

Plant Patterning in the Chilean Matorral: Are the Roles of Native and Exotic Mammals Different?¹

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Mammals and the matorral vegetation have reciprocal effects on each other's distribution and abundance. On the one hand, shrubs, herbs, and grasses provide food and cover for matorral mammals (Jaksić and others 1980; see also the chapter by W. Glanz and P. Meserve in this volume). On the other hand, the use that mammals make of the habitat can have several consequences for the plants, affecting their distribution and abundance.

Here, we will examine the question: are the roles played by native matorral mammals the same as the ones shown by alien species recently introduced?

There are at least two reasons why it is important to know the answer to this question. First, the introduced mammals we will be referring to, goats and rabbits, are of economic importance for the subsistence of a relatively large human population in central Chile (Fuentes and Hajek 1979).

Different management procedures would be derived depending on the degree of similarity one discovered. At one extreme, exotic species could produce consequences similar to those of their original "analogues," but at the other extreme, effects induced by both types of herbivores could be completely different. Whereas in the first case the effects of the introduced mammals would, within certain limits, fall within the naturally evolved resilience (Holling 1973) of the system, in the second case the mammalian effects would be a novel perturbation from an evolutionary point of view. In this latter case, extreme care should be taken, since the system might exhibit very little

Abstract: Native and exotic mammals have different effects on the matorral vegetation. (A) Large mammals (guanacos vs goats) differ in that native guanacos are only minor browsers, whereas goats use shrubs more extensively. Differences between goats and shrub-defoliating insects provide additional evidence that goats are a novel perturbation on the matorral vegetation. (B) European rabbits and their native counterparts differ in their effects on shrub seedlings and on native perennial herbs. Native small mammals affect only the periphery of antipredator refuges. Rabbits are infrequently preyed upon, do not exhibit such habitat restriction, and show a more extensive effect. Implications for matorral renewal are discussed.

tolerance to the new species. Here, only pre-adaptive traits would account for any resilience of the system.

The second reason why the question is important relates to the coupling of herbivores to the ecosystem structure.

Herbivores as a link between producers and carnivores have been selected not only for their capacity to eat tissues of certain plants but also for their ability to avoid predation. Hence, only a fraction of all a priori possible links between plants and mammals are usually observable in any given ecosystem. However, since in a field situation there are usually no "controls," it is not possible to disentangle those links related to feeding preferences and from those associated with constraints imposed by predators, the plants, or abiotic factors. We believe that the comparison of native and exotic species of herbivores, with the latter acting somewhat as evolutionary controls, can aid in the understanding of these relationships.

In this paper, we first discuss the role of the European rabbit (Oryctolagus cuniculus), recently introduced to Chile (Housse 1953). This rabbit is compared with its native counterpart, the diurnal rodent degu (Octodon degus) and to some extent with vizcacha (Lagidium viscacia). There are no native rabbits in Chile (see Osgood 1943). After these comparisons, we will discuss some differences between the present ecological impact of introduced goats and the impact of guanaco (Lama guanicoe), a counterpart of goats. Finally, we will discuss the role of mammals within a more general framework of matorral herbivory.

COMPARISON BETWEEN SMALL MAMMALS

Degu as well as vizcachas, two analogues in body size, general food habits, and habitat of the rabbit, are known to exhibit a strong preference for microhabitat in the neighborhood of rock outcrops and large protecting bushes (Pearson 1948, Le Boulengé and Fuentes 1978) (fig. 1a, b). Chin-

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chilla rat (*Abrocoma bennetti*) is the third possible native counterpart to rabbits by size and food habits, but since its density is usually quite low and it is generally found at the same trapping spots as degus (Jaksić and others 1980), its effect is also likely to be very similar to the one we will describe for degus.

Although all the above animals venture short distances away from these refuges, they do so for very short times and apparently incur great predation risks. Vizcachas are taken by foxes (*Dusicyon culpaeus*) (Pearson 1948), and other carnivores (Pearson 1951) whereas degus and chinchilla rat are frequently preyed upon by two species of foxes and several raptors (for a review, see Jaksić and others 1981).

