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**The natural history and ecology of an agave weevil, *Scyphophorus
acupunctatus* Gyllenhal, and other animals associated with wild
and cultivated agaves in southern Arizona**

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The University of Arizona, 1987

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300 N. Zeeb Rd.
Ann Arbor, MI 48106

THE NATURAL HISTORY AND ECOLOGY OF AN AGAVE WEEVIL,
SCYPHOPHORUS ACUPUNCTATUS GYLLENHAL, AND OTHER
ANIMALS ASSOCIATED WITH WILD AND CULTIVATED
AGAVES IN SOUTHERN ARIZONA

by

Gwendolyn Lee Waring

A Thesis Submitted to the Faculty of the
DEPARTMENT OF ENTOMOLOGY
In Partial Fulfillment of the Requirements
For the Degree of
MASTER OF SCIENCE
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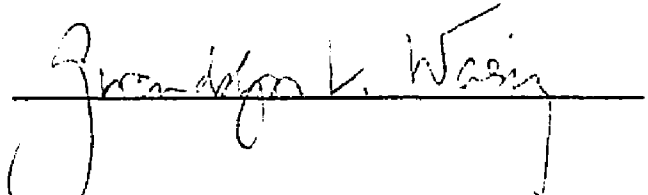
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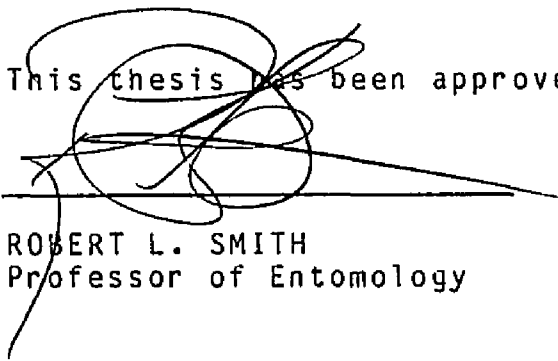
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ABSTRACT

A cultivated plant, Agave americana var. expansa (Jacobi) Gentry, is attacked by the weevil Scyphophorus acupunctatus Gyllenhal prior to flowering, while Agave palmeri Engelman, a wild species, is colonized by the weevil only after it blooms. Microbes associated with the weevil apparently cause "agave decline," a pathological condition that accompanies larval S. acupunctatus infestation. Agave decline kills the afflicted plants.

A survey of arthropods associated with nonblooming and blooming Agave palmeri Engelman revealed that distinct herbivore groups colonize 4 habitats within the plant in a successional pattern. The leaves of nonblooming A. palmeri are colonized by 7 species of leaf feeders. Sixteen species of herbivores and detritivores colonized the boles of blooming plants. The stalk of A. palmeri is colonized by 4 stem boring insects and the inflorescence by yet other species of herbivores.

CHAPTER 1

INTRODUCTION

The genus Agave (Agavaceae) originated in the New World and radiated to produce a very large genus comprised of over 300 species. During this time a number of animals have come to be associated with it, as pollinators, herbivores and predators. As the plant has come to be used by man, these associations have become conspicuous and, in some cases, of major economic importance. Agaves as succulents offer a special ecological opportunity for desert dwelling animals because they are exceptionally nutritious resources. This is due in large part to the fact that they store carbohydrates and water for many years in preparation for their single and dramatic reproductive bout. In light of this, it is worthwhile to understand the nature of the agave's ability to deter herbivores which might otherwise drive it to extinction.

Despite the prevalence of this genus in the flora of the southwestern United States and its commercial use, relatively little is known about how it interacts with

native species of pollinators, herbivores and predators. Thus, this thesis embodies an exploration into ecological aspects of the agave's interactions with native animal species, ranging from cursory associations to more complicated and potentially evolutionary ones.

CHAPTER 2

NATURAL HISTORY AND ECOLOGY OF SCYPHOPHORUS ACUPUNCTATUS (COLEOPTERA:CURCULIONIDAE) AND ITS ASSOCIATED MICROBES IN WILD AND CULTIVATED AGAVES

Introduction

An agave weevil, Scyphophorus acupunctatus Gyllenhal, is the most important pest of cultivated agaves. Both the Agave and S. acupunctatus originated in the New World (Sellers 1951, Gentry 1972). However, agave species have been introduced into many arid and tropical regions as a crop for the production of sisal, and S. acupunctatus appears to have successfully tracked these introductions to the extent that its range is now coincident with the plant's extended range. This weevil has been a major problem in the tequila and henequen industries of Mexico (Halffter 1957); the sisal industry of Africa and Indonesia (Clinton and Peregrine 1963, Hopkinson and Materu 1970a,b,c, Materu and Hopkinson 1969a,b, Lock 1969); and in the nursery businesses and landscapes of the southwestern United States, where the plant is cultivated as an ornamental (Pott 1975). "Agave

decline," a fatal disease in southwestern ornamental agaves is associated with weevil infestations and is a major concern among homeowners (Dave Byrne, U of A personal communication). Although, some weevil control studies have been conducted (Materu and Hopkinson 1969a, Hopkinson and Materu 1970a, Lock 1969), and some taxonomic work has been done on S. acupunctatus (Vaurie 1971; Duges 1881), very little is known about the natural history of this insect and its relationship to the host plant (however, see Duges 1881, 1886).

