SIZE-DEPENDENT PREDATION BY FERAL MAMMALS ON GALÁPAGOS *OPUNTIA*

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Oceanic islands typically possess biotas with high susceptibility to damage by introduced plants and animals (Schofield 1989, Loope et al. 1988). Change in the flora of the Galápagos Islands is a well-documented example of such damage. On most of the larger islands, native vegetation has been significantly altered in composition by feral mammalian herbivores (Hamann 1984, Schofield 1989, Loope et al. 1988).

Previous studies of herbivory by introduced mammals in Galápagos have been concerned primarily with the species of plants consumed, and with effects on vegetation structure (e.g. Calvopiña and de Vries 1975, de Vries and Calvopiña 1977). However, little is known about how food plants are selected within palatable species.

In predator-prey interactions involving animal species, many cases are known in which predation is size-dependent (e.g. Paine 1976). Frequently, both small and large prey individuals are consumed disproportionately rarely by predators; small individuals because they do not provide sufficient food rewards, and large ones because they are too difficult to capture or consume. Although seed size clearly influences food consumption by granivores (e.g. Grant 1986), examples of the effect of whole plant size on rates of herbivory are rare.

In this paper we describe size-dependent predation by feral goats (*Capra hircus* L.) and burros (*Equus asinus* L.) on the tree cacti *Opuntia echios* var. *gigantea* Howell and *O. galapageia* var. *galapageia* Hensl. in the arid zone of Galápagos. (Hereafter, varietal epithets of these *Opuntia* taxa will be omitted). These animals damage cacti by biting into the cladodes or through the bark of the trunk to reach the pulp. The only large native herbivores, land iguanas (*Conolophus subcristatus* and *C. pallidus*) and giant tortoises (*Geochelone elephantopus*), eat fallen pads and fruits, but are not known to damage trunks in this way (Carpenter 1969, Rodhouse et al. 1975, Christian et al. 1984). As suggested by Snell et al. (1994), introduced mice can also be a threat to *Opuntia* populations because they consume the roots and may accelerate mortality.

Opuntia echios was studied on Santa Cruz Island, in a zone where introduced herbivores are typically uncommon, and the vegetation is relatively stable (Eliasson 1982; Hamann 1984). *O. galapageia* was studied on Santiago Island, where large populations of feral goats and burros are present and have caused significant damage to the native vegetation (Schofield 1989, Hamann 1993). Goat populations are very high, estimated at 60,000 to 80,000 individuals on the 572 km2 island (unpublished analysis by W. Pittroff, based on data of L. Calvopiña).

STUDY SITE AND METHODS

Opuntia echios was studied on Santa Cruz, about 0.7 km north of the Charles Darwin Research Station. The approximate elevation is 30 m. The vegetation is low (less than 2 m tall, with the exception of occasional cacti), with about 80% total plant cover. *O. echios* was common at the site and reached a maximum height of 5 m. Dominant plants were *Cordia leucophlyctis, Cordia lutea, Prosopis juliflora, Acacia rorudiana, Ipomoea triloba,* and *Lantana peduncularis* (Wiggins and Porter 1971). Burro droppings were found, but no signs of goats were encountered. The droppings and bites on *Opuntia* trunks appeared to be at least several months old.

Opuntia galapageia was studied in the north-central part of Santiago, near La Bomba. This site was also in the arid zone, at an elevation of about 2 to 10 m. Vegetation dominants were *Bursera graveolens, Castela galapageia, Clerodendron molle,* and *Lantana peduncularis.* Although some *Bursera* trees reached 4 m height, this site was quite open, with vegetation covering only about 30%. The very high frequency of droppings and sightings of animals suggest an abundance of goats and burros. Much evidence of recent damage to *Opuntia* plants, from near ground level to about 1.8 m height, was found, and prob-

Table 1. Relationship between spine cover of *Opuntia* and probability of damage to the trunk by feral goats and donkeys. The number of damaged plants expected was calculated on the assumption that the same proportion of plants would be damaged in each size class. Obs = observed, Exp = expected, N = number of plants examined, % = percent damaged.

	Number of Damaged Plants			
Spine cover	Obs	Exp	N	%
O. echios, Santa Cruz				
Heavy	0	5.6	21	0
Moderate	8	5.1	19	42
Light	22	19.3	75	29
(Chi Square = 33.1, $p < 0.001$)				
O. galapageia, Santiago				
Heavy	5	12.9	76	7
Moderate	7	4.6	27	26
Light	8	2.5	15	53
(Chi Square = 21.5, $p < 0.001$)				

ably represents a combination of burro and goat attacks. It was not possible to visually distinguish between burro and goat damage.

In both areas, *Opuntia* plants with heights of ≥ 2 m were surveyed. This cutoff was chosen because these plants begin to form definite terete trunks and to produce flowers at about this size. Furthermore, plants < 2 m height showed no bite damage by large animals. We recorded the diameter of the trunk at a height of about 0.5 m, the degree to which spines covered the trunks ("heavy" = 75-100% cover by spines, "moderate" = 25-75% cover, and "light" = < 25% cover), and the presence of bites on the trunk and cladodes. We also recorded the diameter of plants killed by bites. On Santa Cruz, data were collected within an area of approximately 0.5 ha. On Santiago we walked a circuit of about 2 km length, recording data on all cacti of appropriate height.

Statistical tests and calculations were done by the program SPSSPC. Values reported are means +/- standard deviations.

RESULTS

At the Santa Cruz site, 30 of 115 living plants (26%) displayed burro damage to the trunk; none had damage to cladodes. On Santiago, 20 of 118 living plants (17%) had trunk damage, 21 (18%) had cladode damage, and 2 (2%) had both.

