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Genetic consequences of specialization: yucca moth behavior and self-pollination in yuccas

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Abstract Reciprocal specialization in interspecific interactions, such as plant-pollinator mutualisms, increases the probability that either party can have detrimental effects on the other without the interaction being dissolved. This should be particularly apparent in obligate mutualisms, such as those that exist between yucca and yucca moths. Female moths collect pollen from yucca flowers, oviposit into floral ovaries, and then pollinate those flowers. Yucca moths, which are the sole pollinators of yuccas, impose a cost in the form of seed consumption by the moth larvae. Here we ask whether there also is a genetic cost through selfish moth behavior that may lead to high levels of self fertilization in the yuccas. Historically, it has been assumed that females leave a plant immediately after collecting pollen, but few data are available. Observations of a member of the *Tegeticula yuccasella* complex on *Yucca filamentosa* revealed that females remained on the plant and oviposited in 66% of all instances after observed pollen collections, and 51% of all moths were observed to pollinate the same plant as well. Manual cross and self pollinations showed equal development and retention of fruits. Subsequent trials to assess inbreeding depression by measuring seed weight, germination date, growth rate, and plant mass at 5 months revealed significant negative effects on seed weight and germination frequency in selfed progeny arrays. Cumulative

inbreeding depression was 0.475, i.e., fitness of selfed seeds was expected to be less than half that of outcrossed seeds. Single and multilocus estimates of outcrossing rates based on allozyme analyses of open-pollinated progeny arrays did not differ from 1.0. The discrepancy between high levels of behavioral self-pollination by the moths and nearly complete outcrossing in mature seeds can be explained through selective foreign pollen use by the females, or, more likely, pollen competition or selective abortion of self-pollinated flowers during early stages of fruit development. Thus, whenever the proportion of pollinated flowers exceeds the proportion that can be matured to ripe fruit based on resource availability, the potential detrimental genetic effects imposed through geitonogamous pollinations can be avoided in the plants. Because self-pollinated flowers have a lower probability of retention, selection should act on female moths to move among plants whenever moth density is high enough to trigger abortion.

Key words Mutualism · Coevolution · Self-pollination · *Tegeticula* · *Yucca*

Introduction

Ecological specialization in interspecific interactions, such as plant-pollinator mutualisms, intrinsically increases the susceptibility to detrimental effects conveyed by the interacting species (Bull and Rice 1991; Pellmyr and Huth 1994; Thompson 1994). Such effects should be particularly apparent in obligate mutualisms, where either species may be unable to reverse dependence on the other, even if escalated exploitation increases the cost of the interaction.

The obligate pollination mutualism between yucca plants and yucca moths is a pertinent system for addressing this issue, in that yuccas appear to have evolved from dependence on a broad spectrum of

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nectar-drinking insects to depend solely on yucca moths for their pollination (Riley 1892; Pellmyr and Huth 1994; Pellmyr et al. 1996). In the yucca-yucca moth interaction, the female moth uses specialized mouthparts to actively collect pollen from yucca flowers. Carrying this pollen, she oviposits once or more into ovaries of yucca flowers. The moth then actively pollinates the flower in which she has oviposited, thus assuring that lack of pollen will not limit the availability of yucca seeds, which is the only food source for her larvae. The larvae only consume a small portion of the developing seeds, thus creating a benefit that outweighs the cost to the plant.

Cost estimates of the dependence on moths for the plants have so far been confined to levels of seed destruction (Riley 1873a, b; Rau 1945; Johnson 1983; Keeley et al. 1984, 1986; Addicott 1986). There is the possibility, however, that the plant may suffer a genetic cost as well in the form of inbreeding depression if yucca moths self-pollinate flowers to any extent. This possibility was first raised in 1881 by Charles Darwin (F. Darwin 1903), who read Riley's early papers of the yucca-yucca moth interaction (Riley 1873a, b; references in Davis 1967) while concluding his own studies into inbreeding depression (Darwin 1877). He noted the possibility based on available reports that moths may perform geitonogamous pollinations and suggested that Riley look into this possibility.

Riley (1892) subsequently reported that the moth indeed cross-pollinated flowers, but this statement was in error because his description of moths moving among flowers within plants implies geitonogamous self-pollination. For a century, authors generally have assumed that moths leave a plant immediately after collecting pollen (e.g., Addicott et al. 1990; Powell 1992), but little empirical data have been compiled to resolve the issue of yucca moth movement patterns and their consequences for plant mating patterns. In this paper, we first provide behavioral data for one yucca moth species, and experimental data on self-compatibility and inbreeding depression in its host. We then use allozyme analysis of an open-pollinated progeny array to assess the frequency of self-pollinated seed under natural circumstances, and discuss the genetic consequences to the plant of moth pollination patterns.

