Variation in the costs and benefits of mutualism: the interaction between yuccas and yucca moths

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Summary. Yucca moths are both obligate pollinators and obligate seed predators of yuccas. I measured the costs and net benefits per fruit arising for eight species of yuccas from their interaction with the yucca moth *Tegeticula yuccasella*. Yucca moths decrease the production of viable seeds as a result of oviposition by adults and feeding by larvae. Oviposition through the ovary wall caused 2.3–28.6% of ovules per locule to fail to develop, leaving fruit with constrictions, and overall, 0.6–6.6% of ovules per fruit were lost to oviposition by yucca moths. Individual yucca moth larvae ate 18.0–43.6% of the ovules in a locule. However, because of the number of larvae per fruit and the proportion of viable seeds, yucca moth larvae consumed only 0.0–13.6% of potentially viable ovules per fruit. Given both oviposition and feeding effects, yucca moths decreased viable seed production by 0.6–19.5%. The ratio of costs to (gross) benefits varied from 0% to 30%, indicating that up to 30% of the benefits available to yuccas are subsequently lost to yucca moths. The costs are both lower and more variable than in a similar pollinator-seed predator mutualism involving figs and fig wasps.

There were differences between species of yuccas in the costs of associating with yucca moths. Yuccas with baccate fruit experienced lower costs than species with capsular fruit. There were also differences in costs between populations within species and high variation in costs between fruit within populations. High variability was the result of no yucca moth larvae being present in over 50% of the fruit in some populations, while other fruit produced up to 24 larvae. I present hypotheses explaining both the absence and high numbers of larvae per fruit.

Key words: Mutualism – Yucca – Yucca Moths – Gest-benefit analysis – Seed predation

An important problem in the study of dynamics and evolution of mutualism is how gross costs and benefits and net benefits vary and are regulated (Addicott 1979, 1981, 1984, 1985a, 1985b; Boucher et al. 1982; Dean 1983; Howe 1984; Keeler 1981). Study of this variation is hampered by two practical problems. First, it is difficult make direct comparisons of gross costs and benefits, because they usually arise in different biological currencies. For example, a major cost for many animal-pollinated plants is the production of nectar (Southwick 1984), while the major benefit is the transfer of pollen leading to seed development. Similar problems exist with other mutualisms, including ant-plant systems and coelenterate-algal symbioses. Second, it is difficult to determine sources of costs and benefits in mutualisms involving a number of species, particularly where the number, kind and interdependence of mutualists may vary in time and space. In many pollination systems plants are associated with a whole suite of pollinators and pollinators with whole suites of plants. In ant-homopteran mutualisms, homopterans must interact with different species of ants, given the mosaic distribution of ant species.

There are relatively few mutualisms in which costs and benefits can be easily compared and in which there is also a small and consistent group of interacting species. Obvious examples are those systems in which a mutualist enhances seed production of a plant through one effect and diminishes seed production with another effect (e.g. Janzen 1979; Louda 1982). The interaction between yucca moths (*Tegeticula* spp., Prodoxinae, Incurvariidae) and yuccas (*Yucca* spp., Agavaceae) is one such system. Like fig wasps for figs, yucca moths are both obligate pollinators and obligate seed predators of yuccas (Powell and Mackie 1966; Riley 1892), and therefore most costs and benefits for yuccas are measurable in the same biological variable, seeds. The structure of this pollination-seed predation mutualism is also very simple. Two yuccas, *Y. whipplei* Torr. and *Y. brevifolia* Engelm., are each pollinated by their own species of moth, *T. maculata* (Riley) and *T. synthetica* (Riley), respectively, and with the exception of *Y. schottii* Engelm., each of the 20–30 other species of yuccas is apparently only pollinated by *T. yuccasella* Riley) (Davis 1967; McKelvey 1938, 1947; Webber 1953; but see below).

In this paper I describe and compare the costs and net benefits to eight species of yuccas interacting with *T. yuccasella*. The purpose of this study was to identify patterns, if any, in the interactions among yuccas and yucca moths. Are there differences between species or between populations within species in the interaction between yucca moth and yucca, and if so, what factors are associated with the differences? How variable are the number of yucca moth larvae and net seed production per fruit within populations of yuccas?

Methods

Yuccas and yucca moths

In July and August 1980, I collected a total of 690 mature fruit from eight species of yuccas in Arizona, Colorado, Montana, New Mexico and Utah, U.S.A.: *Y. schottii* Engelm., *Y. arizonica* McKelvey, *Y. baccata* Torr., *Y. glauca* Nutt., *Y. baileyi* Woot. & Standl., *Y. angustissima* Engelm., *Y. kanabensis* McKelvey, and *Y. elata* Engelm. The first

three species belong to the Sarcocarpa section of the genus *Yucca*, the fruit of which are large, fleshy and indehiscent. I will refer to these as baccate species. The last five species belong to the Chaenocarpa section. Their fruit are capsular and dehiscent, and I will refer to them as capsular species. I also collected fruit from *Y. brevifolia* Engelm., but since it is pollinated by *T. synthetica* rather than *T. yuccasella*, I have excluded it from the analysis. There are five other yuccas within the region where I collected: *Y. whipplei* Torr., *Y. schidigera* Roezel, *Y. neomexicana* Woot. & Standl, *Y. gilbertiana* (Trel.), and *Y. torreyi* Shafer. Either these species did not bloom and set fruit in 1980, or I did not encounter them.

