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Phenology and Pollination Biology of Five *Ranunculus* Species in Giessen, Central Germany

By

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With 16 Figures

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Summary

STEINBACH K. & GOTTSBERGER G. 1994. Phenology and pollination biology of five *Ranunculus* species in Giessen, Central Germany. – *Phyton* (Horn, Austria) 34 (2): 203–218, 16 figures. – English with German summary.

Five *Ranunculus* species, *R. acris*, *R. auricomus*, *R. bulbosus*, *R. flammula* and *R. repens* were studied in respect to phenology and pollination biology at several places in their natural habitats around Giessen, Central Germany and at gardenbeds of the Giessen University in 1989. Population phenology was compared with weather conditions. For *R. auricomus*, *R. bulbosus*, and *R. acris* quite distinct phenology was observed at the two sites, with a much longer flowering period at the bed site. Differences in longevity of individual flowers were observed, even within the same species. In *R. acris* and *R. bulbosus*, early and late flowers of the flowering period lasted more than twice as long as flowers from the middle of the flowering period. In *R. flammula* this situation was inverted. Flower visiting insects, belonging mainly to the Diptera, Hymenoptera, and Coleoptera, varied considerably in the natural habitats and at the bed sites. Frequency of flower visiting at the natural sites was highest in *R. flammula* (45 insects per hour), followed by *R. acris* (12), and *R. bulbosus* (8). *R. repens* has a strong vegetative propagation by runners in addition to generative reproduction, and *R. auricomus* has asexual (apomictic) reproduction in addition to generative reproduction. The two latter species showed a flower visita-

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tion frequency of only 6 and 4 insects per hour, respectively. The great variety of flower visiting insects and the substitution of insect species at different sites are an expression of a generalistic pollination syndrome of the studied *Ranunculus* species.

Zusammenfassung

STEINBACH K. & GOTTSBERGER G. 1994. Phänologie und Bestäubungsbiologie von fünf *Ranunculus*-Arten in Giessen, Mitteldeutschland. – *Phyton* (Horn, Austria) 34 (2): 203–218, 16 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Im Jahr 1989 wurden in Giessen, Mitteldeutschland, fünf *Ranunculus*-Arten, nämlich *R. acris*, *R. auricomus*, *R. bulbosus*, *R. flammula* und *R. repens* hinsichtlich ihrer Phänologie und Bestäubungsbiologie an natürlichen Standorten und auf Beeten der Universität Giessen untersucht. Die Phänologie der Populationen wurde unter Berücksichtigung des Witterungsverlaufes analysiert. *R. auricomus*, *R. bulbosus* und *R. acris* verhielten sich an den verschiedenen Standorten unterschiedlich bezüglich ihrer Phänologie, wobei die Blühperiode am Beet erheblich länger war. Die Blühdauer einzelner Blüten variierte, sogar innerhalb derselben Art. Frühe und späte Blüten von *R. acris* und *R. bulbosus* blühten mehr als zweimal so lang wie Blüten der Hauptblütezeit. Bei *R. flammula* war dieses Verhältnis umgekehrt. Die Spektren der blütenbesuchenden Insekten, die hauptsächlich zu den Diptera, Hymenoptera und Coleoptera gehören, waren an den natürlichen Habitaten deutlich anders als an den Beeten. Bei *R. flammula* war die Frequenz der Blütenbesuche an den natürlichen Standorten am höchsten (45 Insekten pro Stunde), gefolgt von *R. acris* (12) und *R. bulbosus* (8). *R. repens* weist außer generativer Reproduktion eine starke vegetative Vermehrung durch Ausläufer auf, und *R. auricomus* vermehrt sich zusätzlich zur generativen Reproduktion asexuell (apomiktisch). Die Blüten der beiden letztgenannten Arten wurden von nur 6 beziehungsweise 4 Insekten pro Stunde besucht. Die breiten Spektren der blütenbesuchenden Insekten und die Substitution der Insektenarten an verschiedenen Standorten sind Ausdruck eines generalistischen Bestäubungssyndroms der untersuchten *Ranunculus*-Arten.

1. Introduction

The cosmopolitan genus *Ranunculus* L., with more than 400 species worldwide (BUCHHEIM 1964), is well represented in the Central European flora, where especially the yellow buttercups form a prominent part of the flowering aspect of many meadows, pastures, or ruderal places during spring and summer.

Since *Ranunculus* belongs to the herbaceous part of the basic “*Polycarpicae*” (see “Paleoherbs”, TAYLOR & HICKEY 1992), the flowers exhibit a number of archaic characters, such as a more or less strongly convex receptacle, choricarpy, or primary polyandry. However, some more advanced characters, such as a differentiated perianth, or nectar production at the base of “petals”, are also present. From a functional point of view, many

Ranunculus flowers are nectar-producing pollen-flowers (KUGLER 1970), which are visited and pollinated by a vast array of different insects.

Some native species were investigated with respect to flowering phenology, flower biology, breeding system, pollen-ovule ratio, flower attractivity, investment in reproduction, and reproductive success (Steinbach 1990). In the present paper we address the following questions: How long do individual flowers live and how long do they need to produce fruits? How long does flowering of whole populations last, and how do phenological events vary at different sites? Another approach involves flower attractivity, the flower visitor spectra, feeding preferences of individual insects or species during their visits, and the frequencies, with which particular *Ranunculus* species are visited.