Materials and methods

Study organisms and study sites

All observations and experiments were performed in 1992–1994 on *Yucca filamentosa* (Agavaceae) and its exclusive pollinator, *Tegeticula yuccasella* (Lepidoptera: Prodoxidae). A native of the eastern North American seaboard, *Y. filamentosa* was naturalized across eastern United States during the 1800s, and has been established in the study area in Cincinnati, Ohio, for at least 150 years. Inflorescences of this species have 150–500 flowers arranged in a branched raceme that open in overlapping succession over a period of 10–20 days. Individual flowers are open for 1–2 days.

The pollinator is one species within an unresolved complex of closely related taxa (Miles 1983; Addicott et al. 1990; O. Pellmyr unpublished work); voucher specimens are deposited in the collection of O. Pellmyr and The Smithsonian Institution (USNM). The moth quickly colonized the extended range of its host, and collection records show that it has been established in Cincinnati for >90 years. Behavior and compatibility studies were almost exclusively performed in an artificial population in a discrete part of the Cincinnati Zoological Gardens; it contained 35–50 inflorescences each year. Two observations were made in Spring Grove Arboretum, 2.5 km away from the main site, where a large yucca population (350–850 inflorescences/year) has been established for >120 years.

Moth behavior observations

Moths in the study population generally became active around 2045 hours (LST) and remained active for 1–3 h, depending on temperature conditions. Data on movement patterns and behavior after pollen collection were extracted from a total of 52.2 h of moth behavior data collected during the periods 9 June–5 July 1992, 14 June–7 July 1993, and 25 June–1 July 1994. Behaviors following pollen collection were characterized as oviposition attempt, pollination, search, or rest, and we also recorded whether the female flew off the plant at some point before resuming oviposition and pollination. It should be emphasized that pollination invariably is preceded by oviposition into the same flower in this and other studied yucca moths (Aker and Udovic 1981; Addicott and Tyre 1995). When a female went to rest, she was dropped from further observation after 5 min. In our experience, such females rarely became active again in the course of the night.

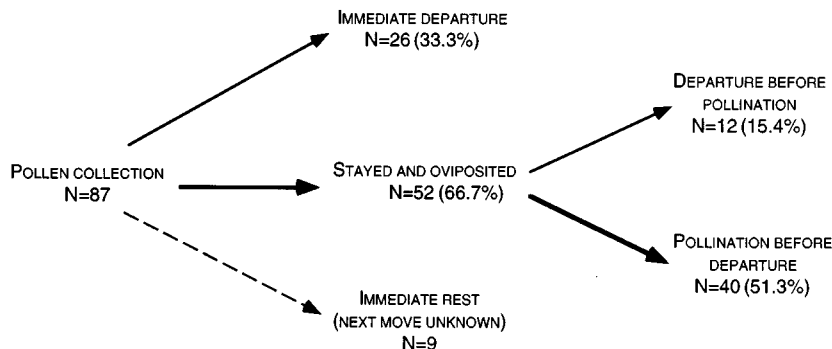
Tests of self-compatibility and inbreeding depression

Tests for self-compatibility were done by controlled self- and out-cross pollinations of ten randomly selected plants at their flowering peak in 1992. For each plant, two just-opened flowers on each of 20 side branches of an inflorescence were identified; one was self-pollinated and the other cross-pollinated with ample pollen. After treatment, each flower was given a 3×3 mm plastic label indicating treatment, and any developing fruits on the same side branch were removed to prevent within-branch competition (Huth and Pellmyr, in press). A plastic straw (length 20 mm, diameter 7.5 mm) was slipped over the ovary and kept in place for 2 days to prevent moth ovipositions and pollinations. Fruit set was scored 5–7 days after treatment; at that point, high levels of selective abortion of fertilized flowers that characterize this species is >95% complete (Pellmyr and Huth 1994), while abortion of young fruit caused by *Carpophilus melanopterus* (Coleoptera; Nitidulidae) was kept to a minimum.