The European rabbit, on the other hand, exhibits a somewhat different behavior contrasting to that of the native species (fig. 1a, b). In the matorral, adult rabbits tend to use the open spaces far from the above-mentioned refuges (Jaksić and others 1979). Simonetti and Fuentes (1981) confirmed these results and have also shown that small, juvenile rabbit individuals tend to use the neighborhood of refuges, just like degus, and that as they become progressively larger they concomitantly become users of the open spaces (fig. 1b, c). Nevertheless, in the Chilean matorral actual predation upon rabbits seems negligible (Jaksić and others 1979, Jaksić and Soriguer 1981) in spite of the existence of a conspicuous array of potential predators. That is, there are potential predators but these do not eat rabbits.

On the other hand, in Spain where the rabbit is native, its microdistribution pattern is similar to that exhibited by degus and vizcachas in Chile; it is restricted to the neighborhood of protecting refuges (Jaksić and Soriguer 1981). In Spain, rabbits are known to be heavily preyed upon by several predators (Jaksić and Soriguer 1981). Moreover, whereas in Spain rabbits strongly prefer habitats with high shrub cover, presumably protecting them from predators, in Chile they exhibit just the opposite trend (Fuentes and Jaksić 1980, Jaksić and Soriguer 1981). It therefore seems that juvenile rabbits born in Chile behave as they would in the Spanish maquis and only later use the open, predation-safe spaces of central Chile (Simonetti and Fuentes 1981).

These differences between rabbits and native matorral species, plus the differences exhibited by rabbits in similar habitats in Chile and Spain, but under different predation pressures, suggest that in Chile rabbits exhibit habitat release associated with reduced predation pressure (Fuentes and Jaksić 1980, Jaksić and Soriguer 1981). Thus, the lack of an effective coupling between Chilean predators and rabbits can be related to an important extension in the pattern of microhabitat use by rabbits in Chile. This habitat release also occurs in zones where degus are absent, indicating that it is not competition that drives rabbits out of the refuges.

