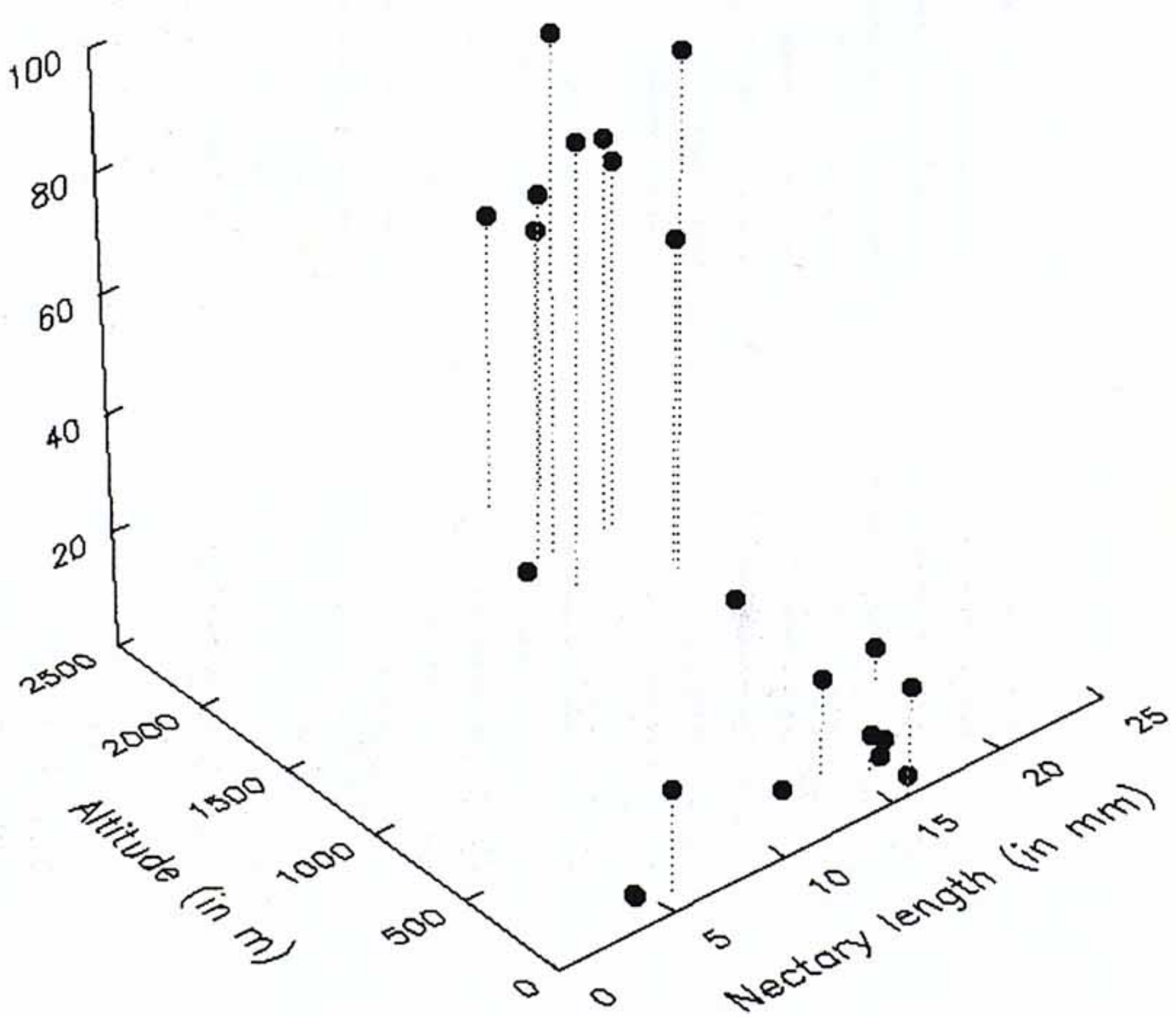


Fig. 4. Relationship between nectary length, altitude and percentage *Bombus* visits over the total number of insect visits in each population.

Generally, the perennial taxa studied showed a higher insect activity than the annual ones (see Fig. 5, presented as number of insect visits/hour), except for *D. montanum*. We attributed this slow activity to unfavourable meteorological conditions on the days on which field work was performed. Plants with the shortest spur –*D. pictum* and *D. staphisagria*– foreseeably less specific, showed a markedly inferior activity. The greater rate of visits was concentrated in the morning and, especially, at midday. In the afternoon, insect activity decreased progressively. Some vectors however, such as *Macroglossum stellatarum* or some *Bombus*, remained active throughtout the diurnal period. No nocturnal pollinator was recorded.

