

Vertebrate herbivores as predators of insect herbivores: an asymmetrical interaction mediated by size differences

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We have analysed the effect of wild goat (*Capra pyrenaica*) on the reproductive success of a chalcid gall maker (*Systasis encyrtoides*), both species being herbivores of *Hormathophylla spinosa*, a stunted mediterranean high-mountain shrub. The gall's position on *H. spinosa* is very specific, reflected in the fact that the gall maker attaches principally to the basal floral buds of the inflorescence, and in the lower sector of the plant. We labelled inflorescences with and without galls in order to quantify goat herbivory and gall predation. The goat feeds both on plants and infructescences with or without galls, resulting in gall destruction and larval death (phenotypic selection). The browsing behaviour of goat was influenced by the general stunted growth of the plant, as well as by the abundance of spiny stems. This fact allows chalcids to escape goat herbivory on a very fine spatial scale. Gall survival strongly depends on gall position in the inflorescence, being greater in the lower position. Furthermore, galls situated in the lower sector of the plant have a greater survival chance than galls situated in the upper sector.

The goat acted as a true predator of the gall maker wasp, becoming a potential selective agent conditioning the reproductive success of *Systasis*. The relationship between goat and gall-maker is an asymmetrical hierarchy mediated by size differences, the bigger one conditions the smaller one, but the reverse does not occur. We propose that under low herbivore pressure, the gall makers (and similar invertebrate sessile forms) will show a spatial oviposition preference which is less selective than under strong herbivore pressure.

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Plants provide both the food and the templet where herbivorous interactions take place. The modular growth of plants produces different patterns of structural development and a varied size hierarchy. The resulting plant architecture is a major determinant of the diversity of herbivores, animals that show an impressive array of differences with regard to taxonomic identity, size, and life-history strategies (Crawley 1983, Strong et al. 1984, Huntly 1991). In spite of this ecological complexity, the trophic level of herbivores has long been considered as a "black box" where competition is the prevalent interspecific interaction, and where results of paired competitive interactions might be symmetrical,

or nearly so (Abrams 1987). This idea comes from the classic studies on interspecific competition, which have traditionally been concerned with interactions between closely related species (Connell 1983, Schoener 1983, Hochberg and Lawton 1990).

Nevertheless, many studies indicate that asymmetrically competitive interactions are more common among herbivores than are symmetrically competitive interactions (Seifert and Seifert 1976, Lawton and Hassell 1981, Stamp 1984, Karban 1986). Now it is widely recognized that interspecific relationships between two herbivorous species may range from mutually competitive to mutually beneficial, including amensalism and

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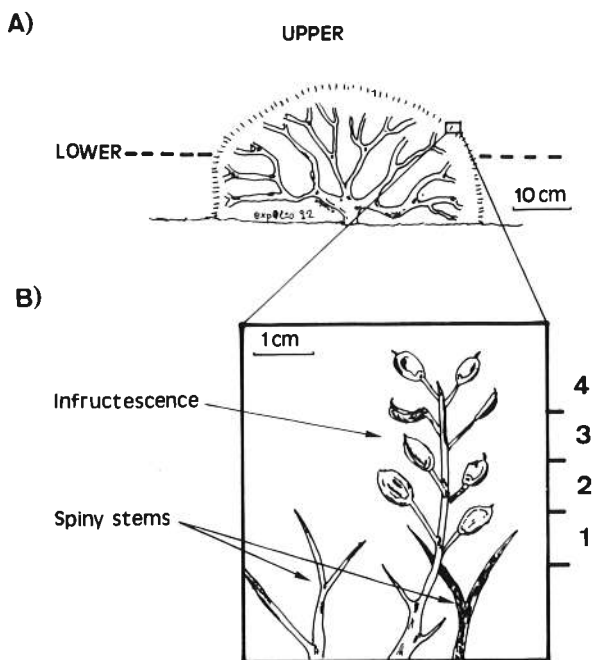