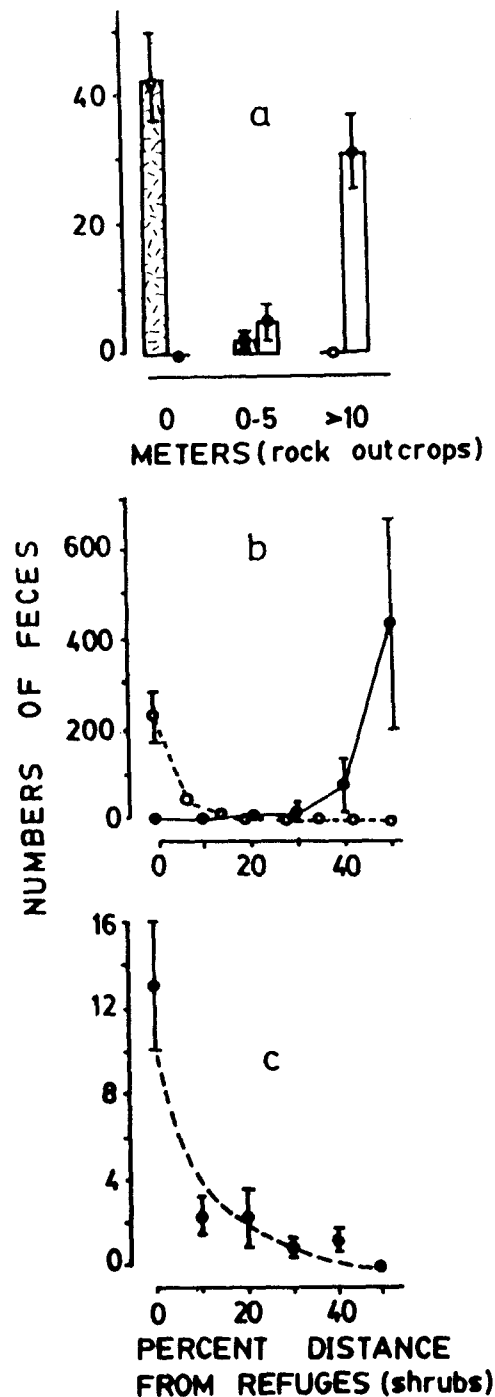


Figure 1--Relative activity of small mammals. Ordinate is density of feces ± 2 SE of the mean, whereas abscissa is distance to nearest refuge (rock outcrop or large shrub). (a) Vizcachas (dark columns) versus adult rabbits (light columns). (b) Degus (light dots) versus adult rabbits (black dots) (redrawn from Jaksić and others 1979a). (c) Small rabbits under 250 mm length (redrawn from Simonetti and Fuentes 1981). Curves were drawn by eye. Notice that vizcachas, degus, and small rabbits tend to use the neighborhood of refuges preferentially, whereas adult rabbits do exactly the opposite. See the text for discussion.

We will now discuss the question: are the preferences of these two mammals for the vegetation the same or not? The significance of this question lies in that both niche dimensions, microhabitat use, and food preferences are important in comparing the potential impacts of the species on the vegetation.

The answer to the above question was obtained through pairwise "cafeteria tests" using four common species of matorral shrubs: Colliguaya odorifera (Euphorbiaceae), Kageneckia oblonga (Rosaceae), Lithraea caustica (Anacardiaceae), and Quillaja saponaria (Rosaceae). Methods as well as results are explained in detail by Fuentes and Etchégaray (1980) and Fuentes and Simonetti (unpublished manuscript). In brief, results show that rabbits and degus eat mature leaves of all four shrub species, although they clearly exhibit different preferences in the pairwise comparisons (table 1a). In addition Simonetti and Montenegro (1980), following a somewhat different methodology, report that degus distinguish less between young leaves of these species than between old leaves, and they do discriminate between new and mature leaves within one species. The extent to which this latter pattern holds for rabbits is unknown, but it is not unlikely that its preferences for young tissues are broader than for the older sclerified ones.

At any rate, the cues used by these animals in selecting leaves are likely to be different. Moreover, both mammals seem capable of eating a broad spectrum of shrub species.

How do the above-mentioned differences in microhabitat use and leaf preferences express themselves in the field?

Jaksić and Fuentes (1980) proved experimentally that in Chile rabbits exhibit a preference for native perennial herbs over the mediterranean grasses, and consequently are capable of removing all unprotected native herbs before their reproduction. Only the native herbs growing under bushes with ground level branches, which can be reached only with difficulty by rabbits, attain sexual maturity and reproduce. That is, where degus are absent, rabbits restrict native herbs to the areas under bushes, whereas spaces between these shrubs are occupied by introduced grasses (Keely and Johnson 1977). Where degus are present, they remove native perennials only from under the shrubs or at most from their periphery (personal observations). Before this effect of rabbits on native herbs was known, the microhabitat restriction of native herbs, clearly differentiating the California chaparral and the Chilean matorral, was thought to be a discrepancy in convergent evolution.

It is not known what effect vizcachas have on the herb cover surrounding the large outcrops where they live, although preliminary observations at Cajón del Maipo, east of Santiago, suggest that they might have an effect that is distinguishable

from the microclimatic effect produced by the rock outcrops.

In addition to the effect on herbs, rabbits and degus modify the distribution of shrubs by altering the survival chances of some seedlings. Simonetti and Fuentes (unpublished data), by planting protected and unprotected Q. saponaria seedlings on equator-facing, ridgetop, and polar-facing slopes, were able to show that even here rabbits do have an important effect on shrub renewal. On north-facing slopes, where rabbit densities are highest, their killing effect is considerably higher than on the high cover south-facing slope, where rabbits are known to be scarcer. Moreover, the ridgetop situation is intermediate in both effect and rabbit density (see fig. 2).