Given the intergradation between species of yuccas in many regions of the southwest (McKelvey 1938, 1947; Webber 1953; Cronquist et al. 1977), assignment of populations to a particular taxon can be difficult. Populations in central Arizona, that are apparently hybrids between *Y. angustissima* and *Y. elata*, are particularly confusing. I have assigned them to *Y. elata*, based upon fruit shape, oviposition patterns, and branching of inflorescences. The yuccas near Kanab, Utah also present a problem. Some authors consider them as a variant of *Y. angustissima* (e.g. Cronquist et al. 1977). However, based upon fruit and inflorescence characters, I place these plants close to *Y. baileyi*. In this paper I use the name *Y. kanabensis* (McKelvey 1947). Because of the confusing state of taxonomy of the genus *Yucca*, I present precise collection localities in Appendix 1. I grouped collection sites into regional populations (see Appendix 1). Until the population structure of *T. yuccasella* is studied, designations of populations will remain arbitrary.

All eight yuccas in this study are pollinated by *T. yuccasella*. However, there is some question about the homogeneity of the taxon *T. yuccasella* (Davis 1967; Miles 1983). Until the taxonomic status of these variants is clarified, it is appropriate to refer to the yucca moths in this study as *T. yuccasella*.

Procedures

Each fruit was dissected, and the numbers of viable, inviable, eaten and uneaten seeds, and the number of yucca moth larvae per locule counted. Viable seeds are dark, usually black, while inviable seeds have white seed coats and lack endosperm. For some analyses I excluded those fruit for which I could not determine whether seeds were damaged by yucca moth larvae or by other insect seed predators. Locules were classified as being constricted or unconstricted.

Data were analyzed by one-way non-parametric ANOVA with nesting, and two-way non-parametric ANOVA, using the Kruskal-Wallis test. Koch (1970) and Scheirer (1976) provide examples of the extension of the Kruskal-Wallis test to complex ANOVA designs, and they provide confirmation that tabled probability levels are appropriate. Mariscuilo and McSweeny (1977) discuss partitioning the Kruskal-Wallis test statistic, as well as procedures for planned comparisons. I made planned comparisons between baccate and capsular species and pairwise comparisons between species within each group. Other analyses involved the use of 2-way contingency tables to test for heterogeneity, and a multi-sample sign test (Mariscuilo and McSweeny 1977).

Results

Net seed production

The total number of ovules per fruit varied between ($H_7 = 291.0$, $P < 0.001$) and within ($H_{17} = 96.9$, $P < 0.001$) species of yuccas (see Tables 1 B, 2 B). Species with baccate fruit (*Y. schottii, Y. arizonica* and *Y. baccata*) had fewer ovules than species with capsular fruit (*Y. glauca, Y. baileyi, Y. angustissima, Y. kanabensis* and *Y. elata*). Species with thick-walled, capsular fruit (*Y. baileyi* and *Y. kanabensis*) had more ovules than species with thin-walled, capsular fruit, particularly *Y. angustissima*. There was also significant variation between populations within *Y. baccata, Y. glauca, Y. angustissima,* and *Y. elata*.

Net seed production in yuccas is measurable either as the absolute number or proportion of seeds that are viable and escape predation from yucca moth larvae. Absolute net seed production differed between species ($H_7 = 91.8$, $P < 0.001$) and between populations within species ($H_{17} = 154.3$, $P < 0.001$) (Tables 1 C, 2 C). The number of viable, uneaten seeds was lower in baccate species than capsular species, while *Y. kanabensis* and *Y. elata* produced more viable, uneaten seeds than did the other three capsular species. These differences existed despite significant variation between populations of *Y. baccata, Y. glauca,* and *Y. elata*.

A better comparative measure of the net benefits of the interaction between yuccas and yucca moths is proportional net seed production per fruit: the ratio of the number of viable, uneaten seeds to the number of ovules. Values per species ranged from 0.36 to 0.60 (Table 1 D), but were not significantly different ($H_7 = 13.5$, $P = 0.06$). However, there were differences between populations within species ($H_{17} = 142.7$, $P < 0.001$), particularly between populations of *Y. baccata, Y. glauca,* and *Y. elata*. Values per population ranged from 0.36 to 0.81 for *Y. glauca* and from 0.23 to 0.73 for populations of *Y. elata* (Table 2 D). There was also high variation between fruit within populations. For example, the range for *Y. baccata* was from 0.051 to 0.901, and in both *Y. glauca* and *Y. elata* there were fruit in which proportional net seed production was zero. A pattern typical of this variation is shown for *Y. baccata* in Fig. 1.

