

**REPRODUCTIVE BIOLOGY OF
HELIANthemum APENNINUM (L.) MILL.
AND H. CAPUT-FELIS BOISS. (CISTACEAE) FROM
MALLORCA (BALEARIC ISLANDS, SPAIN)**

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RESUMEN. *Biología reproductiva de Helianthemum apenninum (L.) Mill. y H. caput-felis Boiss. (Cistaceae) de Mallorca (Islas Baleares, España).* El estudio de la biología reproductiva de poblaciones naturales de *Helianthemum apenninum* y *H. caput-felis* en Mallorca ha demostrado que son básicamente entomófilos, aunque también producen numerosos frutos por auto-polinización. Las flores de *H. caput-felis* duran cuatro días, mientras que las de *H. apenninum* duran uno, como suele ocurrir en otras especies del género. En la población de *H. apenninum*, la predación por ungulados afecta al 50% de los individuos. Los test de germinación mostraron una temperatura óptima de germinación de 16 °C para *H. apenninum* y de 23 °C para *H. caput-felis*. *H. caput-felis* muestra una importante variabilidad interanual en su comportamiento germinativo. En las poblaciones naturales de *H. caput-felis*, se ha observado atelechoria, y en relación con ésta, las semillas germinan dentro de la cápsula.

Palabras clave. Fenología, polinización, germinación, dormición, *Helianthemum*, Cistaceae, Islas Baleares.

ABSTRACT. *Reproductive biology of Helianthemum apenninum (L.) Mill. and H. caput-felis Boiss. (Cistaceae) from Mallorca (Balearic Islands, Spain).* The study of reproductive biology of natural populations of *Helianthemum apenninum* and *H. caput-felis* from Majorca, has demonstrated them to be basically entomophilous, although they also produce many fruits by self-pollination. *H. caput-felis* flowers last for four days, while *H. apenninum* flowers last for one day, as usually occurs in other species of the genus. In the *H. apenninum* population, severe ungulate predation affects 50% of the plants. In germination tests, the optimum temperature was 16 °C for *H. apenninum* and 23 °C for *H. caput-felis*. *H. caput-felis* shows high interannual germination variability. In the naturally occurring population of *H. caput-felis*, it has been observed atelechory, and related to this, the germination of the seeds covered by the fruit capsule.

Key words. Phenology, pollination, seed germination, dormancy, *Helianthemum*, Cistaceae, Balearic Islands.

INTRODUCTION

Species belonging to the family *Cistaceae* are characteristic of the Mediterranean area (Heywood, 1968) where they are particularly

common in disturbed environments. Following Raven (1973), this family appears to be related to the Arcto-Tertiary Geoflora and its derivatives, its representatives having evolved up to the present as species endemic to both the

Mediterranean and North America. Its pollen appears in post-Miocene sediments (Cronquist, 1981), represented by *Helianthemum* (Willemstein, 1987), and the species of this genus are characteristic and constant in pollen spectra during the later glacial periods over the greater part of Europe. They disappear almost completely from pollen records later, coinciding with the post-glacial extension of forests (Proctor, 1958). In this last period, populations of the *Helianthemum* species are seen to be displaced, becoming restricted to extreme environments where stable communities developed away from forests such as on mountain tops (as occurred with *H. apenninum* (L.) Mill. subsp. *apenninum*) or along the coast (as *H. caput-felis* Boiss. and *H. organifolium* (Lam.) Pers.) in the Balears. From a reproductive viewpoint, the *Helianthemum* species are characterised by very similar flowering attributes and by producing seeds with dormancy. Some members of the genus *Cistus* have been widely studied (Herrera, 1987b; 1992; Brandt & Gottsberger, 1988; Bosch, 1992; Blasco & Mateu, 1995; Martin *et al.*, 1995), and their main reproductive characters are associated with their presence in areas which are subject to frequent fires (Vuillemin & Bulard, 1981; Troumbis & Trabaud, 1986; Cucó, 1987; Trabaud & Oustric, 1989; Thanos *et al.*, 1992; Valbuena *et al.*, 1992). In this paper, data on some aspects of the reproductive biology of *Helianthemum apenninum* and *H. caput-felis* are presented, such as phenology of flowering and seed dispersal, pollination, fruit production and germination.

