THE YUCCA PLANT AND THE YUCCA MOTH

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Photo and illustration credits: All photographs except the picture of C.V. Riley are by John Richard Schrock. All figured graphs are by Marylee Ramsay.

Cover Photo: The most common yucca in the Midwest and eastern Great Plains is *Yucca filamentosa*, a cultivar limited to towns and graveyard plantings in these regions.

Back Cover: Night view of a female yucca moth resting on a yucca flower. Actual length of the moth is slightly over one centimeter or one-half inch.

In Remembrance

Dr. John W. Breukelman, founding editor of the *Kansas School Naturalist*, died May 18, 1995 at Emporia KS. Born in 1901, he graduated from Yankton College, SD and earned a doctorate from the University of Iowa. Breukelman came to Kansas State Teachers College in 1929 where he headed the Biology Department through 1958 and edited the *American Biology Teacher*. In 1970, the new biology building was named Breukelman Hall. In 1954, he invited E. Laurence Palmer, editor of the *Cornell Science Leaflets*, to visit K.S.T.C. and consult in the formation of a similar journal to serve the Plains region. Breukelman also wrote or co-authored 14 issues of the *Naturalist*. In 41 years, the *Naturalist* has grown to serve 7000 readers and has printed 156 titles. At age 94, Dr. Breukelman still looked forward to reading each new issue. -Editor

THE YUCCA PLANT AND THE YUCCA MOTH

by Marylee Ramsay and John Richard Schrock

At the end of every May, across the Midwest and Great Plains, yucca plants sprout a stalk of white flowers. Inside some of these flowers lurks a plain little white moth. These yucca plant and their yucca moths are the classic textbook example of "mutualism." And it was discovered over a century ago by a famous entomologist from Missouri.

MUTUALISM

Many organisms live together in relationships where one depends upon the other. Some, relationships, such as the coyote and rabbit, represent "predators" that feed upon "prey."

Corn rootworms, corn stem borers, and corn earworms are, of course, all dependent upon their host corn plant. Parasites such as ticks and tapeworms feed on the surface or inside their hosts. And some creatures, such as the follicle mite, live in our eyebrow follicles without doing any harm at all. However, when two organisms have evolved a relationship where both benefit and neither is harmed, that is "mutualism."

Many mutualistic relationships have been documented. Wood termites contain one-celled protozoans that pre-digest wood cellulose in the termite gut. Without the protozoa, the termites starve with a belly full of useless wood fibers. And the protozoa need the moist environment of the termite gut, and the termite's ability to harvest and deliver wood fiber. The termite-protozoa relationship and the yucca-moth relationship are the most common and therefore classic cases of mutualism cited in textbooks.

COEVOLUTION

When an organism becomes totally dependent upon another, they may share the same biological fate. For instance, if a loon becomes extinct, a loon louse specialized to parasitize just this species will also become extinct. The protozoa and termites mentioned above have also locked their future survival together–they have "coevolved." When we discover a coevolved system, it provides scientists an opportunity to play with the system to discover how each organism is dependent upon the other, and to probe how the relationship evolved. For instance, we can clear protozoa from termites using antibiotics, observe how the microorganisms are transferred, and search for similar microorganisms in termite relatives.

But the yucca plant and yucca moth are the textbook case of coevolution. First, the yucca plant has no ability to reproduce seeds without the moth. Yuccas can propagate small rosettes around the parent plant, but these vegetative sprouts are copies of the parent. Over decades, the plant cannot move but a few feet, and there is no possibility for genetic variation. Without the moth, the whole flowering effort (expensive to the plant in energy terms) is a total waste. The only pollinator of the plant is the yucca moth; bees are not attracted and neither wind nor bees can pick up the sticky pollen.

The yucca moth is likewise dependent upon the yucca plant. There are no alternate host plants known for the yucca moth; the yucca moth caterpillars must eat yucca seeds or starve. Without the plant, the moths die off in one generation. Without the moth, the plant cannot reproduce variation or disperse; given any major climate changes, it too will go extinct. The system is therefore tightly coevolved.

Marylee Ramsay earned her masters degree from Emporia State University; she studied the population biology of the yucca and yucca moth-that provides the data for this issue– and currently teaches in western Kansas.

Dr. John RichardSchrock received his doctorate in entomology from the University of Kansas and is Associate Professor of Biology in the Division of Biological Sciences, Emporia State University, Emporia KS 66801.

Figure 1. Yucca moths hide inside yucca flowers during the daytime.

A "TRANSPARENT" SYSTEM

The yucca plant and yucca moth system is very "transparent" to study by biologists. The yucca plant remains in place; it does not rapidly disperse to new fields is not pollinated by other insects. The moth is likewise tied to the plant and does not venture into other flowers. The adult moth resides inside the yucca flowers, allowing an easy census of adult populations. And the active larval stages are all contained inside the developing yucca fruits where they can be easily sampled, and where the amount of food they eat is easily measured. Compared to wide-ranging insects with multiple host plants and hidden life cycles, the yucca-moth association is conveniently packaged for those researchers who know to ask the right questions.