2. Material and Methods

Five species of the genus were studied, *R. acris* L. subsp. *acris*, *R. auricomus* L. s. lat., *R. bulbosus* L., *R. flammula* L. and *R. repens* L. Observation and field-work were conducted during 1989 at several places in the surroundings of Giessen, and at garden-beds in the Botanical Garden of Giessen University (50°35'N, 80°41'E), where several individuals of each species were grown. All five species are perennials with bright yellow, radially-shaped flowers. Typically, the flowers have five sepals and five petals with a basal nectary each. The androecium consists of many stamens and the gynoecium of many free carpels with one ovule each. The fruit, which means the whole flower under fruiting conditions, consists of several to many one-carpellate nutlets.

With exception of *R. flammula*, which was studied only at the garden-beds, phenology of the other four species was examined at both sites: in their natural habitat and at the garden-beds. Fifteen randomly selected plants were marked at each site and all buds, flowers, unripe and ripe fruits of every individual were counted once a week in the natural habitat and two or three times a week at the Botanical Garden site. For technical reasons duration and functioning of individual flowers were studied only in the Botanical Garden. Here 15 to 35 flowers of each species were marked randomly in bud-stage and their opening, final closing and wilting was noted.

Pollination biology of all species was studied throughout the whole flowering period at the sites of the phenological investigations. Observations were carried out always during the same four hours a day, from 9.00 to 10.00 a.m., from 12.00 to 1.00 p.m., from 3.00 to 4.00 p.m., and from 6.00 to 7.00 p.m. (MEST = Middle European Summer Time). During these four hours, every flower visitor was registered. Length of stay of the visitor in a flower, its behavior, collecting or feeding activity (pollen or nectar), and frequency of visits were reported. Some additional observations around the clock, but outside the regular observation times resulted in complementary data for the flower visitor spectra. The catching of flower visitors had been realized only outside the regular observation times. This seemed to be quite the best method to avoid an influence on the frequency of flower visitors. The reference specimens are included in the collection of the Botanical Institute of the Justus-Liebig-Universität Giessen.

3. Results

3.1. Weather Conditions and Population Phenology

The phenological events are viewed in relation to the weather conditions in Giessen (Deutscher Wetterdienst 1989). The whole vegetation period in 1989, with exception of the months March and April, was too dry and too warm (Fig. 1) in comparison with the long-term middle (measured since 1951). The mean number of sunny hours in March was exceeding the long-standing mean considerably, but lowered to about half of the expected value in April. These conditions, together with unusually low temperatures, affected the flowering period of the plants. From May to August duration of sunshine was above the long standing mean. Together with higher temperatures, this stimulated the concomitant onset of flowering of many species.

Although fifteen plants in each population at each site had been marked, only ten plants of them actually were used to show flowering and fruiting behavior (Figs. 2 to 6), because some of the plants were affected – or even destroyed – by the action of predators.

Figures 2 to 6 show the phenology of flowering (distinguishing buds from open flowers) and fruiting. The fruiting process is shown by considering unripe fruits. Each ripened fruit was counted only once and the sum of all ripe fruits is mentioned in the upper right of each figure. A fruit was counted as such when it had at least one fertilized carpel.

The flowering process of *R. auricomus*, *R. bulbosus*, and *R. acris* was very distinct at the two different sites (Figs. 2 to 6). In all three species the flowering period at the bed site lasted longer than in the natural habitat. Moreover, the populations at the bed site showed a second increase – or even peak – of flowering, absent in the natural habitat.

The second flowering peak in *R. auricomus* was due to the so-called “fruiting flowers”. Such flowers were nearly free of petals and had only a

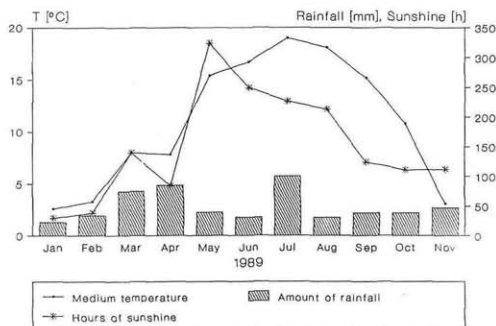


Fig. 1. Weather conditions in Giessen from January to November 1989 (data from Deutscher Wetterdienst 1989).

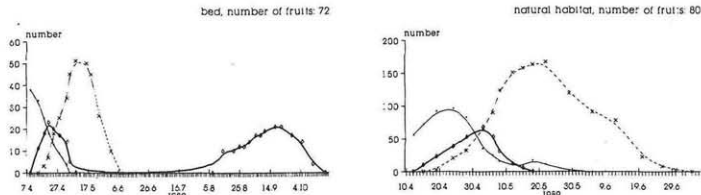


Fig. 2. *Ranunculus auricomus*, phenology at the bed site and at the natural habitat site. – For the symbols see Fig. 6.

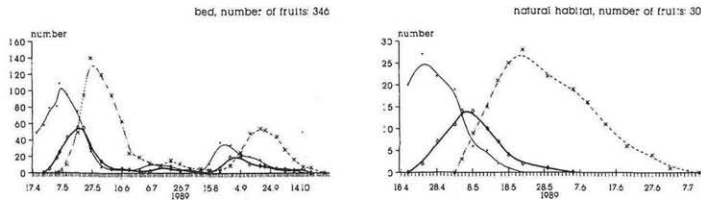


Fig. 3. *Ranunculus bulbosus*, phenology at the bed site and at the natural habitat site.