Some insects produced a hole in the helmet or in the spur to suck the nectar (Fig. 6b). They are considered primary robbers (LØKEN, 1949; INOUYE, 1980a, 1983) like *Bombus wurfleini pyrenaicus*, *Bombus terrestris* or *Xylocopa violacea*. Others used the holes (secondary robbers), such as *Alastor atropos*. Some primary robbers acted as secondary ones in some cases. The incidence of nectar robbery is different, depending on the species. It was higher in *A. lycoctonum* than in the other two *Aconitum* species and it was also frequent in *D. montanum*, *D. bolosii* and *D. gracile*. It seems to be related to bumblebee proboscis length, because the most frequent robbers –*Bombus terrestris* and *Bombus wurfleini pyrenaicus*–, have short tongue (LØKEN, 1949; PEKKARINEN, 1979). This is easily seen if the data are arranged as in Fig. 7, by pairs of proboscis and nectary length. In this graph, *Bombus terrestris* and *B. wurfleini pyrenaicus* lie in the lower right hand corner below a critical value. However, there was no correlation between proboscis length and nectary length of a given species (y=–0.018x+8.078 r=–0.030 p=0.84 n=48). This can be interpreted, probably, because corollas are wide enough not to limit the entry to most insect species, and thus the range

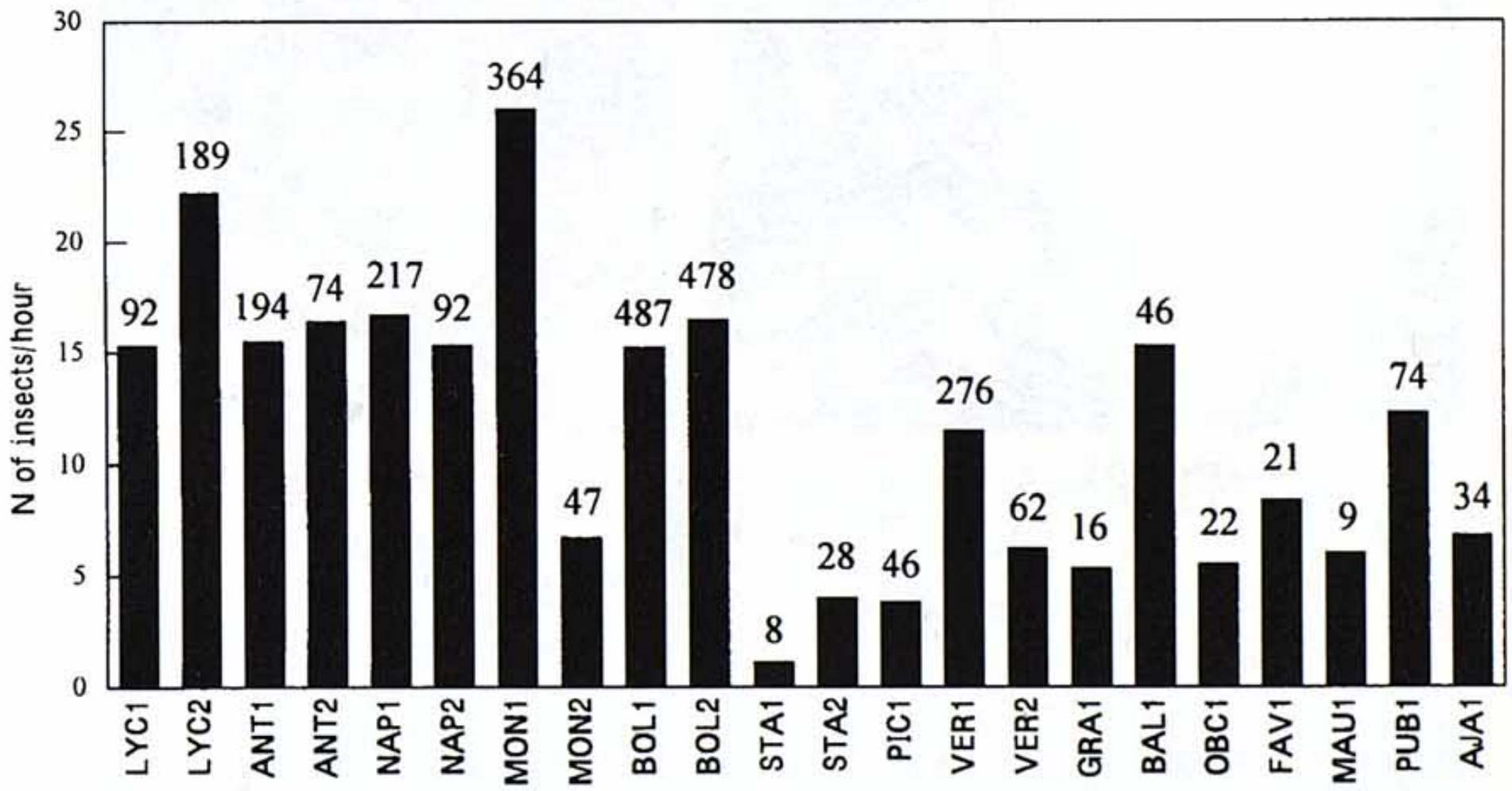
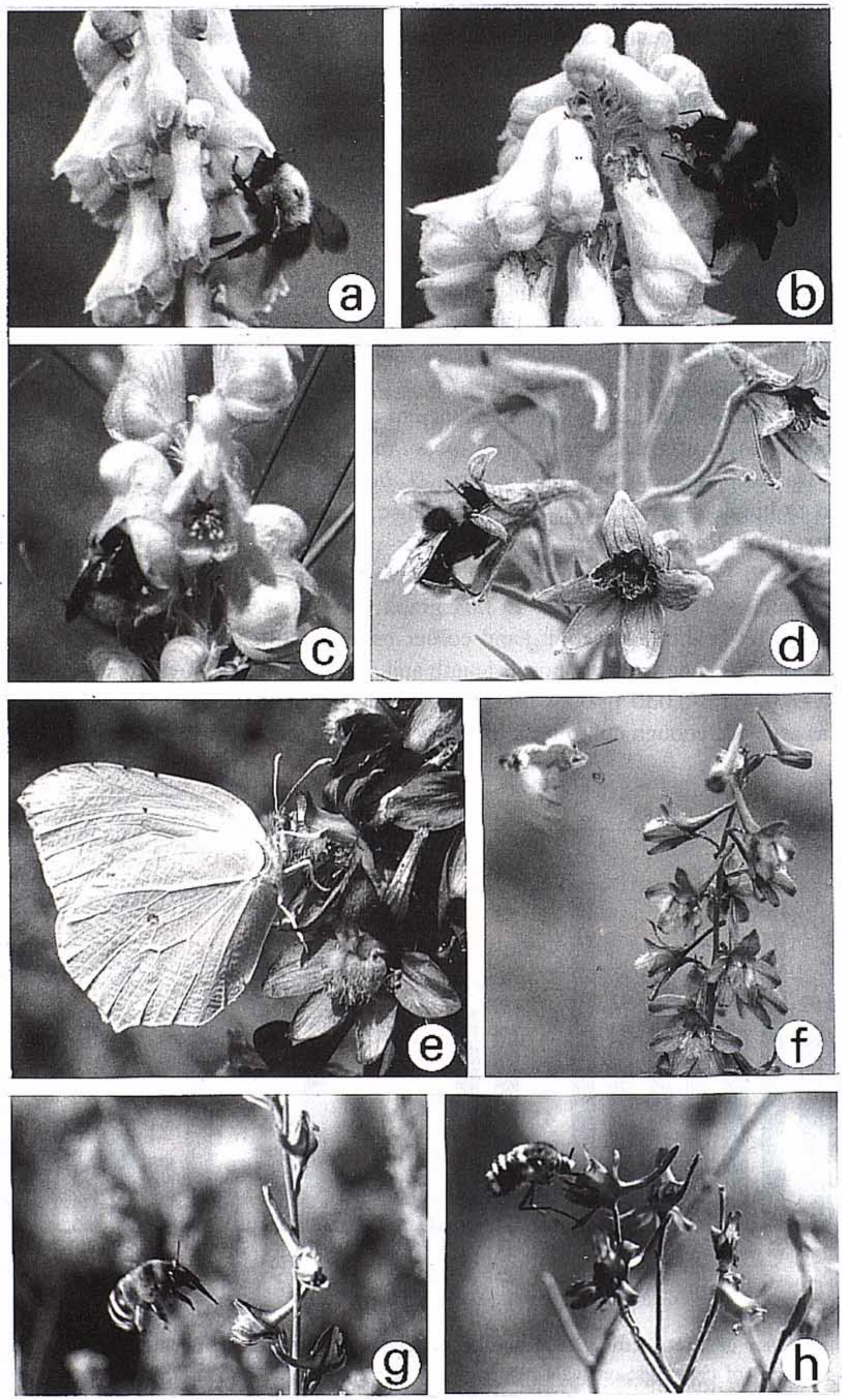