THE PLANTS

H. apenninum is a Mediterranean species with numerous geographical races (G. López, 1993). The Mallorcan populations are integrated by individuals with pink flowers,

and not white as is most common in Europe (Raynaud, 1988), and have been interpreted by G. López (1993) as a local race within the subsp. *apenninum*. In Mallorca, it grows at heights over 1200 m in exposed locations. Populations are known only on Puig Major and Massanella, the two highest mountains in the Balears. *H. caput-felis* is distributed throughout the southwest Mediterranean, being found at Alicante in the Iberian peninsula, in N Africa and Mallorca (Heywood, 1968) as well as in Sardinia (Pignatti, 1982) and Italy (G. López, 1993). In Mallorca, it is found only along the south coast where it grows on sand dunes and occasionally, on the adjacent coastal slopes.

In both species, the inflorescences are bracteate racemes in sparse groups. The androecium consists of many free, yellow-coloured stamens, all fertile. The anthers are tetrasporangiate and dithecal, opening by longitudinal slits. The gynoecium is tricarpic and has parietal placentation. The flowers are homogamous. The fruit is capsular and dehiscent with three valves. The seeds are small, subspherical and without raphe.

MATERIAL AND METHODS

The *H. apenninum* population studied grows on Puig Major (municipality of Escorca), located in the central sector of the Serra de Tramuntana in the N of Mallorca. The experimental plot was set up on Coll de N'Arbona. The *H. caput-felis* population studied was situated at Sa Rápita (municipality of Campos) in the south of the island, the experimental plot being located by Sa Rápita beach. The main features of each plot are given in Table 1. Both localities were visited periodically throughout 1990.

Observations were made of flower colour, morphology, size and floral reward. The size was calculated by measuring the diameter and

Species	<i>H. apenninum</i>	<i>H. caput-felis</i>
Locality	Puig Major	Sa Rapita
Altitude (m)	1250	6
MAR (mm)	1238.4	326.7
MAT (°C)	9.1	15.8
Soil	Lapiaz	Dune
Slope (%)	5-10	<5
Aspect	S	SE
Community	Cushion plant community	Sand dune bush
# studied plants	20	10

Table 1. General characteristics of the study areas (MAR: mean annual rainfall; MAT: mean annual temperature). Data from GUIJARRO, 1986.

the longitude (distance between the base of the calyx and the stigma). The longitude and the width of the petals was also measured. The measurements were carried out with a caliper in the field, sampling one flower per plant for 20 different plants. After dissection of the flowers, the number of ovules per ovary were counted as were the number of stamens and pollen grains per flower. After macerating 10 anthers in 0.5 ml of detergent solution, the number of grains in 10 replicates of 5 μ l were counted and the number of pollen grains per stamen estimated. According to the number of stamens per flower, the overall pollen count per flower was calculated (Herrera, 1987a; 1991). From these examinations, the relation P/O (pollen/ovules) was assessed, as proposed by Cruden (1977) as an indicator of the reproductive system of each taxon. To identify the relative importance of pollination vectors, the percentage of flowers which produced fruits («fruit set») on free branches (controls) and on branches covered with mesh bags was observed in 20 (*H. apenninum*) and 10 (*H. caput-felis*) different plants. By means of dissection under a binocular microscope, the seeds were separated and counted from their capsules. Field observations were made examining the systems of fruit opening and dehiscence, as well as seed liberation. In *H. caput-felis*, the seed germination was also observed.

The phenological follow-up was carried out at different levels: individual flowers, individual plants and populations. The study of individual flowers was conducted by means of observing 1 flower bud marked before anthesis on 10 different individual plants. These observations aided understanding of the entire anthesis process, the opening time of the stamens, the changes in relative position of floral parts, in addition to the flowering time. Individual plant flowering periods were studied for 20 plants in *H. apenninum* and 10 plants in *H. caput-felis*, counting the total number of open flowers per plant every week. The results have been used to produce specific flowering curves and the same process was followed for fruits. In *H. apenninum*, the period of fruit ripening was considered as the time from when capsule development is observed until it opens or falls. After this ripening period, the fruit is considered to be in the dispersal phase. In *H. caput-felis*, observation of the ripening process in the field was not possible, and consequently, only the second, the dispersal phase, is considered. Also, the percentage of herbivory by goats and its frequency of occurrence in the Puig Major population were quantified. All species of visiting insects seen during the field work were collected and identified. In addition, nonconsecutive days during the maximum blooming period of the population, an

additional study was conducted for *H. caput-felis*, in which the number of insects that visited the flowers was counted at a frequency of ten minutes for each hour interval.