Effects of oviposition on seed production

Net seed production is a function of both the proportion of ovules which do not produce viable seeds, and the proportion of viable seeds which are eaten by yucca moth larvae. There were significant differences both between species ($H_7 = 47.3$, $P < 0.001$) and between populations within species ($H_{17} = 118.1$, $P < 0.001$) in the proportion of inviable ovules (Tables 1 E, 2 E). Values were high for *Y. angustissima* compared to *Y. glauca, Y. kanabensis,* and *Y. elata*. However, baccate species did not differ from capsular species. There were also significant differences between populations of *Y. schottii, Y. glauca* and *Y. elata*.

Three factors contribute to seed inviability. First, adult yucca moths could transfer insufficient pollen for fertilization of all ovules within an ovary, or they could transfer pollen of low quality. Second, fertilized ovules may abort because of insufficient resources for seed development. Third, insertion of a yucca moth's ovipositor through the locular wall into the locular cavity may damage ovules or interfere with ovule development, leading to constriction

Table 1. Ovule numbers, net seed production, and components of decreased seed production caused by *T. yuccasella* adults and larvae in eight species of yuccas. Sample size (column A) applies to data in columns (B), (E), (F), and (G). Sample size in column (L) applies to columns (L), (C), (D), (I), and (K). Sample size in column (H) applies to columns (H) and (N)

Species	(A) n	(B) Mean # Ovules per Fruit	(C) Mean # Uneaten, Viable Seeds per Fruit	(D) Mean # Uneaten, Viable Seeds per Ovule per Fruit	(E) Mean # Inviable Seeds per Ovule per Fruit	(F) Mean # Constricted Locules per Fruit	(G) Proportion of Fruit Lacking Constrictions	(H) Mean Difference per Fruit between Constricted and Unconstricted Locules in the # Inviable Seeds per Ovule per Locule (n)	(I) Mean # Eaten, Viable Seeds per Viable Seed per Fruit	(J) Cost of T.y. per Ovule per Fruit	(K) Mean # T.y. Larvae per Fruit	(L) Proportion of Fruit Lacking T.y. Larvae (n)	(M) Maximum # T.y. Larvae per Fruit	(N) Proportion of Fruit with more Inviable Seeds in Constricted Locules (n)
Y. schottii	42	150.0	89.4	0.588	0.305	4.2	0.095	0.055 (26)	0.107	0.145	1.9	0.500 (42)	18	0.731 (26)
Y. arizonica	9	220.1	131.0	0.604	0.336	1.6	0.444	0.023 (5)	0.000	0.006	0.0	0.800 (5)	0	0.600 (5)
Y. baccata	108	196.9	116.1	0.589	0.391	1.9	0.444	0.184 (40)	0.006	0.064	1.5	0.697 (99)	20	0.875 (40)
Y. glauca	124	291.3	137.9	0.482	0.356	3.5	0.145	0.114 (67)	0.120	0.186	3.9	0.295 (95)	19	0.881 (67)
Y. baileyi	14	352.0	139.0	0.362	0.457	2.5	0.429	−0.06 (5)	0.136	0.109	9.2	0.200 (5)	13	0.400 (5)
Y. angustissima	28	285.8	126.0	0.425	0.457	5.0	0.100	0.058 (13)	0.147	0.195	3.3	0.364 (22)	12	0.538 (13)
Y. kanabensis	54	347.9	200.9	0.585	0.293	3.2	0.111	0.124 (42)	0.124	0.190	4.6	0.135 (52)	24	0.857 (42)
Y. elata	250	316.7	179.0	0.567	0.288	0.9	0.636	0.166 (83)	0.138	0.162	2.9	0.333 (246)	23	0.964 (83)

Table 2. Ovule numbers, net seed production, and components of decreased seed production caused by *T. yuccasella* adults and larvae in twenty five populations representing eight species of yuccas. Sample size (column A) applies to data in columns (B), (E), (F), and (G). Sample size in column (L) applies to columns (L), (C), (D), (I), and (K). Sample size in column (H) applies only to column (H)