Fig. 5. Diagram of insect activity in all studied populations. Bars indicate the number of recorded visits per hour of censuses; ordinals placed at the top of each bar indicate the total number of specimens censused in each population.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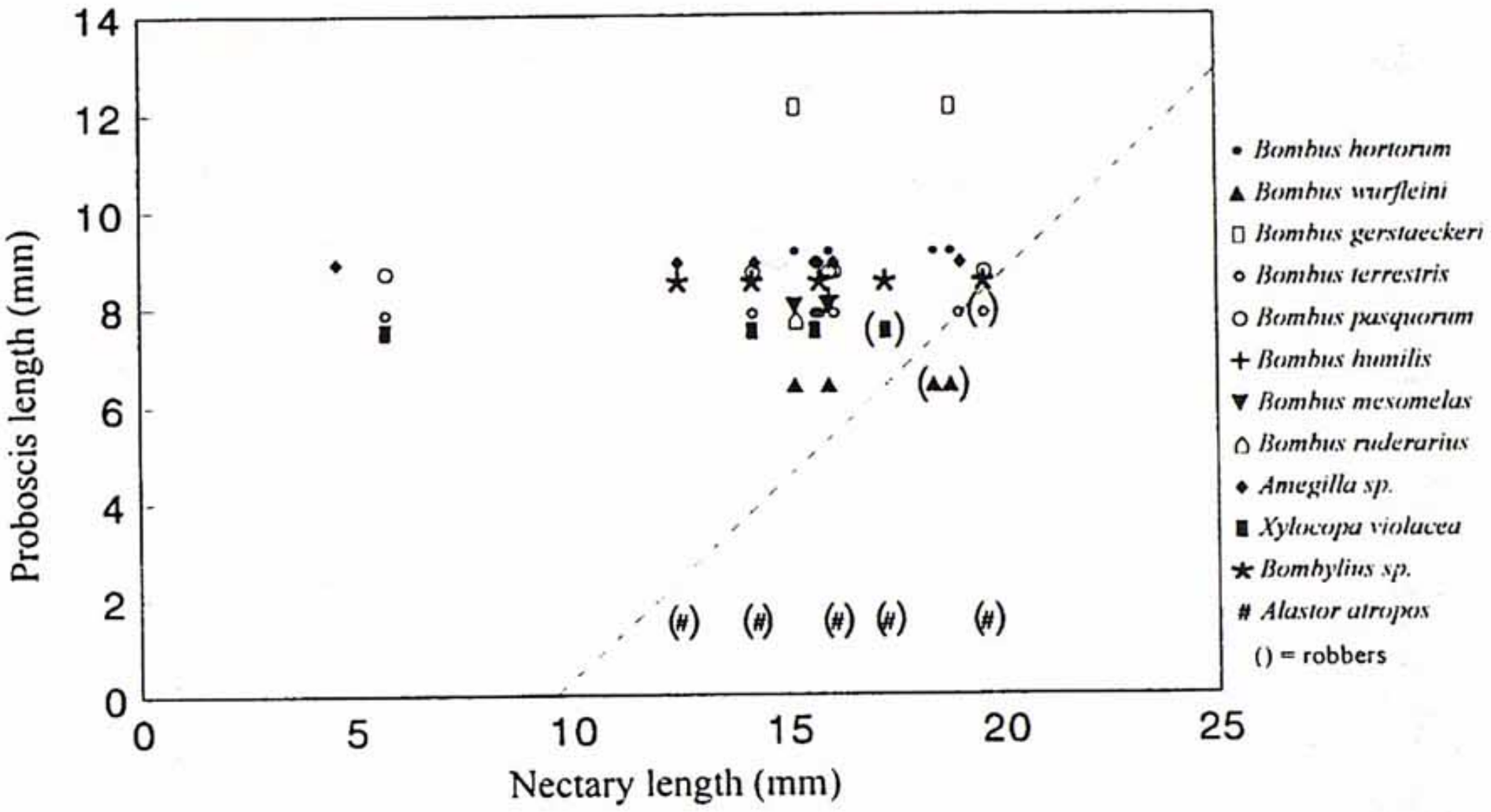