In sum, the evidence available at present suggests that degus have a different effect on the vegetation from that produced by rabbits. The main difference is that predator efficiency at hunting degus confines their effect to the periphery of protecting refuges, whereas predation on rabbits does not impose on them such a restriction. It is reasonable then to suggest that before the recent introduction of rabbits (Greer 1965), seedlings growing beyond 6 m from protecting shrubs or rock outcrops were safe from predation, but that this is no longer the case. Now, all seedlings have high predation risks. Field experience in the matorral shows that in fact very few seedlings can be found, and these are only on mesic slopes with high plant cover, where rabbits are less common. Thus, whereas on these polar-facing slopes few seedlings and very few small plants can be found, on the drier north-facing slopes they are almost nonexistent. Generation time for shrubs may be too long and rabbit introduction too recent for us to know exactly what the future fate of the matorral will be. The situation is complex, however, because we do not know if changes in the plants' physical and chemical composition, or modifications in potential rabbit predators (by becoming more efficient) will occur first and thus modify the whole process. Our present knowledge does not allow us to make an extrapolation.

LARGER MAMMALS

The effects of goats and guanacos have been studied only as far as they concern large, mature shrubs. Studies of their comparative roles on seedling removal are still in progress. Therefore, we mention only one clearcut example that suggests seedling removal is also important here and that it can be measured.

The only place where guanacos are now kept in a semiwild setting, within the matorral type of ecosystem, is in the Forest Reserve at Penuelas, approximately 90 km west of Santiago. Here, the Forest Service (CONAF) keeps two males and three females within a large fenced area of approximately

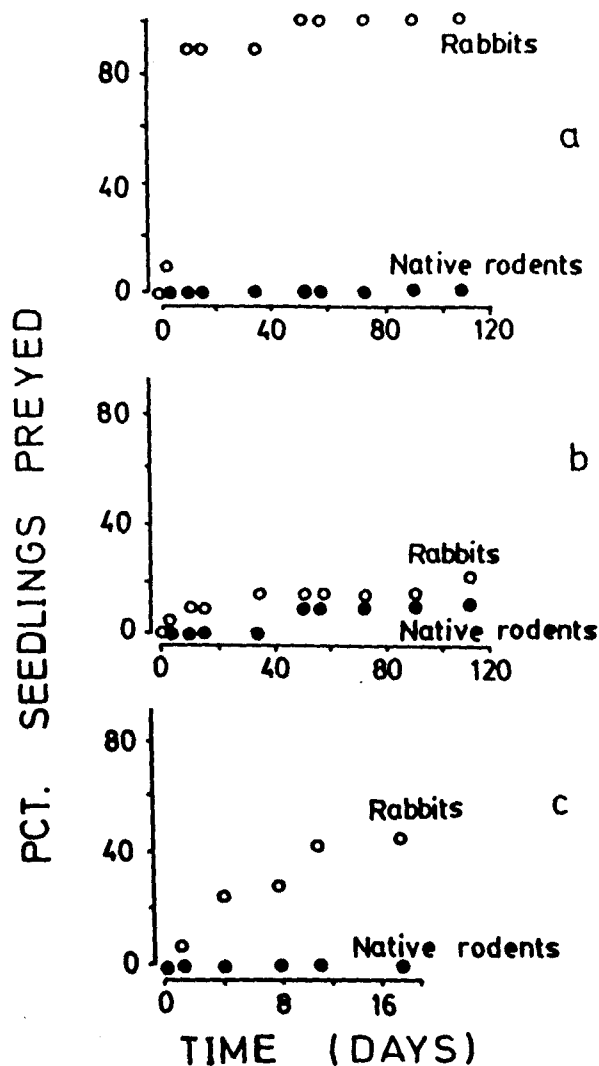


Figure 2--Seedling predation by small mammals. (a) Equator-facing slope. Points shown indicate only results in areas far from refuges where only rabbits are present. No degus effect could be detected here. (b) Polar-facing slope. Here the slope is covered by vegetation. Rabbits kill approximately twice as many seedlings as native rodents (chinchilla rat, degus). Even so, about 70 percent of the seedlings survive herbivore attacks. See text for discussion. (c) Ridgetop. Rabbit effect is intermediate between (a) and (b), but native rodents show no detectable effect.