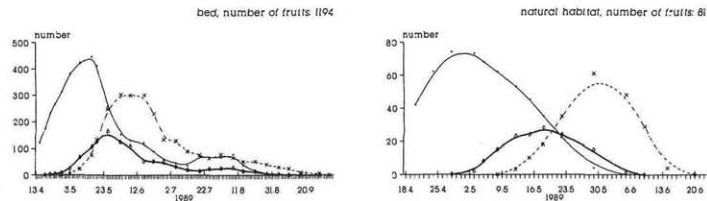


Fig. 4. *Ranunculus acris*, phenology at the bed site and at the natural habitat site.

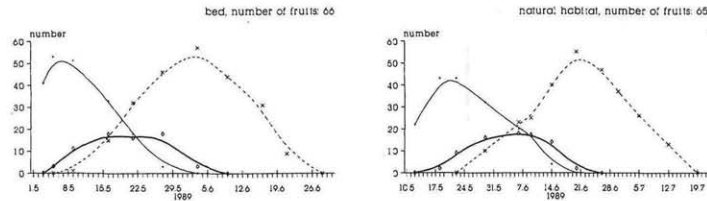


Fig. 5. *Ranunculus repens*, phenology at the bed site and at the natural habitat site.

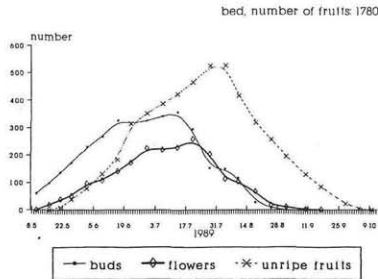


Fig. 6. *Ranunculus flammula*, phenology at the bed site.

few stamens. It was nearly impossible to distinguish whether these "fruiting flowers" were in flower or were in fruiting stages, so in the graph they are handled as flowers. The descending of the flowering curve in September and October indicates the formation of ripe fruits. In contrast to *R. auricomus*, which produced more fruits in the natural habitat, *R. bulbosus* and *R. acris* produced more fruits at the bed site.

R. repens (Fig. 5) did not show essential differences in phenology at the two sites. Duration of the flowering period as well as the number of flowers and fruits was quite similar. Moreover, there was only one flowering peak at both sites.

In the natural habitat, *R. auricomus* was the first of the five species which began to flower during the vegetation period, followed by *R. bulbosus*, *R. acris*, *R. repens*, and *R. flammula*. The flowering period of the species extended between five (*R. auricomus*) and six and a half weeks (*R. bulbosus* and *R. repens*) at the natural habitat sites. At the bed sites the flowering period varied between five and a half (*R. repens*) and twenty-eight weeks (*R. auricomus*). The flowering period of *R. flammula* (19 weeks) and *R. acris* (23 weeks) lies in between these two extremes.

3.2. Flower Phenology

Individual flowers lasted between four (*R. acris* and *R. bulbosus*) and twelve days (*R. flammula*). Furthermore, there was a notable variation in flowering time of flowers which opened at the beginning, at the middle, and at the end of the flowering period of each population (Table 1).

Early and late flowers of *R. acris* and *R. bulbosus* were open twice as long or even twice and a half times longer than flowers in the middle of the flowering period. In contrast to flowers from the last two species, flowers of *R. flammula* from the beginning and the end of the flowering period

Table 1

Flower duration (in days) of *Ranunculus* species. Flowers were uncovered and observed at the beginning (= early), during the peak (= middle), and towards the end (= late) of the flowering period.

Species	Flower duration [d]								
	early			middle			late		
	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n
<i>R. acris</i>	8.5	2.0	17	3.9	1.2	18	6.3	1.4	8
<i>R. auricomus</i>	—	—	—	9.1	2.1	19	—	—	—
<i>R. bulbosus</i>	9.9	2.0	17	4.1	0.9	10	5.7	0.9	10
<i>R. flammula</i>	6.3	1.2	16	12.2	2.0	10	7.4	1.9	9
<i>R. repens</i>	—	—	—	5.9	1.2	13	—	—	—

were open only half to three quarters of the time as flowers from the middle of the flowering period. In *R. repens* and *R. auricomus*, flower longevity during different flowering periods was not evaluated.

3.3. Pollination Biology

3.3.1. Flower Visitors

The flower visiting insects mainly belong to the orders Diptera, Hymenoptera and Coleoptera (Table 2). The list does not only mention visits of a certain insect species at a *Ranunculus* species, but also indicates collection of pollen (p), or nectar (n), or both (pn). A "x" means that no collecting activity was observed during visitation.

With exception of *R. auricomus*, Diptera were the most abundant flower visitors of the investigated *Ranunculus* species, accounting for more than 50 % of the total of the flower visiting species. The family Syrphidae was the best represented Diptera family. The other abundant groups were Hymenoptera (about 25 %) and Coleoptera (about 15 %).

R. acris was the species with the most diverse flower visitor spectrum. At both sites together, a total of 54 species were observed. A larger number of them (about 80 %) fed on nectar or collected pollen or was involved in both activities. The situation was quite similar in *R. flammula*, *R. bulbosus*, and *R. repens*. Differences between the three latter species were only gradual and concerning mainly the number of flower visiting insects, 41, 37, and 28 species, respectively. The spectrum of flower visitors in *R. auricomus* appeared distinct in at least two points. First, only ten species of insects were seen visiting the flowers, and second, Diptera, Hymenoptera, and Coleoptera were represented in about equal numbers.