Germination tests were made in a germination chamber at different temperatures, excluding light. To carry out these tests, mature fruits were collected from 10 different plants and the seeds were removed. These were placed on sterile hydrophilic gauze in 9-cm diameter Petri dishes, 25 per dish, and were periodically moistened with de-ionised water.

RESULTS

1. Floral morphology. Principal morphological characteristics of the flowers are summarized in Table 2. The flowers of *H. apenninum* are bigger and have more stamens and ovules than *H. caput-felis* ones. The number of ovules per flower in *H. caput-felis* is constant, and very low if it is compared with *H. apenninum*.

2. Reproductive phenology

2.1. Description of the anthesis process. On the racemes of both species, the first flowers to open are the lowest. The anthesis includes the extension of the corolla and the freeing and extension of the reproductive structures until the androecium (constituted by the remainder

of the dry stamens) and gynoecium become covered by the persistent perianth. In *H. apenninum*, this happens towards around 05.00 h (GMT), then the anthers begin to open towards 07.00 h and by 08.30 h, they are practically empty, although they have not been visited by insects. Approaching 15.30 h, almost all the flowers cease to be functional and so last only about 10 hours. In *H. caput-felis*, opening starts at 07.30 h and the flowers remain open until 17.30 h. However, most of the pollen is removed by insects during the four first hours. The same flower will re-open for the following three days. In *H. apenninum*, a characteristic for most of the family *Cistaceae* representatives, the flowers last only for one day (Brandt & Gottsberger, 1988; Herrera, 1987b; Bonet, 1991). In contrast, *H. caput-felis* flowers are longer lasting (4.0 ± 0.14 days, $n = 10$).

When the flower is pollinated, fruit development begins immediately after the flower closes and manifests itself by a swelling of the ovary which is permanently protected by the sepals (and petals in *H. caput-felis*) throughout the process. If the ovule is not fecund, capsule development does not take place.

2.2. Phenology of flowering, fruit ripening and dispersal.

2.2.1. At individual plant level. For *H. apenninum*, average flowering duration is 18.9

	<i>H. apenninum</i>	<i>H. caput-felis</i>
Flower diameter (cm)	2.46 ± 0.04 (n=20)	1.62 ± 0.03 (n=20)
Flower length (cm)	0.95 ± 0.02 (n=20)	0.71 ± 0.01 (n=20)
Petal length (cm)	1.27 ± 0.02 (n=20)	0.86 ± 0.02 (n=20)
Petal width (cm)	1.20 ± 0.03 (n=20)	0.81 ± 0.02 (n=20)
Corolla colour	white-pink	yellow
# fertile stamens	72.8 ± 2.50 (n=10)	59.62 ± 0.95 (n=42)
Pollen per flower	24984.96 ± 2111.20 (n=10)	25068.45 ± 1125.85 (n=20)
Ovules per flower	26.8 ± 1.4 (n=10)	6 (n=42)
«P/O»	942.56 ± 83.72 (n=10)	4178.13 ± 187.64 (n=20)

Table 2. Main flower characteristics (all metric parameters are expressed as mean \pm standard error).

± 1.8 days of which 11.6 ± 1.1 can be regarded as intensive (with $>25\%$ of the flowers which one individual produces in all the flowering period). The day with the greatest number of individuals at a maximum flowering state was 15 May, while the greatest number of plants at the maximal fruit ripening stage was on 5 June. The day with the greatest number of plants at the maximal fruit dispersal stage was 26 June. In *H. caput-felis*, the average flowering period was 35 ± 2.4 days of which 26.6 ± 1.3 were intense. The greatest number of individuals in maximum flower was 24 April, while the day with the greatest number of plants at the maximal fruit dispersal stage was 5 June.