12 ha. A recent comparison made by us (unpublished observations) shows that within the fenced area there are no seedlings or small plants of the matorral tree *Maitenus boaria* (Celastraceae), whereas outside the fence and where the vegetation is otherwise similar, these seedlings are common. "Cafeteria tests" showed that unlike what happens with other matorral shrubs and trees (see later discussion), guanacos eat *M. boaria* avidly. Moreover, within the fenced area there are large individuals of *M. boaria*, but all their leaves up to "guanaco height" have been eaten, whereas the

large *M. boaria* individuals outside the fence do have leaves below that level. These larger individuals were probably established in the area before the guanacos were introduced. Since other browsers like rodents and rabbits are equally abundant on both sides of the fence, it is reasonable to suggest that it is *L. guanicoe* that produces the difference in the seedlings of *M. boaria*. It is important that there are no cattle, horses, sheep, or goats in this part of the Reserve, since we have observed that these animals eat *M. boaria* with the same willingness as guanacos. Moreover, they seem capable of producing exactly the same effects we just described for guanacos.

The effects of mammals on large plants are generally not as direct as they are on seedlings or herbs. Whereas grasses, herbs, and seedlings are killed in one or at most a few contacts with the herbivore, thus producing a modification in the distribution of adult plants, in the case of browsing on larger plants the consequence is generally mediated by shrub-shrub competition and takes considerably more time (Fuentes and Etchegaray 1981). This is not to say that the effect cannot be immediate, as when overstocking produces direct elimination of the shrub cover of an area (see Fuentes and Hajek 1979), but as we said above, in general, the influence is more subtle.

If individual shrubs were independent of each other--for example, if there were no competition--the fate of individual phenotypes would, for a given mammal density, depend largely upon relative palatability and capacity to recover from contacts with the browsers. In fact, matorral shrubs differ not only in the amount of new leaves produced after defoliation but also in the pattern of such production (Torres and others 1980). Thus, for example, *L. caustica* and *C. odorifera* exhibit strong dissimilarities in their production of new leaves at 25 and 66 percent defoliation levels, but not at 100 percent. Whereas *L. caustica* exhibits a compensatory response to 25 percent defoliation, not to 66 percent but then again to 100 percent, the second species, *C. odorifera*, responds only to the two higher levels of defoliation.

However, as Gutiérrez and Fuentes (1979) and Fuentes and Gutiérrez (1981) have shown, matorral shrubs also exhibit intraspecific as well as interspecific competition. Furthermore, competitive interactions seem to account for some of the successional patterns observed in the matorral (Fuentes and Gutiérrez 1981).

For example, on mesic slopes species like *L. caustica* and *Q. saponaria* have stronger effects on species like *C. odorifera*, *Baccharis rosmarinifolia* or *Muehlenbeckia hastulata* than vice versa, although they all interact with each other and with themselves (see Fuentes and Gutiérrez 1981).

That is, in addition to the previously mentioned individual responses to defoliation, browsing pressures also modify the competitive performance of shrubs. Defoliation then not only reduces the leaf area and consequently the future energy pool of a given shrub, but has also an opportunity cost related to unrealized root and shoot growth, with an eventual reduction in the competitive performance, and ultimately exclusion from the community (see Fuentes and others 1981, Fuentes and Etchegaray 1981). Fuentes and Etchegaray (1981) present evidence suggesting that shrub herbivory by insects, which are the most important defoliators in the matorral under natural conditions, acts on shrub density by altering interspecific competitive equilibrium. That is, because insects can reduce the photosynthetic apparatus of shrubs, such shrubs exhibit several defense mechanisms which in general keep damage at low levels. As long as the actual level is low enough, the plant is part of the community; otherwise it is excluded by less damaged competing phenotypes.

In the following paragraphs, we will summarize some of the evidence regarding the role that native guanacos might have had and the significance that goats might be having today in the dynamics of matorral plants. This hypothetical approach was taken because guanaco is now extinct in central Chile (Miller and others 1973), except for the recently established Reserve of Penuelas. By contrast, since colonial times goats have been part of the domestic stock of low-income people in this part of the country (Fuentes and Hajek 1979).