More than 300 agave species occur in the southwestern United States and Mexico (Gentry 1972). Agave americana L. and some other large species are referred to as "century plants" because of the popularly held belief that they live for many (100) years, before producing a spectacular inflorescence. In reality, individuals grow vegetatively for 10 to 25 years before producing the tall stalked flower. Semelparity or "big bang" reproduction occurs when a plant expends such a large portion of its resources in one sexual reproductive event that it dies shortly thereafter. Agaves are semelparous. During vegetative growth, photosynthate accumulates in the bole or base of the plant. Up to 59 percent of this stored energy in Agave palmeri Engelmann is used to produce the inflorescence for sexual reproduction (Howell and Roth 1981).

Several aspects of S. acupunctatus biology seem to account for the weevil's role in agave decline. It is a multivoltine species whose adults bore into the bole of the plant, causing mechanical damage as well as consuming the plant's stored resources and it may be involved in symbiotic relationships with microorganisms that break down plant tissues. Most members of the subfamily (Rhynchophorinae) attack monocotyledonous plants almost exclusively and their larvae are always associated with plant tissue necrosis (Vaurie 1971). A fungus, Aspergillus niger van Tiegh, induces rotting in agaves that have been attacked by S. acupunctatus (Wallace and Diekmahns 1952, and Clinton and Peregrine 1963). Thus agaves must contend with microbial infection as well as the mechanical damage of insect herbivory.

S. acupunctatus is considered a pest because it creates conditions that cause cultivated and ornamental agaves to die before they bloom or can be harvested. There is a need to understand this complex ecology involving herbivore, microbial symbiotes/decomposers and host, before any effective management protocol can be developed. These relationships in natural stands of indigenous agaves are also of interest from an evolutionary perspective because of the plant's semelparous form of reproduction. The relationship between the agave weevil and wild native agaves

has not previously been investigated. Agave palmeri is common in, and endemic to, the foothills of mountain ranges in southern Arizona, and Agave americana var. expansa (Jacobi) Gentry (endemic to northeastern Mexico [Gentry 1972]) is widely cultivated as an ornamental in the urban areas of southern Arizona.

The agave weevil is common in both ecosystems. This study was undertaken to elucidate the natural history of S. acupunctatus and its associated microbes and to compare the ecological relationships of these organisms in ornamental and native agaves in southern Arizona.

Methods

Six roadside populations of wild Agave palmeri, all within a 160 km of Tucson, Arizona, were randomly selected for study. The following data were recorded for each plant: (1) plant size (in cm, estimated by length of two leaves arising from the middle of the rosette); (2) presence of S. acupunctatus (if present, densities, distribution on/in the plant, and developmental states represented); (3) condition of the plant, including presence of inflorescence (stalk), rotting tissue, tissue pH, general condition (i.e., healthy, wilting, chlorotic). Additional data on weevil activity were taken by examining the remains of 18 A. palmeri that had bloomed and died in the previous year.

Cultivated Agave americana were studied within a 1.5 km square residential area in Tucson. The same data were taken as for wild plants. In addition, a survey of homeowners provided information on the age of their cultivated plants, and on cultural practices (i.e., watering, fertilization, and use of pesticides). Other agave species and weevil/host associations in and around Tucson were noted.

The natural history of S. acupunctatus in cultivated and native agaves was observed from March through November, 1980. Frequencies of weevils on blooming and nonblooming plants of both species were compared with a contingency table to discern if adult beetles discriminate among plants' reproductive condition. The Pearson's correlation test was applied to these data to determine if the distribution of weevils was influenced by the ratio of blooming to nonblooming plants.

Necrotic and healthy plant tissues from both cultivated and native agaves were collected for laboratory studies. Plant tissues (necrotic and sound) and weevils were sampled in the laboratory for bacteria and fungi, using nonacidified and acidified yeast maltose agar (YM,AYM) (Starmer et al. 1976). Isolated bacteria and yeast samples were cultured on pectate agar to test for pectolytic activity. Yeasts cultured from rotting agaves were identified by W.T. Starmer (Syracuse University). Two water-stressed A. americana were

inoculated with Aspergillus niger to validate earlier reports that A. niger causes pathology in agave.

Results

Natural History and Colonization: Populations of Scyphophorus acupunctatus were observed on A. palmeri from the time that the plants bloomed in April, through September. During this time the weevils occurred on the leaf surfaces of blooming and nonblooming plants. Only one weevil was observed flying between nonblooming plants, but this and the presence of distinctive chewing marks (2-3 mm oval indentations) on the upper leaves of many plants that did not become colonized (infested with larvae) suggested that the weevils regularly "test" plants and find some to be unsuitable as reproductive hosts. A clear viscous acidic (pH 3-4) exudate was often secreted from feeding marks in healthy plant tissue. Weevils stopped feeding on healthy agaves when this material filled feeding excavations.

On suitable hosts, from 1 to 15 weevils were observed boring into the base of the flower stalk. Feeding marks were frequently found on the upper leaves of these plants, but colonization always occurred through the base of the flowering stalks. Colonizing adults were found boring deep into the bole of the plants, presumably to oviposit. Adult weevils fed on the bases of leaves and on bole tissues.

Many infested agaves contained all developmental stages of the weevil (early instar to adult), suggesting that the plants had been reinfested by residents or immigrants. Sisal fibers from the agave leaves were typically incorporated into the cocoons. Most cocoons were found in the bases of the leaves where sisal is readily available to larvae.