Fig 1. Schematic representation of A) a typical individual of *Hormathophylla spinosa*, distinguishing the lower from the upper sector; and B) a typical infructescence, with spiny stems. The numbers to the right divide the infructescence into four parts (positions 1 to 4).

commensalism, where only one species is affected (Crawley 1983, Strauss 1991a). An asymmetrical result may be the consequence of an indirect interaction of any species (competitor, predator, mutualist) upon a pair of symmetrical competitors (Strauss 1991b), or can simply result from the interaction between two unequal competitors (Lomnicki 1988). There are many factors causing inequalities between consumers belonging to the same trophic level, although body size is probably the most common (Ebenman and Persson 1988). When competitors differ in size, an interference mechanism of competition can easily develop (Polis 1988). The ecological and evolutionary consequences of interactions between competitors that also strongly differ taxonomically have hardly been explored (Hochberg and Lawton 1990).

In the case of herbivores, an interference interaction can potentially appear when large herbivores browse on plant tissues where tiny herbivores live. No studies have previously explored this subject. We have analysed the interaction between a vertebrate herbivore (*Capra pyrenaica*) and a chalcid gall-maker (*Systasis encyrtoides*), both species being consumers of a high-mountain woody plant, *Hormathophylla spinosa*.

In this paper we hypothesize that goat herbivory determines the gall maker oviposition site. We have tested this hypothesis studying the following: firstly, we determined the gall-maker oviposition preference on the

plant. Secondly, we analysed the effect of goat browsing on gall survival, in order to determine gall-maker performance as a measure of offspring survival (Craig et al. 1989). Thirdly, we estimated the level of goat selectivity in relation to plants and inflorescences with galls. Fourthly, we explored the ecological mechanism and the possible evolutionary consequences of the goat-chalcid asymmetrical interaction.

Methods

Plant natural history and study site

Hormathophylla spinosa (L.) K pfer (Cruciferae) is a mass-flowering plant of the high Mediterranean mountains. It is a stunted shrub, spherical or ellipsoidal in form (average height = 25 cm, average maximum axial length = 45 cm, average minimum axial length 15 cm, $n = 20$). The inflorescences, up to 8 cm in length, produce 4 to 22 flowers acropetally, so that the flowering sequence corresponds to bud position in the inflorescence. *H. spinosa* produces dry, dehiscent fruits (silicle), with an average length (\pm SD) of 3.7 ± 0.7 mm ($n = 1372$). Each fruit normally has one or two seeds (G mez and Zamora 1992). The stems of the previous years infructescences become woody, acting as mechanical protection ("spiny stems" hereafter, Fig. 1B).

The field work was carried out in a population of *H. spinosa* located at 3100 m altitude in the Sierra Nevada (SE Spain). The plant density was $74.2 \pm 1.3/100$ m² (mean \pm SD), and the plant cover was 25%. The average flowering period lasted 21 d, a typical reproductive individual bearing several hundred inflorescences, with an average of 49.4 inflorescences/100 cm² (G mez 1991). Plants bore inflorescences in all the reproductive phases (floral bud, flower, fruit) during most of the flowering period.

Wasp oviposition pattern

Systasis encyrtoides W. (Pteromalidae, Chalcidoidea; *Systasis* hereafter) is a high-mountain wasp about 2 mm long, that forms galls in *H. spinosa* flower buds, and emerges as adult during the fruiting period. After oviposition, the flower bud swells abnormally, with a generalized androecious and gynecous hypertrophy, forming a spheroid gall of 2.99 ± 0.6 mm (mean \pm SD) in equatorial diameter ($n = 146$). During the study period, we observed galls of *Systasis* only on *H. spinosa* plants.