2.2.2. At the population level. Figure 1 shows the populational phenologies of flowering and fruit dispersal for both species as well as the fruit ripening and percentage of *H. apenninum* which suffered herbivory due to goats and sheep. The two species concentrate their reproductive phases in spring although these occur at notably differing times and for

different durations. *H. caput-felis* flowers between the end of March and the middle of May; *H. apenninum* from the beginning of May until mid June. As far as fruit dispersal is concerned, *H. caput-felis* disperses the fruits from the end of May to the middle of June. The *H. apenninum* population suffers important predation, since 50% of the plants were eaten partially or totally. As a result, the fruit ripening and specially the dispersal percentage is probably underestimated.

3. Pollination, anthophilous insects and floral reward. In both species, most fruiting originates from natural pollination (Table 3). In *H. caput-felis*, the results obtained from the branches covered with bags show that self fertilization, although unusual, is biologically possible. However, *H. apenninum* shows a notable proportion of self fertilization.

Considering the activity of the antophilous insects during the blooming period, flowers of *H. apenninum* were visited exclusively by Hymenoptera (Table 4), although these visits

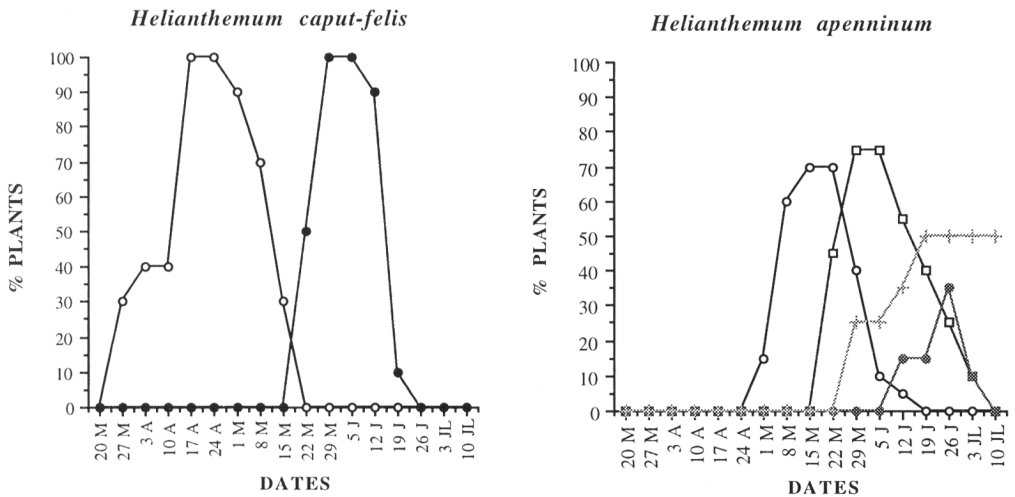


Figure 1. Phenology of flowering, fruit ripening and dispersal in the *H. apenninum* and *H. caput-felis* populations (white circles: flowering; white squares: fruit ripening; black circles: fruit dispersal; crosses: herbivory).

	Natural	Mesh bagged
<i>H. apenninum</i> :		
Flower number	47	47
Fruit number	40	16
Fruit set (%)	85.11	34.04
Seeds/fruit	8.83 ± 1.10	n.d.
Seed set (%)	33.86	n.d.
<i>H. caput-felis</i> :		
Flower number	597	156
Fruit number	549	29
Fruit set (%)	91.96	18.59
Seeds/fruit	4.71 ± 0.06	2.07 ± 0.30
Seed set (%)	72.22	6.41

Table 3. Results of natural and bagged pollination tests (seed set: seeds x 100/ovules; n.d.: no data). The large difference between the size of samples in because of the flower herbivory and the low number of flowers per inflorescence in *H. apenninum*.

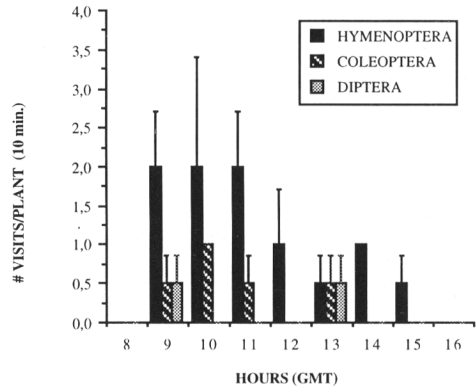


Figure 2. Hourly count (GMT) of visiting insects in *H. caput-felis* (columns: means; lines: standard errors).