Although advanced rots in agave boles are inhabited by a community of many arthropod species (see Chapter 2), S. acupunctatus was the only species observed in five new rots and consistently present in all rots. This suggests that the weevil is the primary colonizer species and has a role in initiating a rot. S. acupunctatus was also found in native Agave schottii Engelm., and Agave parryi (Baker). Agave palmeri, A. parryi var. huachucensis, and A. schottii are all new host records for the weevil.

In Tucson, S. acupunctatus colonized cultivated A. americana from May to October. While adult weevil feeding marks were seen on the upper leaves of these plants, actual colonization occurred through the roots and between lower leaves. No entry holes were found in stalks of blooming A. americana. Pupae were found in the soil beneath the plants and their cocoons usually consisted of more soil than sisal. Thus S. acupunctatus patterns of host entry and cocoon construction varied with host species. Agave

americana var. variegata Trelease, A. lophantha Schiede, and A. vilmoriniana Berger were found to host weevils, and represent new ornamental host records.

Host plant Selection: Of the 155 Agave palmeri studied, 56 (36 percent) were blooming and 41 (73 percent) of those were infested with weevils. None of the 99 nonblooming plants was infested with larvae or boring adults, although adults were found on the leaf surfaces of eleven nonblooming individuals. The preference of weevils for blooming A. palmeri was significant statistically ($\chi^2=55.13$, $p<0.005$). Furthermore, 17 of the 18 dead postbloom plants examined were riddled with insect mines and most contained weevils, adult weevil remains, and/or pupal cases. It is therefore clear that most blooming A. palmeri become infested with Scyphophorus acupunctatus.

Because weevils prefer blooming plants, I assumed that they would occur on nonblooming plants only if few blooming plants were available. However, no relationship between ratio of blooming and nonblooming plants and of weevil occurrence on nonblooming plants was revealed ($r^2=0.06$,/n.s.), suggesting that many or all agaves in a population are examined by S. acupunctatus.

Of the 142 A. americana examined in Tucson, 10 percent ($n=14$) were infested with weevil larvae and were dying. None of these was blooming. Of four blooming plants

examined outside the sample, all were infested with S. acupunctatus. Although weevils may prefer blooming individuals of cultivated as well as of wild species, there was a major discrepancy in infestation of nonblooming plants of the two species (10 percent of nonblooming A. americana vs 0 percent of nonblooming A. palmeri).

Weevil host plant selection patterns were independent of the availability of a particular size class in the urban population of A. americana. Although large agaves were rare, S. acupunctatus colonized larger plants with a greater frequency than could be expected by chance alone ($P < 0.025$, $\chi^2 = 8.7$, $df = 2$). While these larger plants surely represented the amplest resources, the basis for their increased susceptibility is not known.

In more than 40 other instances (within the sample of 142 plants and additional observations), infested plants were adjacent to uninfested healthy conspecifics of similar size. This suggests differential susceptibility of individual plants. Two of the largest plants that died of agave decline were estimated to be 18 to 25 years old, and both were probably near flowering. In both cases, the

Supplemental watering, a cultural practice by homeowners at 20 residences, had no effect on Agave americana susceptibility to weevil infestation ($r^2 = 0.33$, n.s.). No homeowners applied fertilizer or insecticides to

their ornamental agaves. In the urban sample area, 11 of 20 residences landscaped with agaves were losing or had lost them within the preceding years. It is therefore clear that non-blooming urban agaves are regularly infested.

Microbial Activity: All weevil-invested agaves had rotten boles. In field observations and laboratory experiments (n=78 plants), the onset of agave decline began with weevil colonization. Weevils (adults and larvae) observed boring into plants were always surrounded by dark red, foul-smelling tissue; healthy white tissue had a fresh pungent odor. Where measured (n=10 rots) I found that rotting tissues consistently preceded larval excavations by one cm at most. This was true of two plants that had been colonized by weevils in the previous year. In both cases, roughly one-half of the bole was colonized by weevils and only that half contained decomposing tissue, while the other half was sound.

The ability of S. acupunctatus and its associated microbes to induce rotting was also demonstrated in the laboratory. All agave tissue samples (n=5) rotted when weevil larvae were allowed to feed on them; control tissue, not exposed to larvae, did not rot. An adult weevil that was starved for 30 days induced rotting when allowed to bore into a healthy plant.

Cultures from field-collected rot samples (n=15 plants)

yielded a variety of bacteria (not identified), an alga (Prototheca sp. Kruger), and fungi including: Kluyveromyces marxianus (Hansen) Van der Walt, Pichia amethionina var. amethionina, and Pichia nv.sp Hansen. Cryptococcaceae species included: Candida lusitanae van Uden and do Carmo-Sousa, C. valida (Leberle) van Uden and Buckley, and an undetermined species of Candida. Most rotten plants contained at least three yeast species. Yeasts seemed to predominate in early rots, which generally had a pH of from 3 to 4. Bacteria and mycelial fungi were more common in later stages when the pH was higher (>5). The AYM agar used to culture yeasts had a pH ranging from 4 to 5, close to that of newly attacked agaves. This pH precluded bacterial growth on the plates and may likewise have inhibited bacterial development in the plants. Stressed plants (n=2) inoculated with the fungus, Aspergillus niger, did not become infected.

Discussion

Wild Agave palmeri plants are defended against S. acupunctatus during the vegetative phase of their development. A. palmeri are, however, readily attacked once blooming is well under way. This relationship seems to be evolutionarily stable. The plant apparently invests in defensive substances to protect its vegetative parts and

photosynthate store until the onset of flowering and then this defense is relaxed when herbivory and microbial infection are no longer biologically relevant (after blooming is well under way) for the plant. S. acupunctatus is apparently a force that maintains the plant's defenses. By constantly testing nonblooming as well as blooming plants, the weevil selects well defended pre-blooming individuals.