In order to measure inbreeding depression, all fruits that reached maturity were harvested as the capsules began to dehisce. For each plant, an equal number of capsules from the two treatments were picked at random (varying between 0 and 5 among plants, depending upon fruit survival). Twenty seeds were randomly chosen from each capsule, individually weighed and stratified in germination racks at ambient temperature. Germination date was scored for each plant, and seedlings were transplanted to 0.6-L pots as size permitted. Growth rate was estimated by measuring the total length of all leaves at 5 months post-stratification. Inbreeding effects were analyzed for seed weight, germination, cumulative leaf length, and seedling survival, in a three-way mixed-model ANOVA. Pollination treatments were treated as fixed effects, plants as random effects, and pods as random effects nested within both treatment and plant. Subsequent pairwise *t*-tests were used to test for paternal, maternal, and treatment effects. All analyses were performed using SAS (1986).

For all variables, relative fitness of selfs (RFS) was calculated as the ratio of self/cross performance. Inbreeding depression was calculated as 1–RFS, while total inbreeding depression was

Fig. 1 Behavior path in 87 observed events of pollen collection by female yucca moths on *Yucca filamentosa*



calculated by multiplying the independent estimates of RFS and subtracting the product from 1 (Stevens and Bougourd 1988).

Estimates of outcrossing rates in open-pollinated fruits

Moths usually only use a portion of their pollen for individual pollinations, and they occasionally add pollen to their load during their life, so behavioral self-pollinations, i.e., pollination on a plant where pollen pick-up has occurred, need not necessarily equate with genetic self-pollination. For this reason, we estimated realized outcrossing rates among naturally pollinated, mature pods in the study population using several allozyme loci. As seed pods ripened in 1993, leaf tissue and five pods were collected from each of ten plants. Twelve randomly selected seeds were germinated on wet filter paper at 25°C. Both leaves and seedlings were crushed with liquid nitrogen and sand in an enzyme extraction buffer (Wendel and Parks 1982). Enzyme extracts were absorbed on filter paper wicks and stored at -70°C.

Both maternal and seedling genotypes were determined via horizontal starch gel electrophoresis. The gels were stained for seven enzyme loci: phosphoglucose isomerase (PGI), triose-phosphate isomerase (TPI), alcohol dehydrogenase (ADH) (using Poulik buffer), 6-phosphogluconate dehydrogenase (6-P), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH) (using 11 buffer), and diaphorase (DIA) (using modified 8 buffer). Buffer recipes and stains were taken from Soltis et al. (1983) except for diaphorase (Cheliak and Pitel 1984), and Poulik buffer (Mitton et al. 1979).

Single locus and multilocus maximum likelihood estimates of the population outcrossing rate were obtained using the mating-system program of Ritland and Jain (1981). Variances for outcrossing rates were obtained by the bootstrap method.

Results

Moth movement patterns

Eighty-seven pollen collections were observed during the 3 years of study (Fig. 1). This was the least common type of behavior among females, averaging 1.13 collections per hour in the 52.2 h of activity data collected in 1992 and 1993. Moths were seen to either add to an existing pollen load, or start a new load after complete depletion. Nine of the pollen collections were followed by extended rest on the same plant, and subsequent movements were not recorded. For this reason, they were removed from subsequent calculations. Among females that remained active, 33%

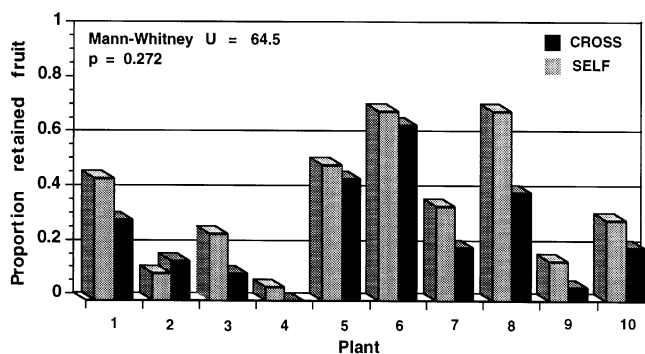


Fig. 2 Fruit set in pairwise self and outcross treatments in ten *Y. filamentosa* plants

($n = 26$) left the plant immediately after pollen collection. The remaining 67% ($n = 52$) stayed on the plant and oviposited into one or more flowers. Of those 52 females 12 left after oviposition, but the remaining 40 pollinated one or more flowers on the same plant where they had collected pollen before flying away. Thus, 51.3% of all instances of pollen collection were followed by pollination on the same plant. This reflects a general behavior pattern in ovipositing *T. yuccasella* females of moving short distances; as a female departs a flower where she has oviposited, she typically inspects adjacent flowers for suitability, and then walks or flits to nearby side branches in search of suitable flowers. On several occasions females spent their entire active period during one evening on one inflorescence.