Order	Family	Species	Frequency
<i>H. apenninum</i> :			
HYMENOPTERA	ANDRENIDAE	<i>Andrena</i> sp. sg. <i>Migrandrena</i>	+
	APIIDAE	<i>Apis mellifera</i>	+
	HALICTIDAE	<i>Lasioglossum planulum</i>	+
<i>H. caput-felis</i> :			
COLEOPTERA	ANTHICIDAE	<i>Anthicus balearicus</i>	++
	CANTHARIDAE	Genus indeterminate	++
	OEDEMERIDAE	<i>Oedemera nobilis</i>	++
	SCARABEIDAE	<i>Oxythyrea funesta</i>	+
		<i>Tropinota squalida</i>	+
DIPTERA	CALLIPHORIDAE	<i>Chrysomia albiceps</i>	+
	SYRPHIDAE	<i>Eristalis pratorum</i>	+
		<i>Eristalis tenax</i>	+
HYMENOPTERA	ANTHOPHORIDAE	<i>Anthophora balearica</i>	+
	APIIDAE	<i>Apis mellifera</i>	+++
		<i>Bombus terrestris</i>	+
		<i>Andrena</i> sp. 1	++
	HALICTIDAE	<i>Andrena</i> sp. 2	++
		<i>Lasioglossum hammi</i>	++
	SCOLIIDAE	<i>Camposcolia ciliata</i>	+

Table 4. Floral visitors (Frequency: percentage of days of phenologic count in which insects were observed; +: 0-33%; ++: 34-66%; +++: >66%. *H. apenninum*: 7 daily counts; *H. caput-felis*: 8 daily counts).

	Temperature (°C):				
	14	16	18	20	23
<i>H. apenninum</i> (seeds 1990):					
Sown seeds (# seeds x # dishes)	25 x 10	25 x 10	-	25 x 10	25 x 10
Viable seeds percent	80.4 ± 4.1	87.6 ± 3.4	-	94.0 ± 1.4	73.6 ± 4.3
Hard seeds percent	67.9 ± 3.3	53.3 ± 3.8	-	79.7 ± 3.6	85.8 ± 2.7
Germination percent	31.7 ± 3.3	46.4 ± 3.8	-	20.0 ± 3.6	13.9 ± 2.7
<i>H. caput-felis</i> (seeds 1990):					
Sown seeds (# seeds x # dishes)	-	25 x 10	25 x 10	25 x 10	25 x 10
Viable seeds percent	-	99.2 ± 0.5	98.8 ± 0.6	98.8 ± 0.6	99.2 ± 0.5
Hard seeds percent	-	99.2 ± 0.5	97.6 ± 0.9	98.0 ± 0.7	96.4 ± 1.1
Germination percent	-	0.8 ± 0.5	2.4 ± 0.9	2.0 ± 0.7	3.6 ± 1.1
<i>H. caput-felis</i> (seeds 1989):					
Sown seeds (# seeds x # dishes)	-	200 x 1 + 25 x 9	-	-	200 x 1
Viable seeds percent	-	99.6 ; 99.6 ± 0.4	-	-	100
Hard seeds percent	-	84.9 ; 84.8 ± 2.5	-	-	59.5
Germination percent	-	15.1 ; 15.2 ± 2.5	-	-	40.5

Table 5. Results of germination tests (± standard error).

were nonfrequent. In *H. caput-felis*, the Hymenoptera were also the most frequent insects although the presence of Coleoptera is notable (Table 4). In Figure 2, the hourly count of visiting insects is shown for *H. caput-felis*. Hymenoptera was the commonest order followed by Coleoptera. The majority of the visits took place between 09.00 and 11.00 h. Throughout the Cistaceae, the main insect reward is pollen; the most notable characteristic is the ready accessibility which insects have to this. They land on the flower and collect pollen with no difficulty whatsoever.