Agaves produce high concentrations of saponins (Gentry 1982) which are toxic to many herbivorous insects. Applebaum and Birk (1979) report that saponin contents of several plant species including Saponaria officinales L. and Polemonium caeruleum L. diminish in underground storage organs during plant reproduction and increase in the reproductive structures. Saponin concentrations are known to change in developing agaves (Dawidar and Fayez 1961). Thus shunting of saponins among plant structures during development may occur in agaves and explain the plant bole's increased susceptibility to S. acupunctatus during reproduction.

Low pH appears to play an important role in plant defense against herbivores. Roever (1964) observed mortality of mining Agathymus spp. larvae (Lepidoptera: Megathymidae) in response to sapping out or the occurrence of acidic exudate in response to wounding. Our

results indicate that this wounding response deters colonization by S. acupunctatus and its associated microbes.

Nonblooming A. americana, particularly larger older individuals, were far more susceptible to herbivory by S. acupunctatus (and agave decline) than A. palmeri (10 percent vs 0 percent infestation rate respectively); this disparity may involve both natural differences and cultivation practices, specifically relaxed selection due to vegetative propagation.

Homeowner practices on ornamental agaves were not correlated with frequency or levels of infestation. However, I observed that A. americana was sometimes colonized through its roots. Perhaps this occurs because soil around landscape plants is less well compacted than in the pristine environment. Weevils also often entered boles of cultivated plants between the leaves rather than through the roots.

Perhaps relaxed selection due to domestication best explains the observed differential susceptibility and higher mortality in A. americana. Intense artificial selection for rapid growth, "showiness," and other desired characteristics can severely compromise a plant line's natural defenses (Pimentel 1976). Ornamental Agave americana is propagated vegetatively by nurserymen and homeowners alike. The "pups" (vegetative propagules that arise from the parent plant)

frequently repopulate urban landscapes after parent plants have died of agave decline.

Weevil larvae are consistently present in rotting agaves, and their associated microbes induce rotting of agave tissues. Although the nature of the weevil/microbe relationship is not fully understood, our data suggest at least a facultative symbiosis. Symbiotic relationships between microbes and rhynchophorid weevils have been reported (Musgrave and Miller 1956, Crawford et al. 1960, Graham 1967). Agaves are patchy in distribution (both temporally and spatially) so rot inducing microbes probably depend on S. acupunctatus for dispersal as well as physical entry into the host plant. S. acupunctatus may depend on the products of microbial activity to break down tissue (e.g. pectin) and synthesize various nutrients as occurs in other herbivores (Barras 1973, Wright et al. 1980, Hagen 1966, Johnson and O'Keefe 1981, Graham 1967). Our data suggest that microbial succession may track changes in pH. Yeasts were more tolerant of acidic conditions that existed at colonization, while later rots contained a higher proportion of bacteria and mycelial fungi. Suberkropp and Klug (1976) found a similar succession in decomposing leaf litter of woodland streams.

The disparate susceptibilities of these two agave species to S. acupunctatus and its complex of associated

microbial symbionts is in need of further investigation. Future studies designed to focus on the precise nature of weevil/microbe interactions as well as the mechanisms that enable A. palmeri to defend itself against this complex may contribute significantly to a general understanding of the evolution of plant-herbivore interactions.

CHAPTER 3

PATTERNS OF FAUNAL SUCCESSION IN AGAVE PALMERI

Introduction

Succession occurs at many levels within biological communities. At the community level, species of plants and animals are replaced as a community moves through seral stages. Within a community, succession takes place as groups of herbivores replace one another on a host plant. As a host plant undergoes its ontogeny a succession of habitats is provided for herbivores. Martin (1966) found successional patterns in the herbivore fauna associated with red pine. His study revealed that herbivore species composition changed dramatically as the trees mature. Waloff (1969) also found successional patterns among herbivores colonizing Scotch broom and again age was an important determinant of herbivore community structure. These studies demonstrate that successional replacement of herbivores takes place on individual host plants.

In community-wide succession, changes in plant species

predictably alter the composition of herbivore species (e.g. Chevin 1966). However, the mechanisms behind changes in the herbivore community of a single plant species represent a more subtle and neglected aspect of community ecology (Connell and Slatyer 1977). For example, why does aging in red pines result in a dramatic displacement of one herbivore group by another? Waloff (1968) investigated the factors driving insect succession on Scotch broom and found that lepidopteran, chrysomelid and curculionid stem miners colonized only green stems, while stem mining scolytids colonized only dead stems. When the chrysomelid beetle, Phytodecta, was forced to mine and breed in old stems rather than young preferred stems, its fecundity was significantly reduced (Waloff 1968). The differences between young and old stems as resources were not elucidated in Waloff's study, however. Apparently, herbivore community succession on a single plant species is the result of changing properties of host plant tissues, but few of these changes are understood for any plant species.