On Santa Cruz, plants with heavy spine cover had a mean trunk diameter of 12.1 ± 2.1 cm (n = 21), versus 15.7 ± 2.9 cm (n = 19) for plants with moderate spine cover and 20.4 ± 5.5 cm (n = 75) for those with light cover. These differences were statistically significant (Kruskal-Wallis test, $P < 0.01$). Diameter also varied significantly with spine class at the Santiago site, although differences were smaller. Here, plants with heavy spines had a mean diameter of 17.6 ± 4.3 cm (n = 18), those with moderate spines 21.8 ± 3.9 cm (n = 30) and those with light spines 20.8 ± 5.0 cm (n = 82). Again, differences were statistically significant (Kruskal-Wallis test, $p < 0.02$).

Table 2. Relationship between trunk spine cover of *Opuntia* and probability of damage to cladodes by feral goats and donkeys, for the Santiago site only. Obs = observed, Exp = expected, N = number of plants examined, % = percent damaged.

	Number of Damaged Plants			
Spine cover	Obs	Exp	N	%
Heavy	12	13.5	76	16
Moderate	5	4.8	27	19
Light	4	2.7	15	27

(Chi Square = 1.03, p = 0.60)

Table 3. Relationship between *Opuntia* trunk diameter and probability of damage by feral goats and donkeys. Plants with heavy spine cover are omitted from this analysis. Obs = observed, Exp = expected, N = number of plants examined, % = percent damaged.

O. echios, Santa Cruz

	Number of Damaged Plants			
Diameter class	Obs	Exp	N	%
<20 cm	24	18.7	58	41
>20 cm	6	11.3	35	17

(Chi Square = 5.9, p = 0.02)

O. galapageia, Santiago

<20 cm	11	10.4	29	38
>20 cm	4	4.6	13	31

(Chi Square = 0.20, p = 0.65)

Presence or absence of damage to the trunk was strongly related to the degree of spine coverage for both sites (Table 1). For the Santiago site, there was no relationship between cladode damage and the degree of spine cover (Table 2).

When plants with heavy spines were omitted from the analysis, a significant relationship between trunk diameter and damage was detected for the Santa Cruz site, with plants having a diameter > 20 cm experiencing less frequent damage than expected. However, we found no relation between size and damage to cacti at the Santiago site (Table 3).

Bite-killed plants were very common on Santiago (40 of 158, or 25%). The diameter of dead plants (17.8 ± 4.6, n = 40) averaged a bit smaller than those of live plants (19.3 ± 4.7, n = 118), but the difference was not significant (Mann-Whitney test, p = 0.10). There were insufficient numbers of dead plants (3 of 118, or 3%) to perform statistical tests for the Santa Cruz site.

DISCUSSION

It is clear that adult *Opuntia* plants are severely damaged by feral animals. Although Eliasson (1968) and Weber (1971) noted damage to trunks by goats, most previous discussions have emphasized trampling or consumption of small plants (van der Werff 1982; Schofield 1989). We did observe a few small plants (diameter ≤ 8 cm) on Santiago that may have been uprooted by feral animals, but this was infrequent in the populations studied. In contrast, damage to trunks and cladodes of large plants was very frequent.

Repeated attacks to an *Opuntia* can girdle the trunk and kill the plant. Cladodes of both *Opuntia* species are capable of rooting after such an event. However, vegetative reproduction from fallen cladodes seems to be very rare in *O. galapageia* on Santiago. This is probably because the cladodes of older plants of this species have bristly, rather soft, spines rather than the long, sharp spines found on younger plants (Wiggins and Porter 1971). Fallen cladodes of older plants are quickly consumed by animals, and usually do not survive long enough to take root.

The selection of cacti as food by feral mammals is clearly size-dependent. Damage was dependent on trunk size, with both small and large diameter stems avoided. The probable reason for avoidance of small trunks is the dense armature of spines. In the Santa Cruz population of *O. echios*, large stems are probably avoided because they exceed the gape size of the animals.

The absence of a significant size effect in *O. galapageia* may be due to differences in trunk size. *O. echios* has a maximum diameter of at least 60 cm, while *O. galapageia* trunks larger than 32 cm were not found in this study. In the study areas, 22% of *O. echios* were > 25 cm diameter, while only 8% of *O. galapageia* were this large. Thus, failure to find a size effect in the latter species may reflect the rarity of large trunks. Another possible explanation for the lack of a size effect is greater herbivore pressure. As *Opuntia* trunks age, patches without spines develop. On Santiago, we saw numerous cases where bite damage occurred in small spineless areas. On Santa Cruz, where food sources other than cacti are common, bites occur mostly on trunks with large patches devoid of spines, or those without spines.

The results of this study have important conservation implications. In both *O. echios* and *O. galapageia*, reproduction is size-dependent. The average diameter of flowering *O. echios* is 26 cm, and that of flowering *O. galapageia* 21 cm. In both species there is a positive correlation between trunk diameter and levels of fruit production (D. Hicks and A. Mauchamp, unpublished data). Damage to medium- or large-diameter individuals could thus constitute a bottleneck in survivorship that prevents plants from reaching reproductive size. In the long term, predation may significantly reduce recruitment to *Opuntia* populations, even though small cacti may not be directly damaged. This appears to be especially crucial in the Santiago study area, where 60% of large *O. galapageia* were damaged or killed by animals. The elimination of reproductive individuals is already occurring on Santiago. In a set of 12 plots from 2 to 135 m elevation, we found only 5.5% of *O. galapageia* individuals to be reproducing sexually. In a similar study on Santa Cruz, 19.2% of *O. echios* were reproductive (D. Hicks and A. Mauchamp, unpublished data).

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