A comparison of the flower visitor spectra of the five *Ranunculus* species showed one common characteristic, namely a notable difference and variation in the natural habitats as compared with the bed sites (Figs. 7 to 11). The Hymenoptera being so abundant at the bed sites strongly diminished or were absent (*R. bulbosus*, *R. auricomus*, Figs. 9 and 11) in the natural habitats.

3.3.2. Frequency of Flower Visitors

All investigated *Ranunculus* species bear more or less cup-shaped flowers. The numerous stigmata of the flowers are not normally pollinated sufficiently by a single visit of one insect. Commonly, several visits are necessary to ensure maximal reproductive success. Therefore, starting from the premise that more frequent visitation promotes reproductive output of a flower and a plant, the number of flower visits of insects was counted.

The frequency of visitation by any insect is shown for each *Ranunculus* species (Figs. 12 to 16). The values represent the number of insect vis-

Table 2

List of all flower visiting insects observed at the *Ranunculus* species. Abbreviations: Ra = *R. acris*, Rau = *R. auricomus*, Rb = *R. bulbosus*, Rf = *R. flammula*, Rr = *R. repens*; p = collecting or feeding pollen; n = sucking or licking nectar; pn = taking pollen and nectar; x = no collecting or feeding behavior observed.

plant species	Ra	Rau	Rb	Rf	Rr	plant species	Ra	Rau	Rb	Rf	Rr
flower visiting species						flower visiting species					
DIPTERA						HYMENOPTERA					
SYRPHIDAE						HALICTIDAE					
<i>Cheilosia albitarsis</i>	pn		pn		pn	<i>Halictus rubicundus</i>	pn				pn
<i>Cheilosia pagana</i>			n	p		<i>Halictus tumulorum</i>	pn		pn	n	p
<i>Cheilosia</i> sp.	n		n			<i>Lasioglossum calceatum</i>	p		p		
<i>Chrysogaster hirtella</i>	pn			p		<i>Lasioglossum fulvicorne</i>	p		pn	p	p
<i>Dasyrphus venustus</i>					pn	<i>Lasioglossum leucopus</i>	pn		pn		
<i>Episyrphus balteatus</i>	p		pn	p	p	<i>Lasioglossum morio</i>	pn		n	p	
<i>Eupeodes corollae</i>	pn		p	pn		<i>Lasioglossum nitidulum</i>	pn				
<i>Helophilus pendulus</i>					pn	<i>Lasioglossum parvulum</i>				pn	
<i>Melanostoma mellinum</i>		p	p	pn		ANDRENIDAE					
<i>Melanostoma scalare</i>	p					<i>Andrena falsifica</i>		p			
<i>Meliscaeva auricollis</i>				pn		<i>Andrena minutula</i>	p			p	
<i>Metasyrphus latifasciatus</i>	p			p		<i>Andrena minutoides</i>	p		p		
<i>Neoscia podagrica</i>	p					COLLETIDAE					
<i>Parasyrphus punctulatus</i>	p					<i>Hylaeus communis</i>	pn				
<i>Pipiza quadrimaculata</i>				pn		<i>Hylaeus hyalinatus</i>	pn				
<i>Pipizella</i> sp.	p		p			APIIDAE					
<i>Platycheirus albimanus</i>	p			pn		<i>Bombus pascuorum</i>	p		p		
<i>Platycheirus peltatus</i>				pn		<i>Bombus pratorum</i>	p			pn	
<i>Platycheirus scutatus</i>				pn		<i>Bombus terrestris</i>	p			pn	
<i>Scaeva pyrastris</i>	p			pn		MEGACHILIDAE					
<i>Scaeva selenitica</i>	pn		p			<i>Osmia rufa</i>	p	p	pn		
<i>Sphaerophoria ruepelli</i>			p			CEPHIDAE					
<i>Sphaerophoria scripta</i>	pn		pn	pn		<i>Calameuta</i> sp.				n	n
<i>Sphaerophoria taeniata</i>				n		FORMICIDAE					
<i>Syrphia pipiens</i>	p			p		<i>Lasius</i> sp.	p	p	x		
<i>Syrphus vitripennis</i>				pn		SPHECIDAE					
MUSCIDAE						<i>Pemphredon</i> sp.	p				
<i>Phaonia basalis</i>				pn	p	ICHNEUMONIDAE					
<i>Phaonia</i> sp.	p		pn	p	p	<i>Ichneumonidae</i> sp.	p				
<i>Muscidae</i> sp. 1	p		p	p	p	COLEOPTERA					
<i>Muscidae</i> sp. 2	pn					COCCINELLIDAE					
<i>Muscidae</i> sp. 3	p		p		p	<i>Calvia quatuordecimguttata</i>				pn	
ANTHOMYIDAE						<i>Coccinella septempunctata</i>	p	p	p		
<i>Botanophila</i> sp.	pn	p	pn	pn	n	BUPRESTIDAE					
<i>Delia</i> sp.	pn		pn	p	pn	<i>Anthaxia nitidula</i>			p		p
<i>Paregle</i> sp.	pn	p	p	pn	pn	BYTURIDAE					
CALLIPHORIDAE						<i>Byturus aestivus</i>					p
<i>Lucilia</i> sp.	pn		p	pn		CANTHARIDAE					
<i>Calliphoridae</i> sp.	p			n	p	<i>Cantharis rustica</i>	x				
EMPIDIDAE						CARABIDAE					
<i>Empis</i> sp. 1				n	n	<i>Nebria</i> sp.				p	
<i>Empis</i> sp. 2	n		n			CURCULIONIDAE					
TACHINIDAE						<i>Larinus</i> sp.			x		
<i>Echinomyia</i> cf. <i>fera</i>				n		MALACHIIDAE					
<i>Tachinidae</i> sp.	n		p	n		<i>Malachius bipustulatus</i>	p				
CECIDOMYIDAE						MELYRIDAE					
<i>Lestremiinae</i> sp.				n		<i>Dasytes</i> sp.					p
DOLICHOPODIDAE						NITIDULIDAE					
<i>Dolichopodidae</i> sp.	n			n	x	<i>Meligethes</i> sp.	p	p	p	p	p
PHORIDAE						OEDEMERIDAE					
<i>Phoridae</i> sp.			x	n	n	<i>Oedemera virescens</i>					p
LEPIDOPTERA						STAPHYLINIDAE					
MICROPTERIGIDAE						<i>Eusphalerum</i> sp.	p	p	p	p	p
<i>Micropterix</i> sp.	p		p			HETEROPTERA					
THYSANOPTERA						CIMICIDAE					
THRIPIDAE						<i>Cimicidae</i> sp.			x		
<i>Thrips</i> sp.	n	n	n		n						