Fig. 7. Relationship between nectary and proboscis length. Each point represents the pair of the mean proboscis length (measured on the captured insects belonging to a given animal species) and the mean nectary length of each plant species. Points lying below the broken diagonal line represents robbery behaviour in all cases, because proboscis length is shorter than nectary length and insects are not able to reach the nectar.

of proboscis lengths available to reach the nectar is too wide to permit a mathematical correlation as stated in the Material and Methods chapter.

Analysis of pollen loading contents showed that these plants were the greatest pollen source, together with small amounts of other neighbouring plants (see Table 2). In general, *Amegilla* (Fig. 6g) and solitary bees seem to be less specific than *Bombus* (Fig. 6a-d).

Finally, concerning the flying patterns of the most important pollinators, two main types have been recognized in relation to inflorescence architecture. In the perennial taxa surveyed, usually bearing simple, long (vertical) racemes (with few or no lateral branching) the vector movements are usually ascending, according to the models described earlier (PYKE, 1978, 1979; WADDINGTON & HEINRICH, 1979; PLEASANTS & ZIMMERMAN, 1990). Bumblebees are more concerned by the directionality of this flight pattern than butterflies. Lepidoptera generally visited fewer flowers per inflorescence

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Fig. 6. Floral visitors of W. Mediterranean representatives of tribe *Delphineae*. a, *Bombus gerstaeckeri* pollinating on *A. lycoctonum* (LYC2); b, *Bombus wurfleini* sucking externally nectar as a robber on *A. lycoctonum* (LYC2); c, *Bombus wurfleini* foraging nectar legitimally on *A. anthora* (ANT1); d, *Bombus hortorum* foraging nectar on *D. montanum* (MON1); e, *Gonopteryx cleopatra* foraging nectar on *D. bolosii* (BOL2); f, *Macroglossum stellatarum* approaching to *D. bolosii* (BOL1); g, *Amegilla* sp. (legitime pollinator) approaching to *D. balansae* (BAL1); h, *Bombylius* sp. landing on lower sepals and legitimally pollinating *C. pubescens* (PUB1).

INSECT	N observations	A	B	C	D
Bombus hortorum	27	11	9	7	–
Bombus wurfleini	17	2	3	4	8
Bombus gerstaeckeri	8	4	4	–	–
Bombus terrestris	3	1	–	2	–
Bumbus pasquorum	7	1	3	3	–
Bombus humilis	1	–	–	1	–
Bombus mesomelas	1	–	1	–	–
Amegilla sp.	21	3	5	12	1
Xylocopa violacea	3	3	–	–	–
Megachile rotunda	2	–	–	1	1
Lassioglossum sp.	18	4	3	7	4
Alastor atropos	2	–	–	–	3

Table 2. Composition of pollen loads. A, only pollen of *Delphineae* (100%); B, pollen of *Delphineae* (>95%) with traces of other plants; C, pollen of *Delphineae* majoritary (50–95%) with amounts of other plants; D, pollen of *Delphineae* minoritary (<50%).

but they spent more time per visit, always in function of the nectar amount available. *Macroglossum stellatarum* (a diurnal hawkmoth) visited more flowers than other lepidoptera, and its visits are more randomly dispersed than those of bumblebees, although a certain preference for ascendent succession of visits was also observed.

In annual taxa, where more open, ramified racemes (with a paniculiform appearance of inflorescences) are found, pollinators repeatedly visited small secondary racemes of the same individual (same genet), then promoting geitonogamy. The general flying pattern of insect visits, although showing a general trend to be ascendent in a given secondary raceme, is much more randomly arranged than in perennials with single racemes. Small solitary bees remained inside the flower for a long time. Their movement between the stamens could produce sporadic self– pollinations.

Discussion

General behaviour

Hymenoptera is the insect order visiting the flowers of tribe *Delphineae* with most frequency in this area and it contains the most effective pollinators (which forage in sternotribic position), mainly belonging to the genus *Bombus*. In annual taxa, the species of *Amegilla* are the most recorded, notably in North-African populations. In alpine areas (*Aconitum* and *D. montanum*), there was a greater diversity of *Bombus*, which decreased markedly in montane and lowerland localities.