4. Fruit dispersal. In both species, when the fruits reach maturity, abscission and fall happen. The opening of the fruit is produced by the separation of the three valves which make up the capsule. In *H. apenninum*, the fruit is removed by the wind, thus freeing its seeds. This is a mechanism common to this genus (Herrera, 1987b). A small number of fruits do

not fall but open and disperse the seeds whilst remaining attached to the plant, a mechanism typical of the genus *Cistus*. In *H. caput-felis*, the fruit remains closed and falls a limited distance from the parent plant (maximum 30 cm, mode = 5-10 cm, n = 10). Some fruits open during summer, but the majority of seeds remain enclosed in the capsule, where they germinate in autumn.

5. Seed germination tests. Germination test results are given in Table 5. In *H. apenninum*, the optimal germination temperature is relatively low (16 °C) whilst at high temperatures (23 °C), germination is markedly reduced. In *H. caput-felis*, the optimal temperature is 23 °C with decreasing germination rates at lower temperatures.

For both species, seeds with developed embryo that failed germinate maintained their initial seed volume and hardness («hard seeds»). In contrast, for germinated seeds a initial seed

volume increment in response to the imbibition was noted. To determine if water penetration through the seed coat of the «hard seeds» induced their germination, they were scarified and reintroduced into the germination chamber with the optimum temperature for each species. As a result, all embryo-bearing seeds swelled and germinated few days later. The seeds of both species are very varied in terms of permeability to water (Table 5). Around 50% of those of *H. apenninum* fail to germinate (at optimum temperature). In *H. caput-felis*, this percentage was around 95% in 1990 and 60% in 1989.

DISCUSSION

Herrera (1992), from the study of fourteen species of *Cistaceae* in the South of Spain, finds the sub-bushes have an average floral diameter of 22.9 mm, low production of ovules per ovary, as well as a relatively high relation of anthers/ovules. The results of our study coincide quite well with these estimations.

The larger fruit set obtained by natural pollination compared with those obtained in the bagging experiments, indicate that both species are basically entomophilous. In *H. apenninum*, despite its flowers with their colourful corolla and important pollen reward, the number and diversity of visiting pollinating insects is low, differing from that which occurs with *H. caput-felis*. Willemstein (1987) maintained that in the family *Cistaceae*, the presence of flowers joined together in inflorescences is a less specialised ecological character than the presence of solitary flowers. In the absence of insects, both species have means of ensuring pollination through self-pollination. These types of mechanism have been noted in other members of the family such as *H. nummularium* (L.) Mill. (Proctor, 1956; Hickey & King, 1981) *Tuberaria guttata* (L.) Fourr. and *T. inconspicua* (Thib.) Briq. (Herrera, 1992). Self-pollination seems to be

possible owing to the proximity of the anthers to the stigma and to their homogamous flowers. In the stamen filaments of both species, the sensitivity to a tactile stimulus has been recognised as had been previously noted in *H. apenninum* (Weberling, 1989). Brandt & Gottsberger (1988) and Bonet (1991) have demonstrated the same phenomenon in other species of this family, interpreting it as a device for avoiding self fertilization which can be triggered by a visiting pollinator. Following Cruden (1977), the result of the quotient P/O would place these species within the range of optional and obligatory xenogamous plants, as is almost certainly the case. Although the floral morphology is not restrictive to any insect group, some authors have recognised a tendency towards cantharophily and melittophily in representatives of the genus (Herrera, 1988, 1992; Bonet, 1991; Bosch, 1992). This has been confirmed in *H. caput-felis*. Knuth (1906-9) recognised that many species within this family were pollinated by *Andrenidae* and *Halictidae*, and that also honeybees may play an important roll in pollination, as we have effectively demonstrated as occurring exclusively in *H. apenninum* and generally in *H. caput-felis*. Coleopterans act as pollinators as is seen in a large number of species of the *Cistaceae* (Gottsberger, 1977; Brandt & Gottsberger, 1988) and in *H. caput-felis*.

The long duration of the individual flower in *H. caput-felis* is exceptional in the family, the same happens with *Cistus ladanifer* L. (Talavera *et al.*, 1993). Flowering is in spring as is true for all members of the family in the Iberian Peninsula (Arroyo, 1988; Brandt & Gottsberger, 1988; Bonet, 1991, Cabezudo *et al.*, 1992; Blasco & Mateu, 1995) and in the majority of species of their communities (Tébar & Llorens, 1992; Tébar, 1992; Gil, 1994).