We analysed the temporal pattern of *Systasis* oviposition by labelling 30 plants at the beginning of the flowering period. We checked periodically (3–4 d) the number of galls that developed in each plant until the

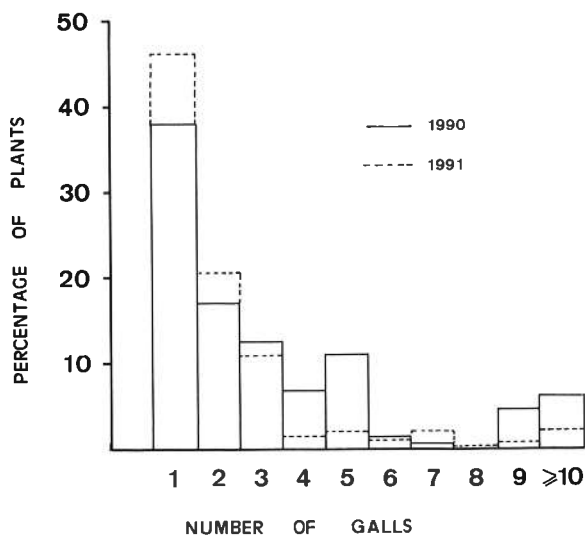


Fig 2. Percentage of *H. spinosa* individuals bearing different numbers of galls in 1990 (n = 226 plants) and 1991 (n = 215 plants).

end of the fruiting period. Therefore, we were able to check the gall formation from the earliest stages of its development.

We determined the intraplant spatial distribution of the galls, looking for them on reproductive plants unbrowsed at the moment of the sampling (324 galls in 1990 and 118 galls in 1991, which correspond to 226 and 215 plants, respectively). We noted the number of galls per inflorescence and their position with respect to the floral buds, as well as the total number of galls per plant and their position within the crown. We defined gall position by dividing the inflorescence into four equal parts, beginning with the first basal buds (position 1) and ending with the uppermost floral buds (position 4, Fig. 1B). In order to locate spatially the inflorescences bearing galls within the plant, each shrub was divided in two sectors depending on the growth patterns of the inflorescences: the upper sector, where inflorescences grow vertically, and the lower sector, where inflorescences grow horizontally to ground level (Fig. 1A). The lower sector included only $36.9 \pm 9.6\%$ of total crown surface (n = 25 plants).

In 1991 we determined the number of larvae per gall by examining 146 parasitized infructescences in the laboratory. We noted the number of larvae per gall and the number of ripe fruit per infructescence. The parasitized infructescences were collected in the field before wasp emergence.

Relationships between goat herbivory and gall distribution on plants

Wild goat (*Capra pyrenaica*, Bovidae) is a native, abundant species of the high-mountain zone of the Sierra Nevada, being the only big vertebrate herbivore present in the study area. When feeding on *H. spinosa*, goats only browsed the current year's infructescences, which completely covered the plant and overhung the spiny stems (Fig. 1).

The possible effects of goat herbivory on gall performance was determined by examining inflorescences with galls labelled at the initial growth stage (63 in 1990, and 113 in 1991, which corresponds to 70 and 215 plants, respectively). Labelled parasitized inflorescences were examined at the end of the plant reproductive period after wasp emergence. We also noted the causes of gall loss, checking whether the goat was the only gall-consuming herbivore. At the beginning of the flowering period we also labelled 100 inflorescences without galls in 1990 and 150 inflorescences in 1991, belonging to 30 arbitrarily selected individual plants in each year, in order to quantify goat herbivory. We also counted the number of galls that developed on these 30 plants in order to test the relationship between the number of galls per plant and the degree of herbivory.

Results

Oviposition pattern

The temporal oviposition pattern of *Systasis* strongly overlapped with the flowering period of *H. spinosa*. In 1990, the flowering period lasted from 15 July to 19 August, and the observed gall formation period from 15 July to 10 August. In 1991, the flowering period lasted from 17 July to 10 August, and the gall formation period from 20 July to 10 August. In 1990 31.6% and in 1991 19.5% of plants had galls. The average number of galls per plant (\pm SD) was 3.4 ± 3.6 (range: 1–19, see Fig. 2) and the average gall number per inflorescence (\pm SD) was 1.1 ± 0.4 ; 36% of the galls contained larvae at the time of collection, with an average of 3.96 larvae per gall (n = 146 galls).