Agave palmeri Engelman is well suited to the study of insect succession with an emphasis on changes in the host and in the composition of herbivores that use it. This agave is a succulent perennial that grows vegetatively for 8 to 25 years (Gentry 1972), and then produces a large inflorescence, reproduces sexually, and dies ("big bang" or

semelparous reproduction, see Ricklefs 1973). The leaves and bole of A. palmeri are moist and starchy, the stalk is woody and the inflorescence produces large fleshy fruits. While the plant is structurally complex, not all of its resources are simultaneously available to herbivores. During the plant's vegetative growth phase, it accumulates a store of carbohydrates in the leaves and bole of its rosette. When the plant reproduces, the succulent leaves lose over half of their water and carbohydrates to the stalk and inflorescence causing a considerable change in resource quality for herbivores (Nobel 1977). The rosettes of many agave species have been found to contain high concentrations of saponins, which are transferred from the rosette to the developing inflorescence as the plant blooms (Dawidar and Fayez 1961) as may be the case for Agave palmeri. Saponins are toxic for many herbivores (Applebaum and Birk 1979), and may function to protect agaves from herbivores.

The purpose of this study was to survey the herbivore community associated with Agave palmeri in its vegetative and reproductive stages, and to document the bases for changes in community structure. Additionally, a complete list of the organisms reported to be associated with A. palmeri has been compiled from the literature.

Methods

Five Agave palmeri populations, all located on rocky rolling hills within 165 km of Tucson, Arizona, were examined in this study. Site 1 was located in the western foothills of the Huachuca Mountains, at an elevation of 1690 m, about 100 km southeast of Tucson. Forty-seven A. palmeri (6 blooming) were examined. Site 2 was located along state Highway 83, ca. 100 km south of Tucson at an elevation of 1400 m. Twenty-nine plants (9 blooming) were examined. Site 3 was also located along Hwy. 83, 50 km south of Tucson. Fifty-four plants (28 blooming) were examined. Site 4 was located ca. 30 km north of Tucson, on the Santa Catalina Hwy. at an elevation of 1540 m. Nine plants (3 blooming) were examined. Site 5 was located in the eastern foothills of the Santa Rita mountains, ca. 120 km southwest of Tucson, at an elevation of 1700 m. Sixteen plants (10 blooming) were examined.

Nonblooming and blooming plants in all populations were sampled in July and August of 1980. Sampling took place between 2 and 6 p.m. Plant leaves, boles and stalks of inflorescences were considered discrete habitats. The flower portion of the inflorescence was not sampled to avoid damaging developing flowers and seeds. Data taken included location of all arthropods on the plants and estimates of their relative densities using density classes as follows:

rare (<5 individuals), occasional (>5<15) and common (>15). Immature insects were reared in the laboratory for identification. The University of Arizona Entomology Department's collection and staff, as well as the relevant literature were consulted to identify specimens. The data collected from all populations were pooled for statistical purposes and to provide an overall qualitative description of the animal species found to be associated with the different plant life history stages. Jaccard's coefficient of community similarity (Southwood 1966) was used to compare similarity of species groups occurring in the leaves, boles and inflorescences of the plants. A computer literature search produced references on animals previously reported to be associated with A. palmeri.

Results

Forty-two species of arthropods and evidence of vertebrate herbivory were collected from 155 nonblooming and blooming agaves in this study. Seven herbivore species were collected from the leaves, 16 from rotting boles and 4 from the flower stalks (Table 1). There was no spatial overlap in species of herbivores between habitats as measured by Jaccard's coefficient (values for all habitat comparisons equalled zero).

The developmental changes which occur during an A.

Table 1. The arthropod fauna collected and reported from Agave palmeri and the density status of each.*

	Density class
1. Herbivores in and on the agave leaves:	
<u>Hymenarcys crassa</u> Uhler (Hemiptera:Pentatomidae)	1
<u>Prionosoma podopioides</u> Uhler (Hemiptera: Pentatomidae)	2
<u>Acanthocephala</u> sp. (Hemiptera:Coreidae)	2
<u>Agathymus</u> sp. (Lepidoptera:Megathymidae)	3
<u>Acmaeodera</u> sp. (Coleoptera:Buprestidae)	1
<u>Tettigoniidae</u> , <u>Acrididae</u> (Orthoptera)	2
Unknown pentatomid (Hemiptera)	2
2. Predators on the leaves:	
<u>Salticidae</u> , <u>Lycosidae</u> (Araneida)	1
<u>Scorpionida</u>	1
3. Herbivores and detritivores in boles:	
<u>Scyphophorus acupunctatus</u> Gyll. (Coleoptera: Curculionidae)	3
<u>Sphenophorus phoeniciensis</u> Chitt. (Coleoptera: Curculionidae)	1
<u>Metoponium candidum</u> Casey (Coleoptera: Tenebrionidae)	1
<u>M. papagonum</u> Casey	1
<u>Ulosonia marginata</u> LeConte (Coleoptera: Tenebrionidae)	1
<u>Carpophilus humeralis</u> (Fab.) (Coleoptera: Nitidulidae)	1
<u>C. dimidiatus</u> (Fab.) (Coleoptera:Nitidulidae)	1
<u>Ataenius hirsutus</u> Horn (Coleoptera:Scarabeidae)	1
<u>Ataenius</u> sp.	1
<u>Cotinus</u> sp. (Coleoptera:Scarabeidae)	1
<u>Hermetia comstockii</u> Williston (Diptera: Stratiomyidae)	3
<u>Volucella haagi</u> Jaennicke (Diptera:Syrphidae)	3
<u>Drosophila buskii</u> (Diptera:Drosophilidae)	1
<u>Drosophila</u> sp.	1
<u>Spongovostox apicedentatus</u> (Caud.) (Dermaptera:Labiidae)	2