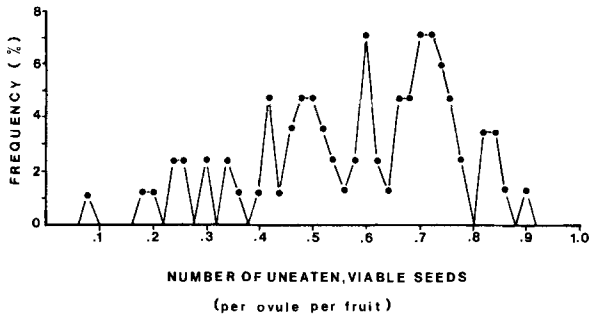| Species	Population	(A) n	(B) Mean # Ovules per Fruit	(C) Mean # Uneaten, Viable Seeds per Fruit	(D) Mean # Uneaten, Viable Seeds per Ovule per Fruit	(E) Mean # Inviable Seeds per Ovule per Fruit	(F) Mean # Constricted Locules per Fruit	(G) Proportion of Fruit Lacking Constrictions	(H) Mean Difference per Fruit between Constricted and Unconstricted Locules in the # Inviable Seeds per Ovule per Locule (n)	(I) Mean # Eaten, Viable Seeds per Viable Seed per Fruit	(J) Cost of T.y. per Ovule per Fruit	(K) Mean # T.y. Larvae per Fruit	(L) Proportion of Fruit Lacking T.y. Larvae (n)	(M) Maximum # T.y. Larvae per Fruit
Y. schottii	Bisbee	4	138.2	87.0	0.629	0.371	5.2	0.000	0.049 (3)	0.000	0.042	0.0	1.00 (4)	0
	Nogales	8	123.1	53.1	0.451	0.547	3.3	0.125	0.037 (6)	0.018	0.032	0.1	0.875 (8)	10
	Portal	30	158.8	99.4	0.619	0.231	4.3	0.100	0.063 (17)	0.149	0.194	2.6	0.333 (30)	18
Y. arizonica	Nogales	9	220.1	131.0	0.604	0.336	1.6	0.444	0.023 (5)	0.000	0.006	0.0	0.800 (5)	0
Y. baccata	Peach Springs	24	145.9	68.0	0.462	0.531	3.6	0.125	0.100 (11)	0.000	0.060	0.1	0.958 (24)	3
	Gateway	35	205.4	132.8	0.664	0.347	0.6	0.743	0.323 (8)	0.014	0.046	2.6	0.613 (31)	20
	Kanab	28	236.8	141.2	0.615	0.370	2.2	0.321	0.184 (13)	0.008	0.075	1.8	0.536 (28)	9
	Moab	21	182.9	115.2	0.609	0.345	1.8	0.476	0.163 (8)	0.002	0.050	1.0	0.750 (16)	5
Y. glauca	Gunnison	31	260.0	93.8	0.363	0.458	5.1	0.032	0.121 (10)	0.161	0.263	4.1	0.226 (31)	11
	Poncha Springs	37	242.0	104.2	0.443	0.397	4.2	0.108	0.107 (20)	0.072	0.146	3.8	0.437 (16)	16
	Wolf Creek	40	349.0	167.7	0.487	0.325	2.1	0.300	0.098 (22)	0.197	0.231	5.6	0.187 (32)	19
	Clines Corners	16	321.5	259.6	0.813	0.161	2.1	0.063	0.140 (15)	0.025	0.074	0.7	0.500 (16)	2
Y. baileyi	Page	14	352.0	139.0	0.362	0.457	2.5	0.429	-0.06 (5)	0.136	0.109	7.4	0.200 (5)	13
Y. angustissima	Peach Springs	11	332.4	138.8	0.417	0.446	4.4	0.000	0.100 (7)	0.154	0.227	4.6	0.167 (6)	12
	Gateway	17	255.6	111.6	0.434	0.463	5.4	0.000	0.010 (6)	0.139	0.148	2.3	0.437 (16)	5
Y. kanabensis	Kanab	38	350.3	197.0	0.573	0.281	2.8	0.158	0.107 (27)	0.143	0.192	5.1	0.111 (36)	24
	Rockville	16	342.4	212.3	0.621	0.321	4.0	0.000	0.154 (15)	0.067	0.169	3.3	0.187 (16)	6
Y. elata	Cottonwood	48	312.2	170.7	0.550	0.375	1.4	0.604	0.122 (15)	0.074	0.102	1.2	0.396 (48)	4
	Sonoita	28	311.2	118.2	0.382	0.312	0.6	0.821	0.173 (3)	0.307	0.347	7.9	0.148 (27)	23
	Portal	12	370.8	194.0	0.526	0.348	0.1	0.833	-0.02 (2)	0.125	0.125	2.7	0.500 (12)	13
	Prescott	24	319.7	72.6	0.237	0.409	0.9	0.583	0.130 (9)	0.350	0.369	7.9	0.045 (22)	22
	Sedona	30	293.0	186.3	0.638	0.255	0.7	0.733	0.102 (8)	0.103	0.114	1.6	0.433 (30)	7
	Wickenburg	28	303.9	199.0	0.656	0.227	0.2	0.929	0.286 (2)	0.111	0.120	1.4	0.393 (28)	4
	Alamagordo	36	333.1	232.6	0.681	0.236	1.5	0.361	0.160 (22)	0.080	0.112	2.1	0.229 (35)	5
	Deming	44	319.7	235.0	0.738	0.198	1.0	0.500	0.245 (22)	0.062	0.102	1.2	0.455 (44)	7

Fig. 1. Percentage frequency distribution of proportional net seed production per fruit ($n=99$) for *Y. baccata* showing high variation between fruit

of the mature fruit at the site(s) where oviposition occurred (Riley 1892).

With the present data set I can only assess the effect of oviposition on seed production. The average number of constricted locules varied between species ($H_7 = 160.2$, $P < 0.001$) and between populations within species ($H_{17} = 71.3$, $P < 0.001$) (Tables 1F, 2F). These differences were due primarily to the proportion of fruit that lacked any constrictions (Table 1G) ($X_7^2 = 147.3$, $P < 0.001$). The fruit of *Y. angustissima* were usually constricted while few fruit of *Y. elata* were constricted. Variation between populations of *Y. elata* was particularly obvious. For example, 92.5% were unconstricted in the Wickenburg population, but only 36.1% in the Alamagordo population.