Inflorescences with and without galls did not differ in number of flowers (8.7 ± 3.2 and 9.5 ± 4.9 flower per inflorescence respectively, mean \pm SD; $Z = 1.24$, $p = 0.22$, Kolmogorov-Smirnov two-sample test). Infructescences having galls produced fewer fruits than infructescences without galls (28.5% vs 65.1%, $U = 1061.5$, $p = 0.0001$, Mann-Whitney). We found a significant negative correlation between the number of larvae per gall and the number of ripe fruit per inflorescence ($r_s = -0.19$, $p = 0.04$, $n = 113$).

Galls appeared most frequently on buds at the base of the inflorescence. In fact, 59.29% in 1990 (n = 324) and 57.07% in 1991 (n = 118) were attached to the lowest

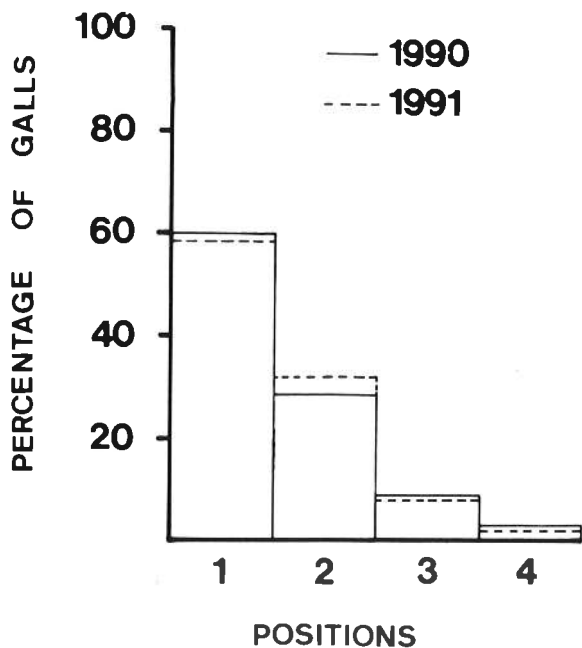


Fig 3. Percentage of galls found in each inflorescence position in 1990 (n = 324 galls) and 1991 (n = 118 galls).

position of the inflorescence (position 1), while only four galls appeared in the distal part of the inflorescence (position 4, Fig. 3). The number of larvae per gall did not change significantly with the gall position in the inflorescence ($H = 4.66$, $p = 0.2$, $n = 146$, Kruskal-Wallis test). Most galls appeared in the inflorescences in the lower plant sector (68% in 1990 and 81% in 1991), despite the fact that this sector represents only $36.9 \pm 9.6\%$ (mean \pm SD) of total inflorescences, representing a significant departure from randomness ($G = 71.67$, $df = 1$, $p = 0.001$).

Asymmetrical interaction between chalcid wasps and goats

Goat herbivory on *H. spinosa* was mainly confined to the fruiting phenophase, when galls are well developed. When browsing on *H. spinosa* infructescences, the goat sometimes cuts stems below the first basal fruit, but at times cuts at a higher point because of the presence of spiny stems, and in these instances the lowermost fruits are not eaten. In this respect, 44.8% of browsed infructescences without galls ($n = 250$) had at least one basal fruit left, and up to four remaining fruits were found in a browsed infructescence. Goats ingested only 38 galls browsing a total of 89 labelled infructescences with galls (20.2%, Table 1). This foraging behaviour caused a different gall survival rate depending on gall position in the inflorescence ($G = 20.47$, $p = 0.0001$): 91% for galls situated in position 1, 59% for galls in position 3, and 0% in position 4 (Table 1). Furthermore, galls situated in the lower plant sector had a greater chance of survival (93.48%) than galls situated in the upper sector (71.43%, $G = 7.01$, $p = 0.001$, data available only for 1991).