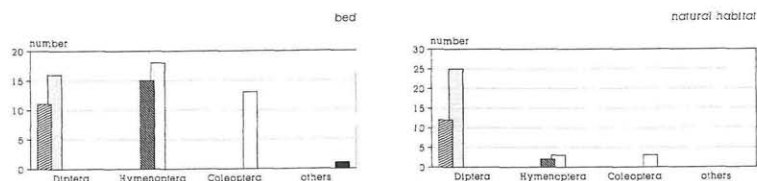


Fig. 7. *Ranunculus acris*, spectrum and number of flower visiting insect species at the bed site and at the natural habitat site. – For the symbols see Fig. 11.

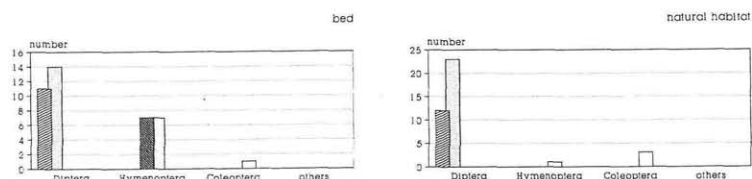


Fig. 8. *Ranunculus flammula*, spectrum and number of flower visiting insect species at the bed site and at the natural habitat site.

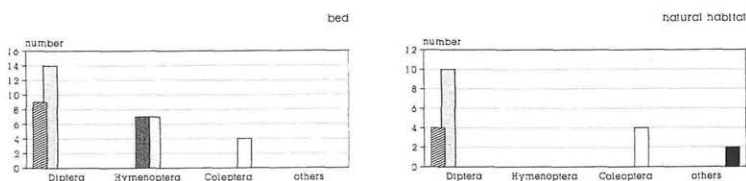


Fig. 9. *Ranunculus bulbosus*, spectrum and number of flower visiting insect species at the bed site and at the natural habitat site.

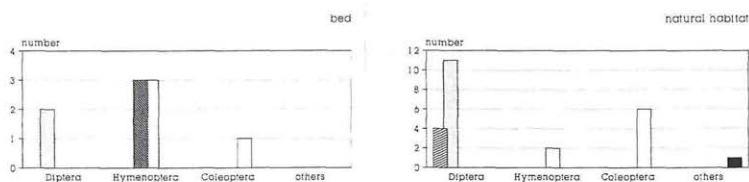


Fig. 10. *Ranunculus repens*, spectrum and number of flower visiting insect species at the bed site and at the natural habitat site.

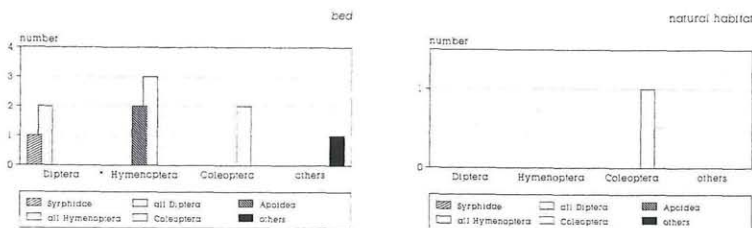


Fig. 11. *Ranunculus auricomus*, spectrum and number of flower visiting insect species at the bed site and at the natural habitat site.

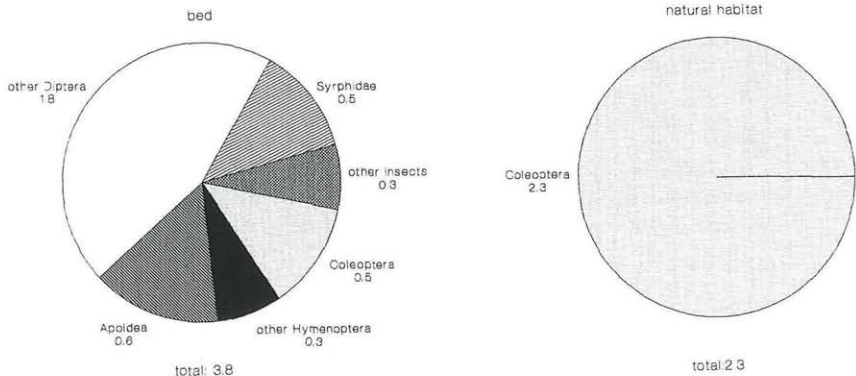


Fig. 12. *Ranunculus auricomus*, frequency of flower visits (per hour and ten flowers) at the bed site and at the natural habitat site.