Table 1, Continued

	Density class
<u>Euborellia annulipes</u> (Lucas) (Dermaptera: Labiduridae)	2
4. Predators and parasitoids in and on boles:	
<u>Dinocheirus arizonensis</u> (Pseudoscorpionida: Chernetidae)	1
<u>Parachelifer hubbardi</u> (Pseudoscorpionida: Cheliferidae)	1
<u>Hololepta yucateca</u> Marseul (Coleoptera: Histeridae)	2
<u>Pelosoma capillotum</u> LeConte (Coleoptera: Hydrophilidae)	1
<u>Polistes</u> sp. (Hymenoptera:Vespidae)	1
<u>Iphiaulax</u> sp. (Hymenoptera:Braconidae)	1
<u>Cleridae</u>	1
5. Herbivores in the stalks:	
<u>Peltophorus seminiveus</u> (LeConte) (Coleoptera: Curculionidae)	3
<u>Tragidion armatum armatum</u> LeConte (Coleoptera: Cerambycidae)	1
<u>Valenus inornatus</u> Casey (Coleoptera: Cerambycidae)	1
<u>Xylocopa</u> sp. (Hymenoptera:Xylocopidae)	1
6. Predators in the stalks:	
<u>Enoclerus zonatus</u> (Klug) (Coleoptera:Cleridae) (Powell 1975)	1

Table 1, Continued

	Density class
7. Herbivores in the inflorescence:	
<u>Peltophorus adustus</u> Casey (Coleoptera: Curculionidae) (Cicero, pers. comm.)	1
Coreidae (Hemiptera) (Gentry 1972)	1
Microlepidopterans (Lepidoptera) (S. Sutherland, pers. comm.)	
*see text for additional associations	
8. Additional species collected from agave with habits unknown:	
<u>Omalodes grossus</u> Marseul (Coleoptera: Histeridae)	1
<u>Carcinops gilensis</u> LeConte (Coleoptera: Histeridae)	1
<u>Geomysparinus</u> sp. (Coleoptera:Histeridae)	1
<u>Scydmaenus</u> sp. (Coleoptera:Scydmaenidae)	1
Numerous species of staphylinids (Coleoptera: Staphylinidae)	2

- * 1 = rare, <5 collected
 2 = occasional, >5<15 collected
 3 = common, >15 collected

palmeri's lifetime lead to the creation or degradation of the leaves, bole and stalk as habitats and it is these changes which lead to the successional faunal patterns we have observed (Table 2). In addition, leaf feeding species in particular seem to be temporally as well as spatially separated from the other herbivore groups, as no leaf feeding species were found on blooming plants.

Agave leaf fauna. Three of the seven herbivore species collected from A. palmeri leaves were sucking insects in the order Hemiptera (Table 1). A pentatomid, Hymenarcys crassa Uhler, was once seen copulating on A. palmeri leaves.

Prionosoma podopoides Uhler (Pentatomidae) and Acanthocephala sp. (Coreidae) were occasionally found on leaves. These hemipterans were typically found on flat, exposed leaf blades. Leaf-mining Agathymus spp. larvae (Lepidoptera: Megathymidae) were common in all agave populations examined except on Site 4. Up to four mines per leaf caused no obvious negative effects such as wilting or chlorosis of the leaves. According to Roever (1964), Agathymus spp. larvae suffered heavy mortality when agaves secreted a clear acidic exudate in response to wounding (see also Chapter 1). Adult buprestids, Acmaeodera sp. (Coleoptera), were found rarely at the bases of the leaves, as were various acridids and tettigoniids (Orthoptera). The orthopterans fed near the leaf bases and left long scraping

Table 2. Some actual and possible changes in morphology and physiology of Agave palmeri coincident with herbivore colonization.

Life history stage	Morphological/ physiological development	Herbivore response
1. Vegetative growth phase:	Carbohydrate and water concentrations in the leaves.	Leaf feeding.
2. Reproduction	A. Carbohydrate and water concentrations reduced by over 50 percent in leaves.	Leaf feeding discontinued.
	B. Saponins shunted from the bole.	Bole is colonized and rotted.
	C. Inflorescence stalk.	Stalk boring insects colonize.
	D. Flower production.	Pollination and herbivory of flowers and fruits.

marks. Predators of arthropods on the leaves occasionally included spiders (Salticidae and Lycosidae) and rarely scorpions. They were found near the bases of the leaves. Herbivores were not found on leaves of plants which had bloomed.

Agave bole fauna. When the agave produces its flower stalk, the bole of the plant is quickly colonized by a large variety of arthropods (Table 1). Agave boles were colonized initially by an agave weevil, Scyphophorus acupunctatus Gyllenhal (Curculionidae). The adult weevil bores into the bole to oviposit, at the same time infecting the plant with micro-organisms that decompose agave tissue. The weevil larvae fed within the bole and also spread microbes.

Following colonization by S. acupunctatus, the bole is rapidly colonized by other herbivores, as well as detritivores, predators and parasites, giving rise to a diverse ephemeral arthropod community (Table 1). The bole tissues decompose rapidly in the presence of the mining herbivores. Although S. acupunctatus was the only insect consistently found in rotting agave boles, larvae of the stratiomyid, Hermetia comstockii Williston, and the syrphid, Volucella haagi Jaennicke, were very common. One fly species or the other was nearly always present in large numbers, although they rarely co-occurred. In numbers and biomass, their larvae were more abundant in advanced rots

than those of S. acupunctatus. In one rotten bole 509 H. comstockii larvae were found and in another, 878 V. haagi larvae were found, while no more than 100 weevil larvae were ever collected from a single rotting bole. Although larvae of both fly species occurred in close proximity to S. acupunctatus in the boles, no antagonistic interactions were observed between them. Adult V. haagi have been collected from various Arizona crops (Butler and Werner 1957), but it is not known that larvae of this species occur in agricultural ecosystems. No information is available on alternative hosts for H. comstockii. Adult H. comstockii is an excellent mimic of Polistes spp. wasps (James 1960) and both the fly and wasp were commonly seen on and near rotting agaves.