Where constricted and unconstricted locules occur on the same fruit, I can assess the importance of yucca moth oviposition *per se* in the decreasing net viable seed production. To assess the qualitative effect of oviposition on seed inviability, I classified fruit into two categories: fruit in which constricted locules had either a smaller or larger proportion of inviable seeds than locules without constrictions. Using the data of Table 1N, I conducted a multi-sample sign test, which showed that constricted locules have a greater proportion of inviable seeds per locule ($X_7^2 = 143.7$, $P < 0.001$).

To assess the quantitative effect of oviposition on seed viability, I subtracted the proportion of inviable seeds in unconstricted locules from the proportion of inviable seeds in constricted locules within individual fruit. I then subjected these values to a 1-way Kruskal-Wallis ANOVA with nesting. There were differences between species ($H_7 = 20.7$, $P < 0.01$) and between populations within species ($H_{17} = 31.1$, $P < 0.05$) (see Tables 1G, 2G). The effect of constrictions on seed inviability is greatest in *Y. baccata* and *Y. elata*, with over 15% of ovules per constricted locule being affected.

Seed consumption and net costs

The effects (if any) of insufficient pollen transfer, insufficient resources, and yucca moth oviposition on seed inviability will have occurred prior to yucca moth larvae consuming any significant number of seeds. Therefore, the effect of yucca moth larvae on net seed production should be measured by the number of potentially viable seeds eaten per ovule per fruit (Tables 1I, 2I). There were significant differences between species ($H_7 = 71.4$, $P < 0.001$) and between populations within species ($H_{17} = 98.9$, $P < 0.001$). Proportional consumption of viable seeds was lower in bac-

cate than capsular species, but there were no differences between species within either group. There was significant variation between populations within species for *Y. schottii*, *Y. glauca*, and *Y. elata*. Consumption of viable seeds was unusually high in the Sonoita and Prescott populations of *Y. elata* and low in the Clines Corners population of *Y. glauca*.

I can estimate the net cost per fruit for yuccas of associating with yucca moths by combining the effects of oviposition and seed consumption. I computed the cost of oviposition as the decrease in seed viability per locule (Tables 1H, 2H) times the proportion of locules constricted, which is the number of constricted locules per fruit (Tables 1F, 2F) divided by six. I added the result to proportional seed consumption (Tables 1I, 2I) to obtain net cost (Tables 1J, 2J). With the exception of one population of *Y. schottii*, baccate species lost less than 10% of their ovules to yucca moths. Capsular species averaged 10–20% loss, but losses were as high as 36.9% in some populations.

Seed consumption per larva

Two factors affect the proportion of viable seeds destroyed by yucca moth larvae: the total number of viable seeds eaten per larva, and the number of larvae per fruit. Data on seed consumption per yucca moth larva were obtained where feeding in one or more adjacent locules could be ascribed unequivocally to just one or two larvae. For feeding zones with a single larva feeding in a single locule, the number of seeds consumed varied from 7.2 in *Y. baccata* and *Y. schottii* to 23.6 in *Y. elata* (Table 3B), while the proportion of the ovules (viable or inviable) consumed per larva per locule ranged from 0.18 in *Y. baccata* to 0.43 in *Y. elata* (Table 3A). In general, small numbers and proportions of seeds of baccate species were consumed relative to capsular species. The only exception to this pattern was *Y. kanabensis*, which had relatively large seeds for a capsular species. An approximate measure of seed size was obtained by dividing the number of seeds per locule by fruit length. Regression of log of the number of seeds eaten on log of seed size was highly significant ($b = -0.892$, $r^2 = 0.453$, $n = 317$, $P < 0.001$). Thus seed size is a good predictor of seed consumption for *T. yuccasella*.
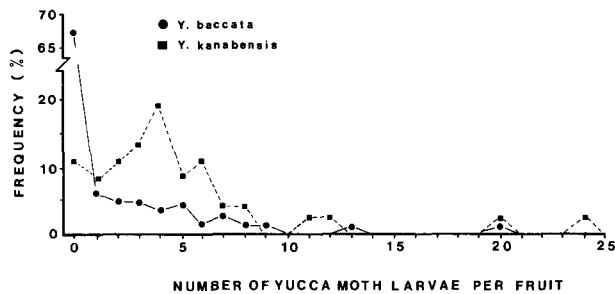
A 2-way Kruskal-Wallis ANOVA for the number of seeds consumed per larvae (Table 3B, 3C) shows that there were significant differences between *T. yuccasella* feeding in different species of yuccas ($H_5 = 44.9$, $P < 0.001$), and that there was a small, but consistent increase in the number of seeds eaten when a larva crosses over to feed in more than one locule ($H_1 = 5.24$, $P < 0.05$). There was no interaction between species and crossovers ($H_5 = 3.97$, NS). In general, only about 10% of all larvae fed in more than one locule. There was no increase in the number of seeds eaten per larva when 2 larvae fed simultaneously in the same locule (Table 3B, 3D) ($H_1 = 0.25$, NS).