Lepidoptera only forage nectar and their pollination effectiveness is much lower, the pollen carry-over being smaller as, is the amount deposited (as stated by HERRERA, 1987). Occasionally, this low pollen transfer can be compensated by a higher number of visits, which increases its efficiency. A good example is *Macroglossum stellatarum*

(a vector that has coincided in more populations of *Delphinium*), from which a certain parallelism can be established with the effectivity vs. effectiveness pattern between bumblebees and hummingbirds reported for American species of *Delphinium* (WASER & PRICE, 1990). *Macroglossum stellatarum,* a diurnal sphingid, practically does not touch the flower with its body (see Fig. 6f), but true pollen carry– over at the proboscis has been reported in other *Sphingidae* (KISLEV & al., 1972; MILLER, 1981; NILSSON, 1988).

In *Diptera, Syrphidae* only consume pollen and are accidental pollinators; we have classified them as pollen thieves following the terminology of INOUYE (1980a, 1983). *Bombylius* (Fig. 6h) has a long proboscis, and can thus reach the nectar and finally legitimally pollinate, although MACIOR (1975) considered it is a less effective pollinator.

Heteroptera and *Coleoptera* are scarce and clearly accidental. They may consume pollen and are occasionally floral predators (as *Oxythirea funesta*, in *D. pictum*).

Differences in spectrum of visitors to each species seem to be due more to the fauna available in a given population than to its own morphological differences. These, like disposition of floral pieces, degree of floral aperture, number of stamens, colour, etc., do not affect the foraging behaviour of floral visitors, except for length limitations to robbers. However, differences in floral structure could be related with other ecological needs (not necessarily with pollination ecology), as for example light, protection against drought or rain, or energy accumulation promoting pollen maturation (MALYUTIN, 1969).

In the course of tribe evolution, a trend to simplification and reduction of lateral petals (changes of colour, shape, disposition, loss of indument) until its disappearance in *Consolida* can be observed (see Fig. 2 and Fig. 8). Lateral petals, often used as taxonomic characters (see MALYUTIN, 1987 or TAMURA, 1995) probably indicators of entry to nectar (nectar guides, MACIOR, 1975; WASER & PRICE, 1985) and acting as landing surface, surprisingly did not show such reproductive significance in our field observations, at least in the 22 populations surveyed.

In *D. staphisagria* and *D. pictum* we detected the lowest activity of insects. These species present the shortest spur in the tribe and become less specific. Morphologically the perianth is more open (Fig. 2d) and adopts a more regular shape. Other sources of evidence, as data coming from the survey of breeding systems, showed a great tendency to autogamy in this group of species belonging to the subgen. *Staphisagria* (up to 80 % of seed production in bagged flowers, BOSCH, *unpubl.* data), mainly due to the very imperfect herkogamy permitting a certain overlap between stamens and stigmata. Thus, if they are selfers the low rate of insects activity on their flowers is not noticeable.

Finally, after examination of the nectar robbers effects, only on very few occasions the damage produced on the flowers rended them unavailable for pollination. Many times, they do not affect the sexual organs nor the seed set production. The decrease in reward quantity could improve the number of the legitimate pollinator visits (HAWKINGS, 1961) because their energetic needs can oblige them to visit a higher number of flowers. In this way, robbers are cross–fertilization promoters. The incidence of nectar robbery can show important fluctuations one year to another, depending on seasonal climatic conditions and on the availability of suitable fauna.

Specificity of visits

From all insect species censused, only *Bombus gerstaeckeri* (Fig. 6a) showed oligolectic behaviour for *A. lycoctonum,* according with other authors (DELMAS, 1976; ORNOSA, 1984; RASMONT, 1988; ROUSSEAU, 1994). Sometimes it visited *A. napellus,* more occasionally. A parallel case takes place between *Bombus consobrinus* and *A. septentrionale* Koelle (LØKEN, 1949, 1950, 1960; MJELDE, 1983). They are two closely related bumblebee species of allopatric distribution (RASMONT, 1988). *Bombus hortorum* (Fig. 6d), which belongs to the same group and was practically the most frequent bumblebee foraging on alpine *Delphineae* species, was more generalist (similar behaviour to the reports of LØKEN, 1949; MJELDE, 1983; CASTRO, 1988). However, *Delphineae* pollen is larger in all examined specimens captured on these plants (see Table 2).