The ripening and liberation of fruits is rapid. The dissemination distance in several *Cistus* does not exceed 40 cm (Troumbis & Trabaud, 1986), as has been confirmed in *H.*

caput-felis, in which most of the seeds are never released from the capsule to germinate. The phenomenon of atelecory observed in *H. caput-felis* is frequent in arid environments, being interpreted as an adaptative answer to the great mortality of the diaspores that go away from the safe place where the plant lives, or to the low benefits of investing in long distance dispersion mechanism in arid conditions (Kigel, 1992).

Germination is one of the critical mechanisms by which a plant adapts to its environment. In *H. apenninum*, germination is greatly reduced at relatively high temperatures as has also been noted in other species of the genus *Cistus*. This is interpreted as a problem of oxygen uptake by the embryo at high temperatures (Vuillemin & Bulard, 1981). *H. caput-felis* does not show this effect like other species such as *Tuberaria guttata* (Paul, 1975), *H. vesicarium* Boiss. and *H. ventosum* Boiss. (Gutterman & Agami, 1987; Gutterman & Edine, 1988), and *H. squamatum* (L.) Pers. and *H. thymiphyllum* Svent. (Pérez-García & Durán, 1989), so this is not constant in the genus. This difference in germination rate could be a determining factor in the species distribution in areas of differing ambient temperatures.

The seeds possess physical exogenous dormancy. In an important number of Cistaceae, this phenomenon is linked to the nature of the integuments which are modified with high temperature treatment. This is traditionally interpreted as an adaptation to environments prone to periodic fires (Vuillemin & Bulard, 1981; Troumbis & Trabaud, 1986; Thanos & Georgiou, 1988; Thanos *et al.*, 1992) and with summer-dry climatic conditions (Thanos *et al.*, 1992). However, in these communities this plays an even more important role in avoiding massive simultaneous germination. This means that not all the small plants are simultaneously exposed to the rigorous and unpredictable environmental risks which are commonplace in the Serra de Tramuntana and

coastal dunes. This has been noted in *Cistus* species (Troumbis & Trabaud, 1986).

The commonest type of pastoral practice in the Mallorcan mountains is based on setting deliberate fires from time to time to promote regrowth in *Ampelodesmos mauritanica* (Poiret) Durand, T. & Schinz. This could have negative repercussions on *H. apenninum* populations because the reserve of hard seeds which remain in the soil are notably fewer than the majority of the family representatives, as occurs in some species of the genus *Cistus* (Bellot & Escarré, 1980; Troumbis & Trabaud, 1986, 1987; Vuillemin & Bulard, 1981) and *Helianthemum* (Gutterman & Agami, 1987; Gutterman & Edine, 1988; Maya *et al.*, 1988; Pérez-García & Durán, 1989). However, *H. scoparium* Nutt., a species characteristic of the Californian chaparral whose seed dormancy is broken by thermal shock, shows germination rates, without pretreatment, similar to those of *H. apenninum* (Keeley, 1991). Braun-Blanquet (1951) on experiments of *H. apenninum* seed germination, a relict species in the centre of Germany, noted that their colonies did not increase despite excellent seed germination. This was explained as being due to its scarcity and competition from other plants and not to low seed production. In the Mallorcan populations, the situation is similar to that described in central Germany. On the other hand, like other members of the family such as *Cistus* sp. (Cucó, 1987) and *Helianthemum nummularium* (Grime *et al.*, 1988), herbivore predation pressure is compensated by the ability of the plants to produce new shoots which allows them to recover significantly.

H. caput-felis occupies localities in which fires are uncommon. In the absence of fires, germination can be induced by abrasion of the seed coat by soil particles or alternating moisture (by dew, mist or rain) and drought and/or major soil temperature changes. Yearly differences in the percentage of hard seeds are pronounced in *H.*

caput-felis and the hypothesis of environmental control of resource availability for seed integument production must be studied in the future.

In conclusion, one could confirm that *H. apenninum* agrees with enough precision in the reproductive pattern that characterizes the genus, while *H. caput-felis*, which belongs to a monospecific section, has important different distinguishing characteristics: a floral anthesis of several days, constant number of ovules and germination of many seeds into the fruit.

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