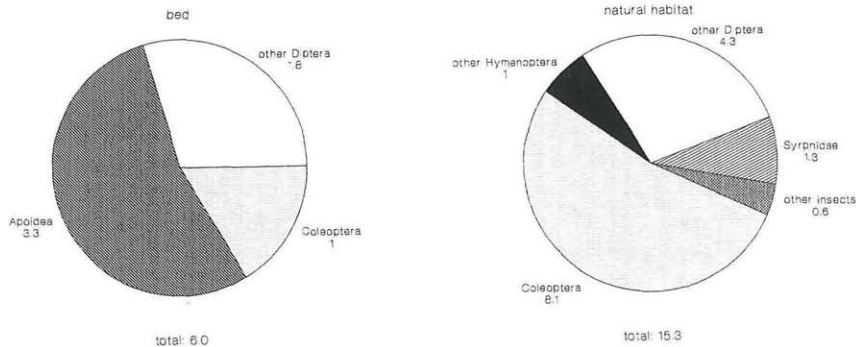


Fig. 13. *Ranunculus repens*, frequency of flower visits (per hour and ten flowers) at the bed site and at the natural habitat site.

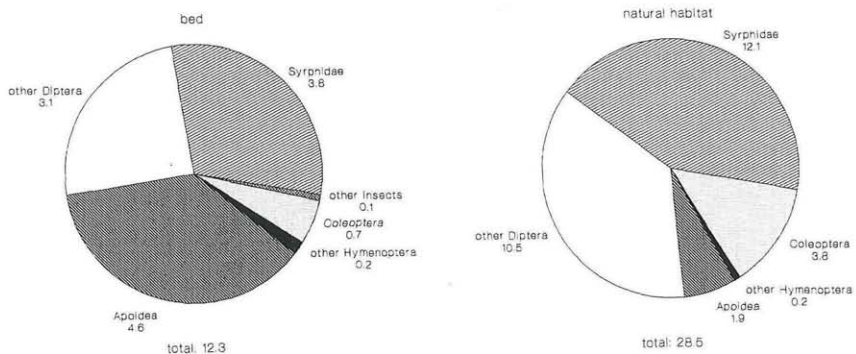


Fig. 14. *Ranunculus acris*, frequency of flower visits (per hour and ten flowers) at the bed site and at the natural habitat site.

its in ten flowers per observation hour and have been calculated as the arithmetical mean of all observation hours and days. For this part of the study, only the major orders (sometimes with superfamily or family) of insects have been taken into account.

R. auricomus was visited more frequently at the bed site than at the natural habitat site, however, visitation rate was low with 3.8 and 2.3 visits at both sites, respectively. These numbers quantify the low attractivity of the flowers.

R. repens had a higher visitation rate than *R. auricomus* (Fig. 12), with 6.0 at the bed and as many as 15.3 visits at the natural habitat site. A shift from predominant Apoidea at the bed site to predominant Coleoptera at the natural habitat site (Fig. 13) was apparent.

In *R. acris*, visitation frequency was higher at the natural site than at the bed site, with a diminishing visitation frequency of Apoidea (Fig. 14)

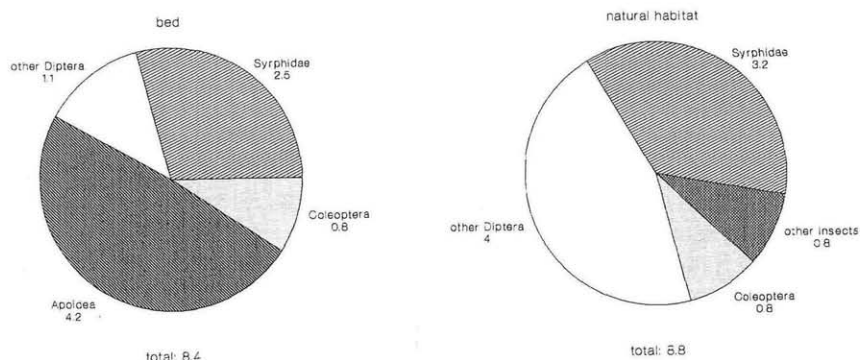


Fig. 15. *Ranunculus bulbosus*, frequency of flower visits (per hour and ten flowers) at the bed site and at the natural habitat site.

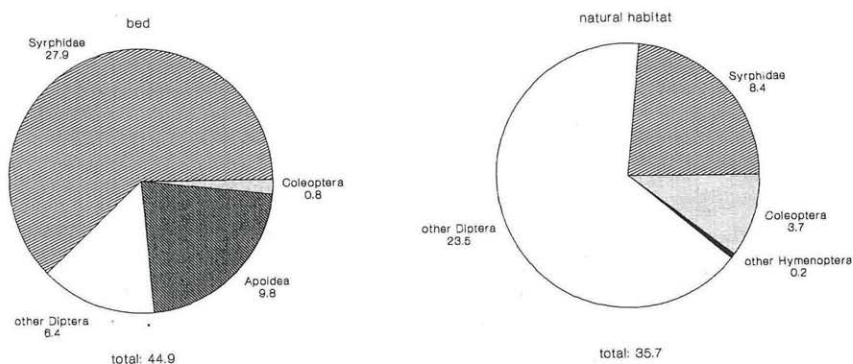


Fig. 16. *Ranunculus flammula*, frequency of flower visits (per hour and ten flowers) at the bed site and at the natural habitat site.

at the latter. In *R. bulbosus*, visitation frequency was not very high with about 8 to 9 flower visits per site. A shift of predominant Apoidea at the bed site towards predominant fly visitation at the natural habitat site (Fig. 15) could be observed.