Comparatively with *Bombus* (which are reported by the literature as the best pollinators for the *Delphineae*, i.e. MÜLLER, 1883, PESSON & LOUVEAUX, 1984), the *Amegilla* species (which seem to be the frequently susbtitutes of *Bombus* on the annual species) are less specific, at least after the examination of pollen loads (see Table 2). This is relevant because this more polylectic behaviour of *Amegilla* could be responsible for a decrease in the number of seeds set by saturation of the stigmata surface by alien pollen and it is a confirmation that bumblebees are the most fitting pollinators for the *Delphineae*.

Solitary small bees (as *Lassioglossum*) are less specific, and they probably tended to visit species with more accessible reward, given their shorter proboscis. These insects often remain moving between the stamens and could promote accidental autogamy. Other species as *Alastor atropos*, acted as secondary robbers of nectar.

In the shortest spur species (subgen. *Staphisagria*), the visitors like *Megachile* or *Lassioglossum* were less specific, as expected.

Some nectar robbers such as *Bombus wurfleini* or *Bombus terrestris* also collect pollen by the legal way and became pollinators. This can explain the presence of corbiculae in these species, also observed earlier in *Aconitum septentrionale* (LØKEN, 1949) or in *Aquilegia* sp. (MACIOR, 1966).

Macroglossum stellatarum is a less specific visitor and it has been found in a much diverse range of ecological situations, practically on all species of *Delphinium* sampled, whereas it has been not detected on *Aconitum* or *Consolida*.

Concluding remarks

a, The true pollinators of the *Delphineae* species, in addition to the general morphological architecture of its flowers acting as attractant, are chosen, in a given population, among the available fauna and no direct relationships of specific insect–plant can generally be found. Although bumblebees seem to be the most fitting pollinators, there is enough evidence for other effective pollinators, as hummingbirds reported by WASER & PRICE (1990) or *Amegilla* and *Macroglossum* and other Lepidoptera pollinations (reported here) in several species.

b, The flowers of *Delphinium* and *Consolida* are better adapted to the visits of Lepidoptera than those of *Aconitum* (because these bear much more hidden nectaries of difficult access, thus forcing the butterflies to curve their long spiritrompae to reach the nectar). The higher accessibility of the nectar of the first two genera to the Lepidoptera, however, does not have to be interpreted as favourable, because of the lower pollinator effectivity of butterfly visits.

c, The main adaptive features reached by the tribe *Delphineae* in relation to its pollination ecology should be placed at the moment of the primary differentiation of each genus in Central Asia (TAMURA, 1995) and, then, the W. Mediterranean representatives should be interpreted as the Western extreme remaining of the fitness reached by its ancestors. Thus, only the high mountain species –as the *Aconitum* species or *D. montanum*, considered as the most primitive in the W. Mediterranean (MOLERO & PUIG, 1990; BLANCHÉ, 1991)– retained a similar fauna and floral adaptations. *D. montanum* (Fig. 6d) is a good example of this, presenting a classical bee-flower (the only species with brownish lateral petals bearing yellow hairs) and being effectively pollinated by bumblebees (Fig. 3b).

In contrast, the remaining perennial taxa, truly mediterranean (or steppic derivatives as the *D.bolosii*-group, *cf.* BLANCHÉ, 1991) and the widely mediterranean annuals of *Delphinium* and *Consolida,* presumably more evolved (TRIFONOVA, 1990) adopted morphologies, colours, shapes quite different from the high mountain species. Other reproduction-related strategies (such as the passage to the annual cycle, the seed size reduction, the flower size reduction, the increased ramification patterns, etc., *cf.* BLANCHÉ, 1990) seem to have evolved to a better adaptation to the new ecological sites to be colonized in the Mediterranean. Certainly, the available fauna is also different and it may be a possible explanation for the development of new features such as the most pallid colours found in South Mediterranean species (as *D. balansae, D. gracile* or *D. favargeri*) or the progressively loss of importance of the lateral petals (loss of hairs and size from Mediterranean perennial to annuals in *Delphinium* and complete loss of lateral petals in *Consolida* in relation to annual *Delphinium*) as drawn in Fig. 8.