In order to determine whether the presence of galls affects goat browsing behaviour, we compared the frequency distribution of undamaged fruits after herbivory on infructescences with galls to that without galls, finding no significant differences ($Z = 1.35$, $df = 2$, $n = 572$, $p = 0.1779$, Kolmogorov-Smirnov two-sample test). Thus, infructescences with galls were browsed by the goat in the same way as infructescences without galls. In addition, the goat consumed similar proportions of infructescences with labelled galls (58.3%) and without galls (55.0%) in 1990 ($G = 0.17$, $p = 0.68$, $n = 160$). In 1991, infructescences with galls were less browsed (42.6%) than control infructescences (58.7%, $G = 6.26$, $p = 0.012$, $n = 263$). However, there were no differences between years in the proportion of infructescences with labelled galls browsed by goats ($G = 2.22$, $p = 0.135$, $n = 173$). Nor does the goat appear to discriminate between parasitized and non-parasitized plants, since a significant correlation does not exist between the rate of browsing per plant and the gall number per plant

Table 1. The effect of goat herbivory on gall survival. The columns indicate the number of infructescences with labelled galls in each position, the number of these infructescences that were browsed by goat and the number of galls eaten in each inflorescence position. The survival probability was calculated as $1-(a/b)$, where a is the number of galls eaten and b is the total number of galls labelled in each position. Results from the two years sampled did not differ statistically, thus, we show combined data.

Inflorescence position	No. infruct. labelled	No. infruct. browsed	No. of eaten galls	Survival probability
1	87	46	8	0.909
2	52	25	13	0.750
3	33	14	13	0.589
4	4	4	4	0.000
Total	176	89	38	0.798

($p > 0.3$, $n = 30$, each year, Spearman Rank Correlation).

Discussion

The position of the galls on *H. spinosa* is very specific. The gall maker selects principally the basal floral buds of the inflorescence, and the inflorescences situated in the lower sector of the plant. This preference cannot be attributed to a temporal limitation of oviposition, since the growing period of the galls broadly overlaps plant flowering. Nor can we attribute this oviposition behaviour to a limitation in the number or position of the inflorescences, because a plant typically bears hundreds of floral buds, flowers and fruit throughout the reproductive cycle, and individual plants broadly overlap in their reproductive phenology.

The mortality of wasp larvae in their earliest developmental stage, depending on position within infructescences, could be a possible cause of the observed gall distribution. However, as Rey (1992) has pointed out for hymenopterous species, galls without larvae usually develop. For this reason, the distribution of galls may be an accurate estimate of the female oviposition behaviour. Craig et al. (1989) showed that stem gall makers selected the longest, most vigorous shoots to oviposit. Nevertheless, *Systasis* oviposition preference with respect to floral buds was not related to the number of flowers per inflorescences (an estimate of the inflorescence vigour), because inflorescences with and without galls bear similar numbers of flowers. On the other hand, the selective oviposition in basal floral buds could be due to resource limitations, because a basal inflorescence position of the gall ensures priority access to nutrients (Lee 1988). If this hypothesis is correct, then basal galls should contain more larvae than galls at the top of the inflorescence. However, the number of larvae per gall did not change with gall position on the inflorescence. Furthermore, this hypothesis could not explain why *Systasis* preferentially oviposited in inflorescences situated in the lower sector of the plant.

We propose an alternative hypothesis that the spatial pattern of *Systasis* oviposition is affected by the wild goat browsing on *H. spinosa*. The goat feeds on more than 50% of the total *H. spinosa* infructescences in our study area, and this plant is frequently eaten by the wild goat throughout the high mountain areas of the Sierra Nevada (Martínez 1985). The goat feeds on inflorescences with or without galls, despite the fact that parasitized inflorescences bear a smaller proportion of ripe fruit than unparasitized ones. This herbivory pressure is the quantitative factor determining the ecological importance of the gall-goat interaction, resulting in gall destruction and larval death (phenotypic selection). Because *Systasis* is monophagous on *H. spinosa*, the goat

becomes a potentially selective agent on oviposition site of this chalcid species.