The ideal experiment to compare guanacos and goats would be to have large separate areas with only one of these in each area, with otherwise comparable vegetation. This however cannot be done. On the one hand, there are no extensive areas in central Chile where either goats, wood-cutting, or artificial fires, singly or in combination, have not been present within the last 30 years or so. In addition to the rabbits mentioned earlier, introduced hares (*Lepus europeus*) are more or less common everywhere and their effect is only partially understood. Moreover, presently existing herds of goat have large fluctuations in number between locations and between years, without any reliable record of them.

On the other hand, the few guanacos existing in the matorral in a semiwild state are at Penuelas Reserve. But here there exist no detailed records, either on the initial and past vegetation, or on the guanaco loads at various times. Because of these constraints, we have approached the question of differences between the two mammals by analyzing (a) relative amounts of browsing and grazing, (b) preferences for various shrub species during browsing, and (c) field densities of the two herbivores.

(a) Browsing/grazing ratios. The best known studies of guanacos feeding were made by Raedecke (1978) in Patagonia. He describes these animals

as mostly grazers that use the taller vegetation mostly for cover. Along the same lines, direct observations of guanacos feeding during late summer in the matorral Reserve of Penuelas show that at most 37 percent of the bites of the average feeding sequence are on shrubs, with the remaining 63 percent being very selective feeding on herbs. This 37 percent is likely to be the maximum proportion of browsing, since during the summer the relative attractiveness of the herb cover over shrubs is at its minimum (Fuentes and Jaksic 1981).

In contrast to guanacos, goats have a much higher browsing percentage. Measurements at a matorral site with high shrub cover reveal an average 87 percent of bites on shrubs. At Penuelas reservation, with a lower shrub cover, the corresponding figure is 62 percent, but still considerably higher than the percentage given above for guanacos.

In sum, the evidence available suggests a strong difference in the browsing/grazing preferences exhibited by goats when compared with guanacos.

(b) Shrub preferences. "Cafeteria tests" similar to those previously reported for rabbits and degus are shown in table 1b. It can be seen that preferences by the two herbivores are clearly dissimilar. Both species prefer *C. odorifera* over *L. caustica*, but whereas the guanaco does not distinguish between the other shrub species pairs, goats exhibit a stronger dislike for *L. caustica*.

Notice that these are preferences, when eating shrubs, but do not refer to consumption rates. Actually, during the experiments goats ate shrubs 5 to 10 times faster than guanacos, even if there was nothing else to eat. Guanacos frequently preferred to nibble the surrounding *Eucalyptus* fence instead of the shrubs.

(c) Field densities. We do not have direct evidence on the former densities of guanacos in the matorral, but they seem to have been relatively low compared with the present densities of goats (see Gay 1847). Goats are managed at very high densities.

In sum, there is little reason to expect that browsing effects of goats are comparable to those of guanacos. The high goat densities we see today, and their broad dietary preferences compared with guanacos, are too different. It is not surprising, therefore, that the traditional, un-informed "management" of such a novel evolutionary perturbation as goats has had such disastrous effects on the matorral vegetation. The evergreen/drought-deciduous matorral mixtures north of Santiago have been turned into a desertlike vegetation, to a large extent due to overstocking with goats (UNCOD 1977, Fuentes and Hajek 1979). This is an unfortunate example of the desertification process where solutions are still to come. Further south, however, in the mostly evergreen

Table 1--Relative preferences for shrubs in 1 cafeteria tests on native and exotic species

(a) SMALL MAMMALS	CQ	CK	CL	QK	QL	KL
<u>O. degus</u>	+1	0	0	0	-1	0
<u>O. cuniculus</u>	0	0	-1	0	-1	0
(b) LARGER MAMMALS	CQ	CK	CL	QK	QL	KL
<u>L. guanicoe</u>	0	0	+1	0	0	0
<u>C. hircus</u>	0	0	+1	0	+1	+1

