

13. THE GOAT AND THE COCCID: INTERACTIONS BETWEEN TWO
INTRODUCED HERBIVORES AND THE VEGETATION OF
ALDABRA ATOLL

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Abstract

Feeding preferences of two introduced, taxonomically remote herbivores were examined on Aldabra Atoll, in the western Indian Ocean. Both the feral goats (Capra hircus) and the coccids (Icerya seychellarum) exhibited clear preferences as to which plant species were fed upon, and these preferences overlapped to some extent. Although the individual actions of goats and coccids did not contribute directly to plant mortality, the combined effect of these two herbivores may be enough to jeopardize the survival of preferred, susceptible plant species, and thus may alter community structure on the atoll. When given a choice, a captive goat preferred coccid-infested vegetation to uninfested vegetation.

Introduction

Interactions between herbivores of very different taxonomic orders have been seldom investigated, though their importance is often suspected in many ecosystems. Situations rarely arise in which their effects can be separated from many other environmental interactions. We present here an unusual example of such an interaction which may generally be more common than previously realized. This paper summarizes our knowledge of the feeding preferences of two taxonomically remote but extremely important herbivores on the atoll of Aldabra and discusses their combined impact on the island ecosystem.

Aldabra is a large, raised coral atoll in the western Indian Ocean (46°20'E, 9°24'S). Its geology and ecology have been extensively reported elsewhere (e.g., Westoll & Stoddart, 1971; Braithwaite et al., 1973; Gould & Swingland, 1980; Hill & Newberry, 1980).

The only introduced vertebrate herbivore on the atoll has been and still is the feral goat (Capra hircus L.). Although the precise history of the population is uncertain, it probably originated from introductions in the late 19th century (Stoddart, 1981; Gould & Swingland, 1980). Gould (1979) and Gould & Swingland (1980) have described the population dynamics and behavioral ecology of the goats and their interactions with the atoll's major native herbivore, the giant tortoise (Geochelone gigantea Schweiger).

The most abundant invertebrate herbivore on Aldabra is a phloem-feeding insect, the coccid Icerya seychellarum Westwood (Homoptera; Margarodidae). From the time of its first report in 1968, the population rose to epidemic proportions on the atoll in the mid-1970's and has now (1979-82) fallen to a stable, low level (Hill & Newbery, 1980; Newbery, unpublished). The origins of the infestation are uncertain, although accidental introduction on fruit or plant stock is the most likely explanation (Hill & Newbery, 1982). Newbery (1980a, b) found that this coccid could reduce substantially the growth of highly susceptible tree species, but it seems that infestation caused little direct tree mortality (Hill & Newbery, 1980).

Methods

Experiment 1: General vegetation preferences of goats

Experiments on the feeding preferences of goats were conducted from January to May 1977, in a 4m x 4 m mangrove-pole enclosure at the eastern end of Malabar Island, Aldabra. A goat was captured at night, placed in the enclosure and allowed the following day to become accustomed to its confinement, the presence of an observer, and the experimental routine. Data collected from the second day on were used in the analysis. At dawn each day, five forage bundles were hung inside the enclosure at head height for the goat and spaced so that the animal had to take at least several steps to move from one bundle to another. The positions of the bundles were randomized daily. Each bundle was composed of one of five plant species known from direct field observations (Gould, 1979) to be preferred browse species for the goats: Capparis cartilaginea Decne, Pemphis acidula Forst., Phyllanthus casticum Willemet f., Polysphaeria multiflora Hiern, and Sideroxylon inerme L.. An effort was made to have all five bundles approximately the same size each day. Beginning weights of the bundles ranged from 275 to 2280 g over the course of the experiments. The experimental animal was observed continuously throughout the day until dark when the remnants of the bundles were removed from the enclosure. During the day, the cumulative time spent feeding at each species bundle was recorded. Each experiment lasted 2-4 days and three replicate goats were used: a mature male, a mature female, and an immature (sub-adult) male.

Experiment 2: Goat preference for Icerya-infested versus Icerya-free vegetation

To determine if feeding preferences were influenced by the presence of coccids on some of the vegetation, a captive goat was allowed to choose

between infested and uninfested food bundles. Using the same experimental set-up as in the first experiment, two small (25-80 g) bundles, one with Icerya-infested Sideroxylon and the other with Icerya-free Sideroxylon, were hung in the enclosure for two minutes, then removed. Only Sideroxylon inerme was used for this experiment since Experiment 1 had shown that it was the goat's most preferred browse species. The time spent feeding at and the amount eaten from each of the two bundles were recorded during the two minutes. The experiment was repeated 32 times with the same goat, the immature male. The position of the bundles was reversed on successive trials to remove any positional bias.

Field studies on Icerya feeding preferences

Feeding preferences of Icerya were recorded in surveys of the Aldabra vegetation 1976-1978. The abundance of Icerya on 52 common plant species at 79 sites was assessed using a subjective five-point scale (0 = no Icerya present, to 4 = Icerya infestation devastating). The median score for each plant species over the whole atoll may be considered a comparative measure of Icerya preference (Hill & Newbery, 1980).

Results

Experiment 1 and Icerya feeding preferences

Sideroxylon inerme was by far the most preferred food source for both the feral goats and the coccids (Table 1). Agreement between the goat and coccid rankings of the other four species is less clear, especially since the goats showed individual variation. Capparis cartilaginea, however, was least preferred by the goats overall and was not utilized at all by coccids. Polysphaeria multiflora on the other hand had a fairly high preference rank with Icerya (11th out of 52 species in 1978), but was a low choice for two of the goats.