Tests of self-compatibility and inbreeding depression

Fruit set among the experimentally crossed flowers was 25% in the outcrossed flowers and 30.5% in the self-pollinated flowers (Fig. 2; Mann-Whitney U -test, NS). This exceeded overall fruit set among non-treated inflorescences in the population (mean = 8.1%, $n = 25$) because all other fruits on the experimental plants had been removed. There is strong limitation on resources within side branches (Huth and Pellmyr, in press), so this treatment reduced competition. The retention of selfed fruit at non-significantly different levels

Table 1 Fitness of the cross and self progeny of *Yucca filamentosa* (means; 95% confidence level below), RFS is the relative fitness of selfs (calculated as ratio of self/cross performance), and inbreeding depression is $1 - \text{RFS}$. Overall RFS is the product of the individual estimates of RFS

Variable	Self-pollinated	Cross-pollinated	RFS	Inbreeding depression
Seed weight (mg)	10.30 (8.7–11.9)	11.61 (9.3–13.9)	0.887	0.113
Germination, %	54.04 (40–67.1)	67.69 (57.5–77.8)	0.798	0.202
Leaf length	546.94 (466–628)	676.30 (565–899)	0.809	0.191
Survival, %	75.62 (63–88)	82.45 (72.3–92.6)	0.917	0.083
Cumulative effect			0.525	0.475

Table 2 Results of mixed model ANOVA of inbreeding depression data for *Y. filamentosa*

Variable	df	Seed weight		Germination, %		Cumulative leaf length		Survival
		MS	F	MS	F	MS	F	MS
Treatment (self/cross)	1	2.34×10^{-4}	15.27***	3.31	5.21*	2.58×10^5	0.83	0.344
Plant	7	3.74×10^{-4}	24.45***	1.19	1.87	3.07×10^5	0.92	0.474
Plant \times treatment	7	4.42×10^{-5}	2.88*	0.746	1.17	1.61×10^5	0.48	0.389
Pod	18	1.54×10^{-6}	4.5***	0.635	3.09***	3.86×10^5	3.46***	0.225

* $P < 0.05$, *** $P < 0.001$

suggest that selfed fruit may be as likely as outcrossed fruit to mature when overall fruit set of a plant is low.

A total of 34 pods (balanced for treatments within plants) were available to estimate inbreeding effects in the germination experiment. Seeds resulting from cross-pollination were heavier, had higher germination frequency, higher growth rate, and lower risk of death within five months than those from self-pollination (Table 1). In the mixed-model ANOVA (Table 2), the treatment effect was significant for seed weight and germination frequency. There was also a significant plant effect on seed weight and a plant by treatment effect. Individual plant mean seed weights were calculated before analyzing the variance between treatments and before calculating RFS. This eliminated the bias introduced by unequal pod numbers, and thus seeds, per plant.

Cumulatively, the estimated inbreeding depression was 0.475, i.e., fitness of selfed seeds was 52.5% of the outcrossed seeds.

Outcrossing rates in open-pollinated fruits

Allozyme analyses of the progeny arrays of the 10 seed plants indicated complete outcrossing among seeds in naturally pollinated, mature fruit in the study population. The multilocus estimate for outcrossing rate in the population was 0.961 (SE = 0.07), and the mean single locus estimate was slightly higher at 1.061 (SE = 0.10). Neither estimate differs significantly from 1.0, indicating that the population was randomly outcrossing.

Discussion

The moth behavior data suggest that Darwin's caution about geitonogamy may have been well-founded; almost two-thirds of the observed yucca moths stayed on a plant after pollen collection, and over half of all collections were followed by one or more pollinations on the same plant. This picture differs somewhat from the three previous quantitative observations available in the literature (Table 3); in 26 cases for three different moth species, only one occasion of behavioral self-pollination was observed. Fuller (1990), however, like Riley before him, stated that geitonogamous pollinations were observed but did not provide quantitative data.

The present data set, which is 3 times the size of all prior data sets combined, would suggest that self-pollination may be common in *Y. filamentosa*. The fact that fruit set was not significantly different between self-pollinated and cross-pollinated flowers in the controlled experiments suggests that this would translate into proportional levels of self-pollinated seeds in open-pollinated fruit. Given the high level of inbreeding depression found, this should carry a considerable genetic cost to the plant. Contrary to the expectations from behavior data and hand pollination experiments, however, the proportion of self-pollinated progeny in the open-pollinated seed pods did not differ significantly from zero.