¹Each entry shows the result of a pairwise comparison. (Goat data from Fuentes and Etchegaray 1980.) Statistically significant preferences are indicated by either +1 or -1. An entry with 0 means differences are not statistically significant. C = Colliguaya odorifera, Q = Quillaja saponaria, K = Kageneckia oblonga, L = Lithraea caustica. Entries are to be read as follows: +1 means the preference detected favors the first species in the plant species pair shown above; -1 means the second species is preferred. Thus, O. degus prefers Colliguaya odorifera over Quillaja saponaria, but prefers Lithraea caustica over Quillaja saponaria. None of the four species coincide in their preferences, and there are no closer similarities by either the native/exotic nor the size similarity criterion. See text for discussion.

matorral, more recent overstocking is also starting to show its effects. In areas around Casablanca and Melipilla (Fuentes and Hajek 1979), there is already some heavy destruction of vegetation up to the point of strong sheet and gully erosion.

Even in the few places where goats have been introduced only recently and in comparatively low densities, there are still concomitant changes in the vegetation. These are partly related to selective feeding but are also a by-product of the earlier-mentioned competitive equilibrium between shrubs.

THE TWO KINDS OF EFFECTS OF MAMMALS ON THE VEGETATION

Mammals, either large or small, are capable of exerting important effects on the matorral structure.

One the one hand, by selectively removing seedlings or small individuals of some species from exposed areas, herbivores can modify the "seedling shadow" and thus the later distribution of adult individuals. The available evidence here

points towards different roles for native and introduced herbivores.

The situation with larger shrubs is more complex. As we described earlier, the effects produced by browsers depend upon relative palatabilities, response patterns to defoliation, and overall competitive performance under browsing pressure. In the matorral, where mammalian browsing does not seem to have been evolutionarily important, these factors do not all follow parallel trends.

On the other hand, the evolutionary responses of shrubs to insect herbivory are most likely to be tied to the insect's actual and potential damage to the shrub's photosynthetic apparatus. Lithraea caustica and C. odorifera are the two extreme species in terms of insect damage to leaves. In the former, about 13 percent, and the latter only about 2 percent of the yearly produced photosynthetic apparatus is eliminated by insects. Based on these results, Torres and others (1980) hypothesized that L. caustica, but perhaps not C. odorifera, should exhibit compensatory responses at low defoliation levels comparable to the ones naturally experienced during their evolutionary history. This was shown to be the case. Moreover, species that are intermediate with regard to insect defoliation also seem to exhibit intermediate responses to defoliation.

Thus, before the arrival of goats, the shrubs usually exhibiting the largest damage on their leaves also compensated the most and thus an equilibrium was established. But goats are a truly new perturbation in the evolutionary sense. Not only were there no comparable mammalian browsers before, but goat attack on shrubs is completely different from that of insects. Whereas insects attack L. caustica the most and C. odorifera the least, goats prefer to eat C. odorifera and all the other available shrub species over L. caustica. In addition, L. caustica is the strongest plant competitor in mesic matorral slopes (Fuentes and Gutiérrez 1981). It is not surprising therefore that on mesic slopes goats initially produce a strong modification in the plant community by favoring an overdominance of L. caustica (Torres and others 1980). Later, after their browsing pressure has even eliminated L. caustica, the less palatable cacti (Trichocereus spp.) are favored as dominants (Fuentes and Hajek 1979). This sequence at its various stages is a common phenomenon throughout distributional range of matorral.

Clearly then, goats, even if managed at low densities, are likely to change the composition of matorral. Moreover, Fuentes, Espinosa, and García (unpublished manuscript) provide evidence that overgrazing can accelerate erosion of the rather steep slopes where goats are kept. This is a second process that, when added to the ones described earlier for plant cover, also points in the direction of matorral degradation. In addition, Yates and Valencia (1980) have shown that the plant composition of the matorral has an

important effect on the goats' rate of weight increase and on their milk's fat content (Yates and Valencia 1980). Therefore, the degradation of the vegetation produced by these mammals in turn affects the goats' productivity and their economic return. More research is therefore needed to establish a viable long-term goat management technique, or if it ultimately becomes necessary, to replace goats with some other source of income.

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