Two earwig species, Spongovostox apicedentatus (Caud.) and Euborellia annulipes (Lucas), were common in rots. They are described as scavengers by Borror et al. (1976) and Langston and Powell (1975). However, according to Jackson (1964) both species eat insects in captivity. Spongovostox apicedentatus has been collected from rotting cacti including Cereus sp., Echinocactus sp. and Opuntia sp., as well as the liliaceous Yucca whipplei Torr. Euborellia annulipes has been found in garden plants and stored foods (Langston and Powell 1975). The coincident presence of most instars of these species suggests that they have multiple

generations in a single agave rot.

Other herbivore and detritivore species were found only rarely (Table 1). Three species of tenebrionid beetles collected are considered to be generalist feeders occupying habitats such as rotting wood and decaying vegetable matter (Glen et al. 1943). Nitidulid beetles, Carpophilus humeralis (Fab.) and C. dimidiatus (Fab.), have been collected from stored grains, ripe nuts and fruits (Connell 1975). A weevil, Sphenophorus phoeniciensis Chitt. (Curculionidae), has been collected from other monocots including grasses (Vaurie 1951). The scarab beetles (Scarabaeidae) are also considered to be generalists. Many species of staphylinid beetles (Staphylinidae) in a variety of sizes were collected. When more than one staphylinid species was collected from a given plant, they often differed in length by a millimeter or more. None of these was identified. Drosophila buskii Coquillett larvae were reared from agave rots and are known to colonize other plant rots as well (W. Heed, pers. comm.).

Ten species of predators and parasitoids of arthropods on and in the boles were collected. Hololepta yucateca Marseul, recorded as a predator of S. acupunctatus (Woodruff and Pierce 1973), was found in most rots. It has also been collected from Cereus sp., Echinocactus virescens Nuttall, Opuntia occidentalis Engelm. & Bigel., Ferocactus sp. and

from fruits and compost, where it preys on other arthropods. The braconid, Iphiaulax sp., was reared from S. acupunctatus, six adult Iphiaulax emerged from a single pupa. This wasp species was seen flying about rotting agaves. The pseudoscorpions, Parachelifer hubbardi (Banks) and Dinocheirus arizonensis (Banks) (Arachnida: Pseudoscorpionida), are known to be predators of dipteran larvae including Drosophila spp., and have been collected from various species of cacti, (D. Zeh, pers. comm.). Other predaceous species included Polistes sp. (Vespidae), a hydrophilid beetle, Pelosoma capillotum LeConte, and an unidentified clerid beetle (Cleridae) (Table 1).

The following beetles of unknown habits were all collected (rarely) from rots: the histerids, Omalodes grossus Marseul, Carcinops gilensis LeConte and Geomysparinus sp. (Histeridae), the scydmaenid, Scydmaenus sp. (Scydmaenidae) and Bitoma sp. (Colydiidae) (Table 1). We assume that the histerids are predators of larvae occurring in rots (Borror et al. 1976).

Agave flower stalk fauna. Four species of stem boring insects were collected from the woody Agave palmeri stalks (Table 1). The weevil, Peltophorus seminiveus (LeConte) (Curculionidae), was common in all 5 agave populations studied. Adults were found copulating on the leaves of rosettes and larvae were reared from agave stalks. Their

association with agaves was first reported by Kissinger (1964). Scyphophorus acupunctatus and P. seminiveus adults were found in close proximity on agave leaves. When disturbed, P. seminiveus moved very quickly while S. acupunctatus was extremely sluggish. Peltophorus seminiveus were never reared from the bole, while S. acupunctatus were never reared from stalks, indicating no niche overlap for larvae of the 2 weevil species.

The hymenopteran stem nester, Xylocopa sp. (Xylocopidae), was collected rarely from stalks. Occupied stalks typically had a row of chambers, each of which contained pollen and a pupa or larva. An adult xylocopid was observed defending a developing agave stalk, whose flowers were almost ready to bloom. Other xylocopids attempting to land on the stalk were attacked by the defender. The extent to which this territorial behavior may influence pollen resource utilization and pollination is not known.

Stem boring beetles, Tragidion armatum armatum LeConte and Valenus inornatus Casey (Cerambycidae), were found along with Peltophorus seminiveus in A. palmeri stalks at one collection site. Linsley (1962) reported T. armatum from yucca and agave stalks and Dillon (1956) reported V. inornatus from yucca stalks. Adults of T. armatum have also been seen feeding on the fruits of A. utahensis Engelm. (L.

Stevens, pers. comm.).

A predaceous clerid, Enoclerus zonatus (Klug) (Cleridae), has been reared from A. palmeri stalks (Powell 1975). Powell (1975) also reared E. zonatus adults from the fruits of Yucca schottii Engelm. and Nolina microcarpa Wats.