When the gall maker and predator are similar in size, a predator-evasion strategy may consist of modifying the gall characteristics in order to reduce the chance of larval predation. This situation occurs when, for example, the predator is an insect parasitoid (Weis et al. 1985, Weis and Abrahamson 1986, Craig et al. 1988) or even when the gall maker interacts with herbivores of similar size (Basset 1991). However, when the gall maker is indirectly browsed by a big vertebrate herbivore, an evasion strategy might consist of ovipositing preferentially in the lesser foraged plant parts, avoiding the more foraged ones (Faeth 1985, 1988). Our results clearly show that galls had different survival probabilities depending mainly on their position in the inflorescence, but also depending on the plant sector where they appear. The browsing behaviour of the goat was influenced by the general stunted growth pattern of the plant, as well as by the abundance of spiny stems. For this reason, galls less than 5 cm apart in the inflorescence – those situated at positions 1 and 4, for example – had dramatically different survival probabilities. This fact allows chalcids to escape goat herbivory within a very fine spatial scale, which corresponds to the scale of the parasite oviposition choice. Thus, there was a strong correlation between the oviposition preference and gall performance in *Systasis* (Craig et al. 1989).

Although both the goat and the gall maker are herbivores of *H. spinosa*, their relationship is not a typically competitive interaction indirectly mediated by the host plant (Faeth 1986, Strauss 1991a). On the contrary, the resulting interaction is direct, the goat acting as a true predator of the chalcids, although this ungulate cannot apparently distinguish the galls from the vegetal tissues. The goat may take advantage of this incidental insect ingestion, obtaining a reward of nitrogen and oligoelements currently scarce in the vegetal tissues. The key factor governing the interphyletic interaction between the goat and the gall maker is the size difference between the two herbivores. Consequently, the asymmetrical relationship between these species is a hierarchy, in which the bigger one regulates the smaller one, but the reverse does not occur. Similar cases have been reported between frugivore vertebrates and invertebrate seed predators feeding on the same fruit species (Lamprey et al. 1974, Drew 1987, Herrera 1989), and can be extended to any herbivorous relationship where the species are of markedly different sizes, especially when the small herbivore is sessile and lives on plants intensely foraged by the bigger one. This idea is similar to the hypothesis of Janzen (1984) concerning the incidental seed dispersion of small plants and grasses by big herbivores, but with the important difference that, in the above case, the indirect interaction does not benefit the gall maker, but instead is true predation.

Finally, the information provided in this study allows

us to advance a more general hypothesis about the effect of large herbivores on small herbivores: under low herbivore pressure, the gall maker (and similar invertebrate sessile forms) will show a spatial oviposition preference which is less selective than under strong herbivore pressure. The testing of this hypothesis relies mainly on three factors: 1) herbivory pressure of large vertebrates on plants, considering also the level of palatability as well as mechanical defences of the plant, 2) the effect of large vertebrate herbivory on both preference and performance of the gall maker (phenotypic selection) and 3) inheritance of female oviposition behaviour.