Number of larvae per fruit

The second component affecting the proportion of viable seeds consumed per fruit is the number of yucca moth larvae feeding per fruit. The mean number of larvae per fruit (Tables 1K, 2K) differed between species ($H_7 = 58.9$, $P < 0.001$), with baccate species producing fewer yucca moth larvae, and *Y. elata* producing fewer larvae than other cap-

Table 3. Seed consumption by individual *T. yuccasella* larvae in six species of yuccas

Species	(A) Mean Proportion of Seeds Eaten per Locule, 1 Larva Present (n)	(B) Mean # Seeds Eaten by 1 Larva Feeding in 1 Locule (n)	(C) Mean # Seeds Eaten by 1 Larva Feeding in 2 Locules (n)	(D) Mean # Seeds Eaten per Larva by 2 Larvae Feeding in 1 Locule (n)
Y. schottii	0.247 (13)	7.2 (12)	19.0 (1)	
Y. baccata	0.180 (40)	7.2 (36)	11.0 (4)	6.7 (10)
Y. glauca	0.344 (53)	21.1 (40)	20.7 (13)	18.3 (7)
Y. angustissima	0.301 (13)	16.5 (9)	17.5 (4)	
Y. kanabensis	0.213 (56)	12.3 (53)	17.3 (3)	13.7 (4)
Y. elata	0.436 (143)	23.6 (125)	30.7 (38)	18.6 (17)

Fig. 2. Percentage frequency distribution of the number of yucca moth larvae per fruit for *Y. baccata* (*n* = 99) and *Y. kanabensis* (*n* = 52)

sular species. There was also significant variation between populations within species ($H_{17} = 80.7$, $P < 0.001$). The Clines Corners population of *Y. glauca* had few larvae, and the Sonoita and Prescott populations of *Y. elata* had many larvae.

The most striking features of the data on larvae per fruit, are that a very high proportion of fruit did not produce any yucca moth larvae (Tables 1 L, 2 L), and the high number of larvae in some fruit (Tables 1 M, 2 M). Analysis of the contingency table of number of fruit with or without yucca moth larvae against species shows highly significant heterogeneity ($X_7^2 = 66.9$, $P < 0.001$). Baccate and capsular species appear to be different, as over one half of baccate fruit produce no larvae. There were five populations of *Y. elata* in which over 39% of fruit lacked larvae. The maximum number of larvae per fruit shows the wide variation that occurred within populations, as many populations had fruit with more than 20 larvae. Representative patterns of the distribution of numbers of larvae per fruit are shown for *Y. baccata* and *Y. kanabensis* in Fig. 2.

Discussion

My results should be compared with Janzen (1979), who studied five species of *Ficus* and their agaonid wasps in Santa Rosa National Park, Costa Rica, and with Keeley et al. (1984), who studied nine species of *Yucca* from California to Texas. Janzen (1979) found that the average proportion of ovules damaged by wasps varied from 41% to 77% per population. These values are much higher than either Keeley et al. (1984) or I found in yuccas. The proportion of seeds per fruit destroyed by feeding of *T. yuccasella* larvae was 3–45% in Keeley's study and 0.6–35% in my

study. Even adding as much as 10% loss for ovules damaged by oviposition, seed loss to yuccas due to their pollinator is considerably less, on average, in *Yucca* than in *Ficus*. However, there is much greater variation in seed loss in *Yucca* than in *Ficus*. Janzen (1979) observed no less than 25% loss in any one fruit. In yuccas a high proportion of fruit showed no loss of seeds to feeding by yucca moth larvae, and in *Y. elata* there were many fruit in which there was no loss of seeds due to oviposition. Alternatively, there were also yucca fruit in which all potentially viable seeds were lost to yucca moth larvae.

The high variation in damage caused by oviposition and feeding by yucca moths is seen between species, between populations within species, and between fruit within populations. Accounting for this high variation requires an examination of the potential causes for both high and low values of seed damage. Since seed damage is most closely tied to the number of larvae per fruit, I will examine hypotheses which could explain both very low numbers and very high numbers of ovipositions and larvae per fruit.

Keeley et al. (1984) suggest three hypotheses for the absence of yucca moth larvae in individual fruit: 1) pollination by agents other than yucca moths, 2) pollination by yucca moths without oviposition, and 3) egg or larval mortality. However, there is no convincing evidence from the literature that agents other than yucca moths pollinate yuccas. Likewise, oviposition scars show that every yucca fruit has been visited at some time by yucca moths. The most obvious sign of oviposition is constriction of a locule, with a characteristic scar on both inner and outer walls of the locule. Although, there are many fruit which lack constrictions, particularly in *Y. elata* (see Tables 1 F–G, 2 F–G), lack of a constriction does not imply the absence of yucca moths at the time of flowering. There is a morph of *T. yuccasella* (or a new species losely related to *T. yuccasella*) which oviposits shallowly into the carpel wall, rather than into the locular space (Addicott 1985 b). Shallow ovipositions cause no constriction of the fruit, and instead leave a welt on the surface of the fruit. They occur in n. Arizona and s. Utah on *Y. kanabensis, Y. baileyi,* and *Y. angustissima,* and may occur in both the presence and absence of the normal mode of oviposition. There are also two morphs of *T. yuccasella* that oviposit in the style rather than the ovary of a yucca pistil, leaving no constriction of the fruit. This apical oviposition is common on both *Y. baccata* and *Y. elata* (Addicott unpublished work). Taking into account the different patterns and locations of oviposition, careful inspection of young fruit invariably shows evidence of inser-

tion of yucca moth ovipositors (Addicott unpublished work). Although ovipositor insertion could take place without oviposition, I have found by dissection that there is close to a 1:1 ratio of oviposition scars to yucca moth eggs (Addicott unpublished work). Small deviations from the 1:1 ratio are not large enough to explain the high proportion of fruit lacking larvae.