Agave inflorescence fauna. Most of the information presented on this group of species has been derived from the literature and personal communications (Table 1). Agave palmeri is alleged to be dependent on nectar feeding bats (Leptonycteris sanborni Hoffmeister and other species in that genus) for pollination (Howell and Roth 1981). It is visited by sphinx moths (Sphingidae) and solitary nectar-feeding bats (Choeronyctis mexicana Tschudi) which may also serve as pollinators (Howell and Roth 1981). Coreids (Hemiptera) feed on agave fruits and rodents rapidly collect seeds from the ground (Gentry 1972, Nobel 1977, Howell and Roth 1981). A weevil that breeds and mines in agave seed pods, Peltophorus adustus Casey (J. Cicero, personal communication), was collected rarely. Several species of microlepidopterans have been observed in seed pods (S. Sutherland, personal communication), and bighorn sheep (Ovis canadensis var. mexicanus Merriam) and deer (Odocoileus spp.) are known to forage on the green stalks and inflorescences (Gentry 1972). At Site 1, inflorescences were removed from over 50 percent of blooming plants by

vertebrate herbivores, illustrating how important herbivory by vertebrates can be to this plant.

In summary, thirty-two of 45 species (70 percent) were observed only rarely, that is, only 5 or fewer individuals per species were collected on or in agaves during the study. Conversely, 5 species (11 percent) were commonly encountered (Table 1). These patterns indicate that many of these species are generalists (or accidentals) while a smaller number of herbivores are consistently associated with and dependent on this plant species.

Discussion

A succession of herbivore groups colonize A. palmeri as it passes from one developmental stage to another. Leaves, boles, stalks, and inflorescences represent discrete habitats and each is utilized by a distinct faunal assemblage (Table 2). The leaves of vegetatively growing agaves were fed upon by seven herbivore species until blooming commenced. Upon blooming, water and energy reserves of the leaves are shunted to the inflorescence and the leaves, as resources, literally dry up (Nobel 1977). Consequently, no leaf herbivores were found after blooming began. While the physiological changes in the agave bole that permit colonization are not known, they are clearly correlated with flowering. I determined that wild,

nonblooming A. palmeri were never successfully colonized by S. acupunctatus, although the weevils did land on many nonblooming plants and apparently evaluated them by tasting leaf tissue. Only after blooming is A. palmeri colonized by the weevil. The basis for this may involve a change in allocation of chemical defense; specifically, saponins may be translocated from the rosette to the inflorescence during the plant's reproduction as found by Dawidar and Fayez (1961) for some agave species. The bole is apparently unavailable as a resource to herbivores until blooming commences by which time the leaf fauna has abandoned the plant because of leaf desiccation.

The agave bole was by far the richest habitat in the plant, as evidenced by the great diversity and biomass of arthropods it supported. Colonization of the bole by many of these species appears to depend on the presence of weevil larvae as well as changes in plant physiology and thus represents a successional process in itself. Weevil larvae were adept at rapidly boring through dense plant tissue thereby spreading microorganisms and plant tissue necrosis as they mined (Chapter 1).

The stalk and flowers of the inflorescence also appear to be discrete habits, although a thorough survey of the floral fauna has not been conducted. The two habitats may be sufficiently distinct that a shift in specialization from

one to the other permitted a speciation event, in the case of the congeners, Peltophorus seminiveus (a stalk borer) and P. adjustus (a fruit feeder). The stalk was colonized only by insects capable of boring through dense fibrous tissue.

I found over 40 animal species, including 27 herbivores, to be associated with A. palmeri through its life history. This is a large list. Many of these associations are perhaps inconsequential evolutionarily, while others have probably affected many of the life history traits which A. palmeri exhibits.

This survey suggests that the plants' structural and physiological ontogeny influences the composition and diversity of its herbivores and their colonization patterns. Moran (1980), Lawton and Price (1979) and others, have found that the architectural complexity of a host plant contributes significantly to the number of species of herbivores it can support. Agave palmeri offers herbivores at least 4 distinct habitats: leaves, bole, stalk and inflorescence, and each of these is colonized by a distinct group of herbivores. Physiological changes within the plant, including transfer of resources and defense compounds, may represent mechanisms which adaptively influence both the diversity of herbivores present at any time and the overall diversity of herbivores associated with Agave palmeri. Future studies of this system might well be

designed to reveal the physiological changes these plants undergo as they develop, in an effort to account for changes in their herbivore community structure.

CHAPTER 4

SUMMARY

Perhaps the most striking finding of this study was the large number of herbivores associated with agaves. Although this plant is relatively simple in architectural structure, and complex in its biochemistry, it is clear that many animals ranging from flies to big horn sheep have come to use its leaves, bole, stalk, flowers and fruit for food or refuge. It is important to recognize that so many different herbivores may be affecting the direction of a plant species' evolution.

The key to the agave's ability to survive these herbivores appears to lie in its defensive biochemistry which may have been selected for by one of its primary natural enemies, the agave weevil, Scyphophorus acupunctatus. The agave maintains a very low tissue pH prior to reproduction, and many species have large concentrations of saponins which have been shown to be toxic against many herbivores. Agave defense breaks down upon reproducing and most Agave palmeri are then colonized--

leading to a potentially evolutionarily stable system.

The agave weevil is a critical precursor to the colonization of agave boles by numerous species of herbivores and detritivores. The weevil penetrates agave tissues with rot--inducing microorganisms which probably render the plant a more nutritious resource for all.

The agave and its associated herbivores offer many insights into the nature of plant-herbivore interactions, and consequently, are worthy of further study. Future research should include a thorough examination of agave defensive chemistry and effects of weevil colonization on agave fitness.

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