The highest visitation rate at both sites was noted in *R. flammula* (Fig. 16) with about 45 and 36 visits. A shift from predominant Syrphidae at the bed site towards predominant non-syrphid Diptera at the natural habitat site was taking place.

4. Discussion

Phenology of all studied *Ranunculus* species, with exception of *R. repens*, differed clearly at the bed site and at the natural habitat site. These differences certainly are caused by varying environmental factors, such as different types of soil, light, wind, humidity, and the lack of competition of other plant species at the bed site. It shows the broad capacity of the studied species to modify and to adapt their phenology.

The usually spring-flowering species, *R. auricomus* and *R. bulbosus*, did not only flower during spring, but also throughout summer until autumn, at the bed site. At the bed site, *R. acris*, a late spring- and early summer-bloomer, continued its flowering period until the beginning of autumn. On one hand a longer flowering period results in a higher flower and fruit production per plant, on the other hand the phenological patterns are changed. Under natural conditions *R. acris* and *R. bulbosus* engage in so-called "mass flowering" strategy (GENTRY 1974) which changes to "steady-state flowering" at the bed site.

The situation in *R. repens* is somewhat different, in that this species showed a similar phenological strategy at both sites. This species shows vegetative reproduction through creeping and rooting runners, in addition to its generative reproduction. This capacity of compensation or stabilization in reproduction might be the cause for a lack of prolongation in flowering and fruiting phenology at the bed site. On the other hand, *R. repens* is known as a species which can vary both, its flowering period and its number of ramets (SARUKHAN 1974, LOVETT DOUST 1981) in accordance with ecological factors of its surroundings (LOVETT DOUST & al. 1990).

In *R. auricomus*, a partly asexual (apomictic) species (see NOGLER 1984), the early peak of flowering at the bed site corresponded with the total flowering period at the natural site. The second flowering peak at the bed site in August and September produced a mixture of flowers and other reproductive units ("fruiting flowers"), which did not depend on pollinators, but formed fruits either by self-pollination or apomixis.

With regard to the flower visitors, all *Ranunculus* species show different participation of the three main insect groups, Diptera, Hymenop-

tera, and Coleoptera in the visitor spectrum between the different natural sites and the garden beds.

The great variety of flower visiting insects and the substitution of species at different sites are expression of a generalistic pollination syndrome of the *Ranunculus* species. It also demonstrates, that observation of flower visiting insects at just one site (MÜLLER 1873, KNUTH 1898) cannot reveal the whole visitor spectrum. Several species of syrphids (KORMANN 1988), other Diptera (HOLLOWAY 1976), Hymenoptera (von FRISCH 1914, WESTRICH 1989), or Coleoptera are more adapted to a special habitat than to any flower. Therefore, at different sites, the *Ranunculus* species studied are exposed to a different range of flower visiting insects, in accordance with the local fauna. The large majority of the insects observed is polyphagous (KORMANN 1988, WESTRICH 1989), using a vast array of different food plants to collect pollen or nectar. Nevertheless, these polylectic insects can learn flower characters, including color of certain plant species in their surroundings (KUGLER 1951). Therefore, they can be as efficient as pollinators as other, more specialized groups. MOTTEN & al. 1981 studied such a situation in the Portulacaceae *Claytonia virginica*. The observations of CRUDEN 1972 and EHRENFELD 1979 point into the same direction. Their studies revealed that in *Nemophila menziesii* (Hydrophyllaceae) and in three *Euphorbia* species unspecialized but efficient pollinators play a role besides the oligolectic andrenic bees known as primary pollinators.

The two species, *R. repens* and *R. auricomus*, with additional reproductive capacities – vegetative and asexual strategies, respectively – were visited by only few insect species. They also showed a low frequency of visiting insects at their flowers. These results are apparently in contrast to a study of KORMANN 1976, who found many insects, especially syrphids (40 species) at the flowers of *R. repens*. However, his observations were made at several very different sites with varying ecological factors and thus, his study is not directly comparable with the present one.

More difficult to explain is the low frequency of flower visiting insects at *R. bulbosus*, despite the presence of a broad insect spectrum. On the other hand, it was noted that the visiting syrphids (mainly Cheilosia species) and beetles stayed inside the flowers for a long time. Besides, their body surface was totally covered with pollen grains after a visit, indicating that they may be efficient pollen vectors. HOLLOWAY 1976 showed that different syrphid flies could transport pollen grains on their hairs for several days. KUGLER 1950 demonstrated flower constancy for the syrphid fly *Eristalis tenax* and our observations suggest that flower constancy is a common capacity of syrphid flies.

Flower constancy is known as well for beetles (GRANT 1950, GOTTSBERGER 1989). However, flower constancy was observed in cantharophilic plant species, which are pollinated exclusively by beetles. In the *Ranuncu-*

lus species, however, beetles only represent a part of the broad visitor spectrum.