This leaves egg and/or larval mortality as the only viable explanation for the high proportion of fruit lacking yucca moth larvae. There is very little parasitism of larvae (Force and Thompson 1984), and Kingsolver (1984) estimated larval mortality of *T. yuccasella* in *Y. glauca* to be only about 9.4%. I am uncertain of sources of egg mortality, but the rates must be high. For example, in *Y. kanabensis* there are frequently 10–15 shallow ovipositions per locule, yet it is unusual to find more than 2 larvae per locule. Similarly, the success rate of eggs placed in the styles of *Y. elata* is low.

Fruit with high numbers of yucca moth larvae present a different problem. Keeley et al. (1984) observed up to 17 larvae per fruit, and I observed up to 24 larvae per fruit from *Y. kanabensis* in this study. I have observed populations of yuccas in other years in which every fruit had at least 30 and up to 50 larvae. Normal (deep), shallow and apical oviposition at the time of pollination do not appear to be responsible for high numbers of larvae. Kingsolver (1984) observed the behavior of ovipositing *T. yuccasella* and found that they avoided oviposition in locules in which an egg had already been placed. However, Aker and Udovic (1981) observed *T. maculata* ovipositing, not just in the ovaries of fresh flowers, but also in young fruit. I hypothesize that these secondary ovipositions are responsible for the high number of larvae per fruit (Addicott unpublished work). When there are high numbers of larvae per fruit, there are usually two cohorts of larvae, the second cohort being numerous relative to the first cohort. Eggs from secondary ovipositions are placed directly into developing seeds (Addicott in preparation), not into the locular cavity, carpal wall or style.

Although I suspect the source for the high numbers of larvae per fruit, I still do not know what causes the secondary ovipositions. Given the differences in oviposition, it could be the result of yet another morph of *T. yuccasella,* for example, a morph lacking maxillary tentacles (Davis 1967). Alternatively, it could simply be a facultative response of *T. yuccasella* when its flight season lasts longer than the flowering season of its yuccas.

The preceding has emphasized variation between fruit within populations and between populations within species, but there were still significant differences between species for all but net seed production. Differences were particularly noticeable between baccate and capsular species. Two lines of evidence suggest that these differences are real. First, the patterns I observed are similar to those found by Keeley et al. (1984) from collections made in 1979. Baccate species have relatively low numbers of yucca moth larvae per fruit and a high proportion of fruit without larvae. Second, variation between species is not just a reflection of habitat differences. For example, the consumption of viable seeds by *T. yuccasella* larvae was lower in *Y. baccata* than *Y. angustissima* at both Peach Springs and Gateway (Table 21). Therefore, differences between baccate and capsular species in how they interact with yucca moths are unlikely to be artifacts of different moth densities in different habitats.

Some of the differences in losses of viable seeds due to feeding by yucca moth larvae may be due to differences in locations where feeding occurs, and a nonrandom distribution of viable and inviable seeds within locules. A high proportion of *T. yuccasella* larvae fed near the apex of the fruit in both *Y. baccata* and *Y. elata.* The low proportion of viable seeds consumed by *T. yuccasella* larvae in *Y. baccata* (Tables 1 H, 2 H) may be a function of the distribution of inviable seeds, there being many inviable seeds towards the apical end of *Y. baccata* fruit.

Proportional net seed production was not significantly different between species, and this could potentially reflect a strong regulation of the interaction between yuccas and yucca moths. First, a small number of pollination events per fruit could be associated with a small proportion of viable ovules, and a small loss due to feeding by yucca moth larvae. Higher visitation would yield more viable ovules but a greater loss of ovules due to oviposition and feeding. Oviposition behavior can change in response to the number of eggs already laid in a given ovary (Kingsolver 1984). Second, there could be selective abortion of pistils carrying large numbers of yucca moth eggs, as fruit abortion is very common in most yuccas (Addicott 1985a, Udovic and Aker 1981). However, the high variation between populations within species of yuccas and between fruit within populations does not support the hypothesis that there is strong regulation of the interaction between yuccas and yucca moths.