Experiment 2

The Icerya-infested bundles of Sideroxylon were preferred significantly to the uninfested bundles both in terms of the time spent feeding at each and the percentage (by weight) of available forage eaten (Table 2).

Discussion

The ranking of plant species obtained in Experiment 1 does not match the frequency of consumption of those same species observed in the field. For example, captive goats preferentially consumed much Sideroxylon and relatively little Capparis. Yet in field observations made at the eastern end of Malabar Island during the same time of year, Capparis was the most frequently observed browse species and Sideroxylon ranked third (Gould, 1979; Gould & Swingland, 1980). This discrepancy is most likely explained by differences in availability of browse species in the field versus in the enclosure. In the enclosure, all five species

were readily and equally available, and the consumption pattern of the goats was an accurate reflection of their preferences. Yet in the field under natural conditions, much more of the low, shrubby Capparis was available to the goats than was the tree-form Sideroxylon with its established browse lines (Gould, 1979). There was also a high procurement cost (in terms of time, energy and risk of injury from browsing on hind-legs) associated with trying to feed on Sideroxylon in the field (Gould & Swingland, 1980).

In detailed studies of Icerya on Aldabra, Newbery (1980a, b) has shown that heavy infestations of this species can reduce the growth rate of two host plant species (Scaevola sericea Vahl, and Euphorbia pyrifolia Lam.) by approximately 50%. The long term effect of this level of infestation upon the survival of these plant species and upon the structure of the plant community is not yet known. Those species which are preferred by both invertebrate and vertebrate herbivores will be subject to even greater levels of stress.

Sideroxylon inerme is an important component of most scrub communities on Aldabra (Hnatiuk & Merton 1979; Newbery & Hill, 1981). Many of the mature trees of this species have clearly defined goat browse lines and are often badly infested with Icerya. In addition, on those parts of the atoll where goat densities are greatest (e.g., the eastern end of Malabar Island) seedling Sideroxylon are rare and restricted to areas of deeply dissected coral limestone inaccessible to goats (Gould & Swingland 1980). The combined impact of goats and Icerya may well have a serious effect upon the competitive ability and survival of Sideroxylon, at least on some parts of the atoll.

Experiment 2 showed that Icerya-infested Sideroxylon was consumed preferentially to uninfested Sideroxylon. This is encouraging, as one pest (the goat) will thereby eat the other (the coccid). However, since the foliage is also consumed in the process, the net result is of dubious benefit to the vegetation. The reason for the preference is unclear, though a likely explanation is that the goat is attracted by honeydew, the sweet excrement characteristic of phloem-feeding insects such as Icerya.

The results suggest that two herbivores of widely differing taxa demonstrate strong feeding preferences which overlap to some degree. The cumulative effect of such taxa being introduced into island ecosystems such as Aldabra may be far reaching, and is likely to affect plant community structure significantly in years to come. Furthermore, successive accidental introductions of herbivores are likely to have an accelerating influence upon plant community changes if certain plant species are typically more susceptible to a wide range of herbivores.

Future research aimed at quantifying the susceptibility of plants to a wide range of herbivores would be of interest, particularly with regard to islands such as Aldabra which have a high degree of endemism (Renvoize, 1971). It has been postulated that plants evolving on islands in the absence of strong herbivore pressure are more likely to lack

Table 1. Daily mean feeding time (minutes) of goats, median abundance of Icerya (Hill and Newbery, 1980), and relative preference ranks for five plant species. Numbers in parentheses for Icerya = preference ranks among the 52 plant species examined for Icerya infestation.

	Goat #1			Goat #2			Goat #3			<u>Icerya</u>		
	feeding time	rank		feeding time	rank		feeding time	rank		infestation median score 1976/1977	1978	rank
<u>Sideroxylon inermis</u>	52.5 (49%)	1		30.5 (57%)	1		62.8 (61%)	1		0.60 (12)	1.35 (5)	1
<u>Pemphis acidula</u>	27.2 (25%)	2		11.6 (22%)	2		16.2 (16%)	3		0.01 (31)	0.05 (24)	3
<u>Phyllanthus casticum</u>	15.6 (14%)	3		0.2	4		16.8 (16%)	2		0	0	=4
<u>Polysphaeria multiflora</u>	4.7 (4%)	5		11.0 (21%)	3		7.2 (7%)	4		0.59 (14)	0.43 (11)	2
<u>Capparis cartilaginea</u>	7.7 (7%)	4		0	5		0.7 (1%)	5		0	0	=4

chemical defenses against herbivore attack (Levin, 1976). If this is true, it is endemic plant taxa such as Sideroxylon inerme (endemic ssp. cryptophlebia (Baker) Hemsley) which are most at risk from introduced herbivores.

Table 2. Chi-square test of time (seconds) spent feeding on infested and uninfested Sideroxylon bundles, plus test for equality of two percentages (Sokal & Rohlf, 1969) based on the grams (g) eaten of each.

Bundles	time	χ^2	g eaten	g not eaten	p(of being eaten)	t_s
Coccid infested	1683		711	679	0.5115	
		14.66*				9.55**
Uninfested	1468		451	903	0.3331	

* = $p < 0.005$

** = $p < 0.001$

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