The contradictory results from moth behavior and genetic analysis need to be reconciled. The explanation may lie with mechanisms involving moth behavior, a subsequent plant mechanism, or both. Because pollen was seen to be added to pre-existing loads on many

Table 3 Prior records of yucca moth movement after pollen collection. Moths were members of the *T. yuccasella* complex, except for *T. maculata* in Aker and Udovic (1981)

Source	Host	Moth behavior after pollen collection	
		Stayed and pollinated	Departed
Aker and Udovic (1981)	<i>Y. whipplei</i>	0	9
Dodd (1988)	<i>Y. glauca</i>	1	7
Addicott and Tyre (1995)	<i>Y. kanabensis</i>	0	9
Fuller (1990)	<i>Y. glauca</i> group	"...sometimes continue to pollinate a <i>Y. glauca</i> plant after collecting pollen..."	

occasions (O. Pellmyr, unpublished work; an observation also made for another moth species on *Y. kanabensis*; Addicott and Tyre 1995), the load carried by moths is likely to often be a mixture from different donor plants. Accordingly, behavioral selfing need not equate genetic selfing. Unless a specific mechanism that allows the female to avoid use of the most recently collected (and thus most superficial) pollen exists, it would seem unlikely that some self pollination can be avoided. There is no evidence to support this hypothesis.

Female moths may deposit mixed pollen loads, but pollen competition may lead to predominant outcrossing even though some self pollen may be present (Marshall 1991; Quesada et al. 1991; Björkman et al. 1995). No data exist to test this hypothesis. As an alternative mechanism, self-pollinated flowers may be more frequently aborted during the period of selective abortion that characterizes all observed yuccas shortly after fertilization (Udovic and Aker 1981; Sutherland and Delph 1984; Addicott et al. 1990; Pellmyr and Huth 1994). Fruit set in *Y. filamentosa* is generally 8–20%, so abortion levels can reach 80–90% when pollinator density is high. The exact abortion level in the study population was not recorded, but an indication can be obtained from a near-by population studied in detail (Pellmyr and Huth 1994). In that population, 38% of the flowers were pollinated, abortion frequency was 47%, and moth density was approximately half that of the study population. Because higher moth density would lead to higher pollination frequency, abortion is likely to have exceeded 47% in the study population.

The results from the hand pollination trials, where self-pollinated flowers were retained at the same level as cross-pollinated flowers, may seem to be at odds with the selective-abortion hypothesis. But the experimental inflorescences had their total number of fruits kept artificially low, for the explicit purpose of producing numerous seeds of known genotypes, and the number of pollinated flowers did not at any point reach the level where resource limitation would trigger fruit abortion. Furthermore, our data indicate that more maternal resources were provided to the outcrossed fruits (higher seed weights; Table 2). The hypothesis that self-pollinated flowers may suffer disproportionate selective abortion is corroborated in recent experimental work where pollen genotypes and quantity were controlled (C. J. Huth and O. Pellmyr, unpublished work).

The genetic cost of self-pollination would thus seem to be largely masked in the plant as long as pollina-

tion levels are sufficient to allow for the mechanism of selective abortion of selfed progeny or for pollen competition. Only if pollination levels are very low, or if rates of geitonogamous pollination increase in the moths, would retention of self-pollinated progeny be more common in the plants. A similar mechanism, where retention of selfed flowers depend on overall pollination levels, has been documented in *Phormia tenax* (Becerra and Lloyd 1993). The other yucca species for which small numbers of moth observations exist (Table 3) are all known to be self-compatible (Aker and Udovic 1981; Dodd 1988; Fuller 1990), but studies of context-dependent abortion mechanisms have only been performed in *Y. whipplei* (Richter and Weis 1995). In this case, selfed progeny was selectively aborted as well.

While the effects of self-pollination may be masked in the plants, it would seem maladaptive on the part of the moths to perform self pollinations, as such flowers appear to have a lower probability of retention. Retention probability is positively correlated with pollination quality and negatively correlated with moth egg number (Pellmyr and Huth 1994, 1995; Richter and Weis 1995), and egg dispersal patterns suggest that there is selection on the moths to reduce egg-induced abortion. It would seem adaptive also to reduce pollination-induced abortion by flying off a plant after pollen collection, but perhaps the benefits of such flights are masked by other factors, such as time lost to oviposition, increased exposure to predation during search flight, or low pollinator density that may reduce the risk of selfed fruit abortion. It is also possible that multiple pollinations by several females, which is common, may result in few flowers actually having only self pollen. These factors should affect the outcome among all yucca moths that encounter self-compatible hosts, and comparative behavioral analysis in other populations within and among moth species may reveal considerable variation in this behavior. Resolution of these issues await extensive data sets from other moth populations, empirical data on pollen composition of moth loads, patterns of paternity in fertilized flowers, and their consequences for the moth progeny.

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