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References

- Abrams, P. A. 1987. On classifying interactions between populations. – *Oecologia* 73: 272–281.
- Basset, Y. 1991. The spatial distribution of herbivory, mines and galls within an Australian rain forest tree. – *Biotropica* 23: 271–281.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. – *Am. Nat.* 122: 661–696.
- Craig, T. P., Price, P. W., Clancy, K. M., Waring, G. and Sacchi, F. 1988. Forces preventing coevolution in the three-trophic-level system: willow, a gall-forming herbivore, and parasitoids. – In: Spencer, K. C. (ed.), *Chemical mediation of coevolution*. Academic Press, San Diego, CA, pp. 57–80.
- , Itami, J. K. and Price, P. W. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. – *Ecology* 70: 1691–1699.
- Crawley, M. J. 1983. *Herbivory: the dynamics of animal-plant interactions*. – Blackwell, London.
- Drew, R. A. 1987. Reduction in fruit fly (Tephritidae: Dacinae) populations in their endemic rainforest habitat by frugivorous vertebrates. – *Aust. J. Zool.* 35: 283–288.
- Ebenmann, B. and Persson, L. 1988. *Size-structured populations*. – Springer, Berlin.
- Faeth, S. H. 1985. Host selection by leaf miners: interactions among three trophic levels. – *Ecology* 66: 870–875.
- 1986. Indirect interaction between temporally separated herbivores mediated by the host plant. – *Ecology* 67: 479–494.
- 1988. Plant-mediated interactions between seasonal herbivores: enough for evolution or coevolution?. – In: Spencer, K. C. (ed.), *Chemical mediation of coevolution*. Academic Press, San Diego, CA, pp. 391–414.
- Gómez, J. M. 1991. *Biología de la polinización de *Hormathophylla spinosa*: análisis cuantitativo y cualitativo de una interacción mutualista*. – Dissertation, Univ. de Granada, Granada.
- and Zamora, R. 1992. Pollination by ants: consequences of the quantitative effects on a mutualistic system. – *Oecologia*, in press.
- Herrera, C. M. 1989. Vertebrate frugivores and their interaction with invertebrate fruit predators: supporting evidence from a Costa Rican dry forest. – *Oikos* 54: 185–188.
- Hochberg, M. E. and Lawton, J. H. 1990. Competition between kingdoms. – *Trends Ecol. Evol.* 5: 367–371.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. – *Annu. Rev. Ecol. Syst.* 22: 477–503.
- Janzen, D. H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. – *Am. Nat.* 123: 338–353.
- Karban, R. 1986. Interspecific competition between folivorous insects on *Erigeron glaucus*. – *Ecology* 67: 1063–1072.
- Lamprey, H. F., Halevy, G. and Makacha, S. 1974. Interactions between *Acacia*, bruchid seed beetles and large herbivores. – *E. Afr. Wild. J.* 12: 81–85.
- Lawton, J. H. and Hassell, M. P. 1981. Asymmetrical competition in insects. – *Nature* 289: 793–795.
- Lee, T. D. 1988. Patterns of fruit and seed formation. – In: Lovett Doust, J. and Lovett Doust, L. (eds), *Plant reproductive ecology, patterns and strategies*. Oxford Univ. Press, Oxford, pp. 179–203.
- Lomnicki, A. 1988. *Population ecology of individuals*. – Princeton Univ. Press, Princeton, NJ.
- Martínez, T. 1985. Utilisation de l'analyse micrographique des fèces pour l'étude du régime alimentaire du bouquetin de la Sierra Nevada (Espagne). – *Mammalia* 52: 465–473.
- Polis, G. 1988. Exploitation competition and the evolution of interference, cannibalism and intraguild predation in age/size structured populations. – In: Ebenmann, B. and Persson, L. (eds), *Size structured populations: ecology and evolution*. Springer, Berlin, pp. 185–202.
- Rey, L. A. 1992. Developmental morphology of two types of hymenopterous galls. – In: Shorthouse, J. D. and Rohfritsch, O. (eds), *Biology of insect-induced galls*. Oxford Univ. Press, Oxford, pp. 87–101.
- Schoener, T. W. 1983. Field experiments on interspecific competition. – *Am. Nat.* 122: 240–285.
- Seifert, R. P. and Seifert, F. H. 1976. A community matrix analysis of *Heliconia* insect communities. – *Am. Nat.* 110: 461–483.
- Stamp, N. E. 1984. Herbivory, timing of defoliation and plant availability: the effect of checkerspot caterpillars and sawfly larvae on their host plants. – *Oecologia* 63: 275–280.
- Strauss, S. Y. 1991a. Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. – *Ecology* 72: 543–558.
- 1991b. Indirect effects in community ecology: their definition, study and importance. – *Trends Ecol. Evol.* 6: 202–210.
- Strong, D. R., Lawton, J. H. and Southwood, R. 1984. *Insects on plants: community patterns and mechanisms*. – Blackwell, London.
- Weis, A. E. and Abrahamson, W. G. 1986. Evolution of host-plant manipulation by gall makers: ecological and genetic factors in the *Solidago-Eurosta* system. – *Am. Nat.* 127: 681–695.
- , Abrahamson W. G. and McCrea, K. D. 1985. Host gall size and oviposition success by the parasitoid *Eurytoma gigantea*. – *Ecol. Entomol.* 10: 341–348.