A detailed cost/benefit analysis of the interaction between yuccas and yucca moths is not possible with the present data set. For example, damage caused by larvae from different patterns of oviposition should be considered separately. This is particularly important, because some populations of yuccas, and even individual fruit, experience three different types of oviposition. Also, I do not yet have direct measurements of the impact of oviposition on seed inviability. This makes it difficult to accurately assess gross benefits of pollination. However, I can make a preliminary estimate of cost/benefit ratios by dividing costs of yucca moth larvae (Table 1 J) by the sum of net seed production (Table 1 D) and costs (Table 1 J). These estimates indicate that costs are about 20–30% of gross benefits for the capsular yuccas, and 0–20% for the baccate yuccas. Therefore, the obligate pollination mutualism between yuccas and yucca moths is clearly beneficial to the yuccas, but up to 30% of the potential benefits are lost to the yucca moths.

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Appendix 1. Collection sites and designations of populations where yucca fruit were collected for this study

Species	Population	Location				
Y. schottii	Bisbee	6.6 km	w	Bisbee	Cochise Co.	Arizona
	Nogales	6.5 km	sw	Patagonia	Santa Cruz Co.	Arizona
		23.3 km	ne	Nogales	Santa Cruz Co.	Arizona
	Portal	4.5 km	w	Portal	Cochise Co.	Arizona
		13.8 km	w	Portal	Cochise Co.	Arizona
		3.0 km	w	Portal	Cochise Co.	Arizona
				Portal	Cochise Co.	Arizona
Y. arizonica	Nogales	3.3 km	e	Nogales	Santa Cruz Co.	Arizona
Y. baccata	Peach Springs	6.7 km	w	Peach Springs	Yavapai Co.	Arizona
	Gateway	16.0 km	e	Gateway	Mesa Co.	Colorado
		12.2 km	e	Gateway	Mesa Co.	Colorado
	Kanab	40.3 km	w	Mt. Carmel Jct.	Kane Co.	Utah
		18.7 km	w	Mt. Carmel Jct.	Kane Co.	Utah
		14.2 km	w	Mt. Carmel Jct.	Kane Co.	Utah
	Moab	2.6 km	e	LaSal	San Juan Co.	Utah
Y. glauca	Gunnison	16.5 km	e	Gunnison	Gunnison Co.	Colorado
		7.1 km	n	Gunnison	Gunnison Co.	Colorado
	Poncha Springs	21.3 km	nw	Saguache	Saguache Co.	Colorado
		3.6 km	s	Poncha Springs	Chaffee Co.	Colorado
		8.8 km	w	Poncha Springs	Chaffee Co.	Colorado
		14.2 km	w	Poncha Springs	Chaffee Co.	Colorado
	Wolf Creek	1.6 km	e	Wolf Creek	Lewis and Clark Co.	Montana
		36.0 km	e	Wolf Creek	Lewis and Clark Co.	Montana

Appendix 1 (continued)

Species	Population	Location				
Y. glauca	Clines Corners	22.3 km	s	Santa Fe	Santa Fe Co.	New Mexico
		7.1 km	se	Clines Corners	Torrance Co.	New Mexico
		25.7 km	se	Clines Corners	Torrance Co.	New Mexico
Y. baileyi	Page	7.1 km	w	Glen Canyon City	Kane Co.	Utah
		24.3 km	w	Black Mesa	Navajo Co.	Arizona
		24.3 km	w	Black Mesa	Navajo Co.	Arizona
		0.3 km	e	Black Mesa	Navajo Co.	Arizona
Y. angustissima	Peach Springs	27.5 km	e	Peach Springs	Yavapai Co.	Arizona
		5.0 km	w	Peach Springs	Yavapai Co.	Arizona
	Gateway	32.0 km	w	Whitewater	Mesa Co.	Colorado
		18.2 km	s	Gateway	Mesa Co.	Colorado
Y. kanabensis	Kanab	18.5 km	w	Mt. Carmel Jct.	Kane Co.	Utah
		21.5 km	n	Kanab	Kane Co.	Utah
	Rockville	11.7 km	s	Rockville	Washington Co.	Utah
Y. elata	Cottonwood	7.1 km	ne	Cottonwood	Yavapai Co.	Arizona
		5.7 km	ne	Cottonwood	Yavapai Co.	Arizona
		7.1 km	se	Cottonwood	Yavapai Co.	Arizona
	Sonoita	0.8 km	s	Huachuca City	Cochise Co.	Arizona
		15.2 km	e	Sonoita	Santa Cruz Co.	Arizona
	Portal	2.1 km	s	Rodeo	Hidalgo Co.	New Mexico
	Prescott	2.8 km	n	Dewey	Yavapai Co.	Arizona
	Sedona	25.8 km	s	Sedona	Yavapai Co.	Arizona
		19.5 km	s	Sedona	Yavapai Co.	Arizona
	Wickenburg	20.0 km	nw	Wickenburg	Yavapai Co.	Arizona
	Alamagordo	24.2 km	sw	Alamagordo	Otero Co.	New Mexico
		42.2 km	sw	Alamagordo	Otero Co.	New Mexico
		53.3 km	sw	Alamagordo	Otero Co.	New Mexico
		31.7 km	ne	Las Cruces	Dona Ana Co.	New Mexico
	Deming	38.0 km	w	Las Cruces	Dona Ana Co.	New Mexico
		44.3 km	w	Deming	Luna Co.	New Mexico
		27.5 km	n	Hachita	Grant Co.	New Mexico