Cantharophily, as manifested in many representatives of the archaic stock of the *Magnoliales* and *Laurales*, was interpreted as an early specialization within the primitive angiosperms, and therefore as a derived condition (GOTTSBERGER 1989). Having identified cantharophily as a derived syndrome, open and unspecialized flowers with a generalistic pollination syndrome are now considered a much more reliable model for the situation of the very early angiosperms (GOTTSBERGER 1977, 1988, BERNHARDT & THIEN 1987). Such open, unspecialized, and generalistic flowers, as borne by many *Winteraceae*, attract a different insect fauna at every new site. This insect fauna consists of varying numbers and species of flies, beetles, moths, or thrips (GOTTSBERGER & al. 1980, THIEN 1980, THIEN & al. 1985). Several of the *Ranunculus* species studied show a similar open, generalistic, and varying pollination syndrome. However, it cannot be determined with certainty whether the pollination mode in *Ranunculus* is directly comparable with, e. g. the *Winteraceae* because the floral structure of *Ranunculus* contains nectar-leaves as a derived element. The visitor spectrum comprises extremely primitive insects such as beetles, flies, thrips, and micropterigid moths (see also KNUTH 1898), as well as derived insects such as syrphid-flies and bees. It cannot be tested whether the latter insects are primarily adapted to *Ranunculus* flowers or have learnt to exploit them secondarily. However, we know that there exist such specialized pollinators. WESTRICH 1989 named *Chelostoma florisomne* (Megachilidae) for example as an oligolectic bee, which only feeds pollen at *Ranunculus*-flowers. This species is a very common one in Central Europe, but it was not registered in the present study.

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6. References

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Recensio

COWLING Richard M. (Ed.) 1992. The Ecology of Fynbos. Nutrients, Fire and Diversity. – Lex. 8°, XI + 411 Seiten, 28 Farbphotos, zahlr. Abb., geb. – Oxford University Press, Cape Town. – £ 30,-. – ISBN 0-19-570661-7.

Fynbos ist eine vom Feuer geprägte, heideartige Vegetation auf sandigen, nährstoffarmen Böden. Bei KNAPP 1973 (Veg. Afr. p. 535) laufen diese Pflanzengemeinschaften unter „Immergrüne Hartlaubgebüsche aus kleinblättrigen Arten; Heide-Gebüsche des südwestlichen Kaplandes“. Da bleibt man auch im Deutschen gerne bei Fynbos. Eine genaue Definition ist offenbar sehr schwierig, insbesondere wegen der Abgrenzung gegen afromontane Vegetationseinheiten; entsprechende Versuche sind auf p. 35 diskutiert, wobei die große Bedeutung von *Restionaceae*, *Ericaceae* und *Proteaceae* sowie von ericoiden Pflanzen, z.B. ericoider *Asteraceae*, von Sträuchern mit gebüschelten, kleinen Blättern, stechenden Blättern etc. hervorgehoben wird. Daß das Gebiet der Kapflora einen der Plätze der Erde mit der höchsten Diversität darstellt [ca. 8500–8580 Arten (vgl. p. 25, 83 und 90) auf 90 000 km²] wird im selben Beitrag auf p. 24 ff. und in einem anderen auf p. 82–87 diskutiert.

Der Band bringt die Ergebnisse von Forschungen im Rahmen des „Fynbos Biome Project“ von 1977–1989. Er enthält 28 Farbphotos, die einen optischen Eindruck von Fynbos vermitteln sollen und 15, reichlich mit Zeichnungen, Schwarzweißphotos, Karten, Schemata, Diagrammen oder Tabellen ausgestattete Beiträge (von 22 Mitarbeitern), die, recht verschieden, den Charakter von Übersichtsreferaten bis Originalarbeiten haben.

Von den vier Abschnitten schildert der erste als Einleitung das Projekt. Der zweite Teil „Biogeography“ enthält vier Beiträge über geologische Geschichte, Topographie, Klima, Flora, Diversität, Endemismus, Vegetationstypen und historische Pflanzengeographie. Die fünf Kapitel im Teil „Ecology“ betreffen ‘plant reproductive ecology’, ‘plant-animal relationships’, ‘competition and coexistence’, ‘plant structure and function’ und ‘functional perspectives of ecosystems’. Der knappe Raum verbietet es, auf diese interessanten und anregenden Beiträge einzugehen; lediglich zum ersten sei bemerkt, daß hier u.a. Stimulierung von Samenfreisetzung, Keimung und Blühinduktion durch Feuer, Bestäubung [Vögel 5%, Kleinsäuger (35 Arten, vor allem *Proteaceae*), Wind 12%], Ausbreitung und Lebenszyklen von Geophyten sowie daß im zweiten Bestäubung [u.a. Käfer, extrem langrüsselige Fliegen, *Xylocopa* (13 Arten), *Rediviva*], Diasporen-Ausbreitung (v.a. Vögel u. Ameisen), Diasporen-Prädation, Herbivorie etc. behandelt werden. Der großen Gefährdung des Fynbos durch Mensch und eingebrachte Pflanzen wird der umfangreiche vierte Teil „Management“ gerecht: ‘human settlement’, ‘plant and animal invasions’, ‘preservation of biotic diversity’ und ‘ecosystem management’. Im fünften Teil wird ein Vergleich zwischen Fynbos und dem kalifornischen Chaparral gezogen.

Wie das gesagte zeigt, liegt ein fachlich vielseitiger, die mannigfachen Aspekte des Ökosystems Fynbos darstellender Band vor; man kann ihn jedem, an Ökologie und Naturschutz im allgemeinen bzw. an Südafrika im besonderen, Interessierten empfehlen.

H. TEPPNER

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