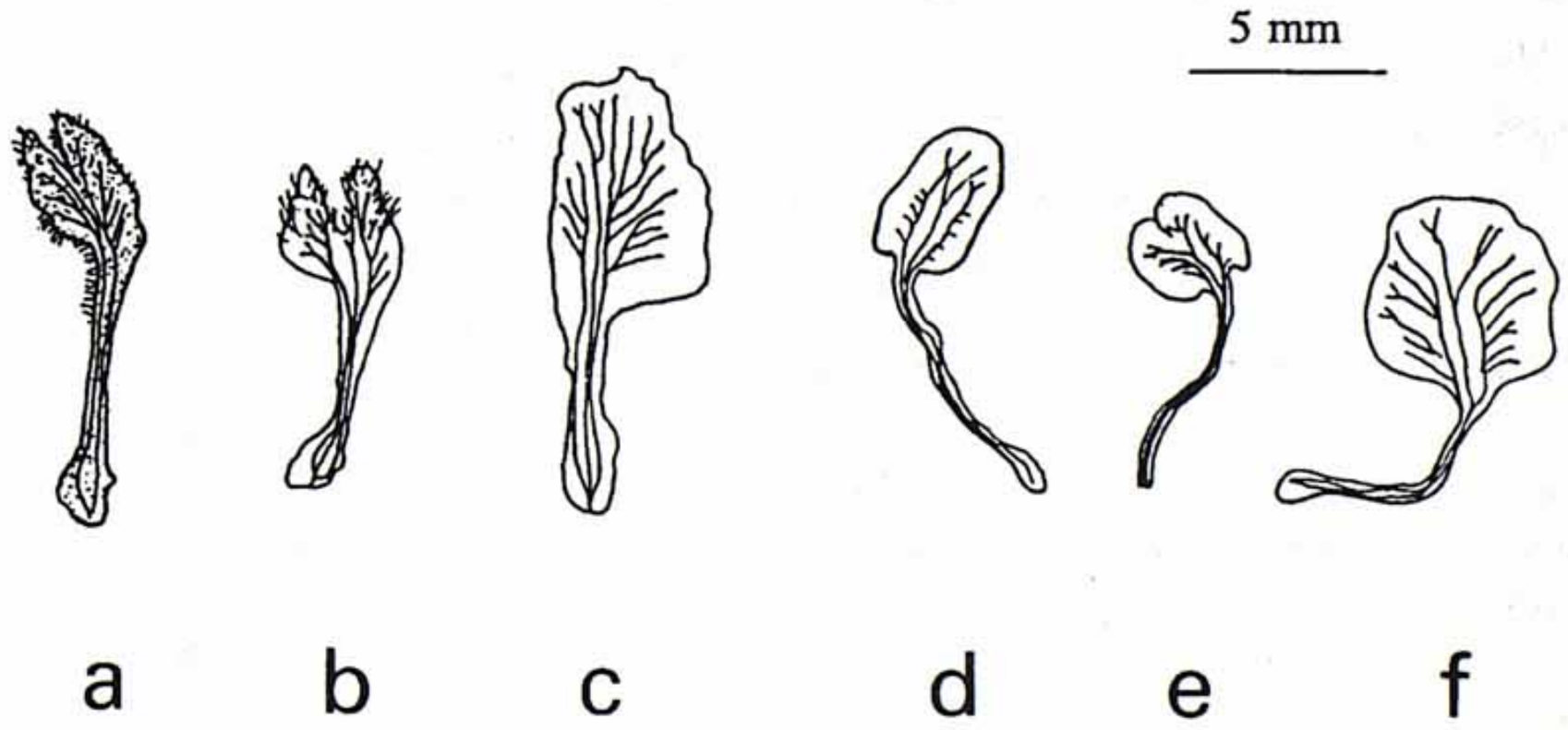

Fig. 8. Evolution of the lateral petals in *Delphinium*. a, *D. montanum*; b, *D. bolosii*; c, *D. pictum*; d, *D. gracile*; e, *D. verdunense*; f, *D. obcordatum*.

The representatives of the subgen. *Staphisagria* (a very isolated group in the genus *Delphinium* with unknown relatives and with the maximum diversity in the W. Mediterranean islands) followed a very distinct evolutive pattern in flower structure: spur shortening in *D. pictum* and its extreme reduction (up to 3 mm only) in *D. staphisagria*; flowers more open in *D. pictum* and nearly dish-shaped in *D. staphisagria*; seed size increase (*D. staphisagria* has the greatest seeds of all the genus), etc. The extremely poor results of pollinator censuses in these plants confirmed a original and divergent evolution of this Mediterranean endemic subgenus that merits further research.

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