YUCCA MOTH POLLINATION

You can watch yucca moths pollinate flowers between dusk and midnight. The female gathers pollen from the flower anthers by using her specially adapted mouthparts, called palps. She forms the sticky pollen into a ball which she carries between her tentacles and her thorax (under her "chin" so to speak). The pollen ball is then "stuffed" or "combed" into the stigma of the various flowers she visits. The stigma is the receptive tip of the female pistil. Without this process, the yucca flower will not develop into the fruit or pod with seeds.

The flower's ovary contains eggs in three chambers called carpels, and each carpel is divided into two locules. When the female moth visits the flower, she backs up to the flower base and inserts her ovipositor to lay an egg in one or more of the six locules. By the time the egg hatches into a microscopic caterpillar, the yucca will have begun to develop a pod with little seeds, just as a fertilized apple blossom develops into a little apple. Many unanswered questions center around how the female moth knows a flower has not been visited before, and how many eggs she lays in how many flowers?

MALE AND FEMALE YUCCA MOTHS

Tegeticula yuccasella is the only true yucca moth found east of the Rocky Mountains and is responsible for pollinating all eastern yuccas and many western species as well. Moths emerge in late May and early June, presumably near a yucca plant. Males may appear a little earlier than the larger females. The smaller males have a blunt tail while the females bear a sword-like ovipositor (egg laying blade). Males and females mate inside a flower after which the male plays no part in the pollination process.

MARK AND RECAPTURE

How far do yucca moths fly at night? And how big are the moth populations? Since we can't place radio collars on little moths, and we can't be certain of collecting all the moths in a locality, scientists have devised a technique for estimating the population by sampling and marking a small portion, and then resampling the population later. Simply, if you capture ten individuals and mark and release them yesterday, and today half of the individuals you catch are marked, then the estimated total population is twenty.

Ramsay has discovered that yucca moths stay very close to their home yucca clusters, and they remain active on the plants for less than a week.

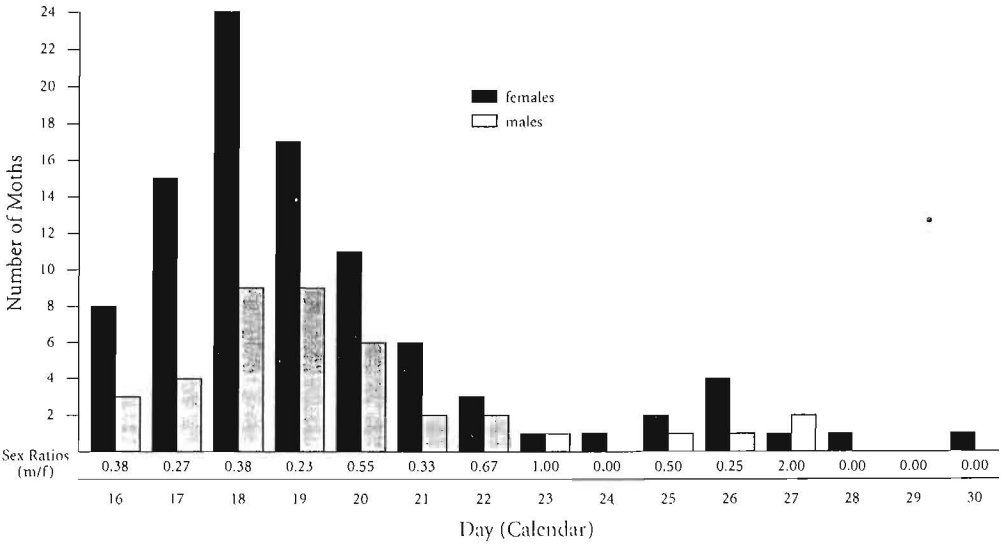


Figure 2. Total number of moths and sex ratios (male : female) per capture day.

THE YUCCA PLANT

About 30 species in the genus *Yucca* are found in North America. Only *Yucca glauca* is common and native to the western Great Plains. It is found from South Dakota down through western Nebraska, Kansas and Oklahoma. Its stiff, broad and short sword-like leaves form green rosettes in the short-grass prairies and sand hills. Because of the lack of moisture, the plants are spaced out across the dry semi-arid hills. *Yucca glauca* only produces from 20-60 white flowers per stalk.

The common yucca found around towns and graveyards in the eastern Plains and across the Midwest is *Yucca filamentosa*. Also known in nursery catalogs as *Yucca smalliana*, *Y. filamentosa* is a cultivar that is native to the humid southeastern U.S. It occurs in the central U.S. only where planted and disperses only a short distance from where it was planted. It forms a rosette with longer narrow blades and produces several hundred smaller flowers.

The greatest variety of yuccas live in the Southwestern U.S. where they evolved as successful semi-desert plants. Arizona is home to 14 species, including the Spanish bayonet and the Joshua tree. There are also many yucca moth species in that area to pollinate the wide range of yucca species. Because of the great variety of yuccas and their moths in the southwestern U.S., biologists believe this is the region where most of the evolution of these groups occurred–a process called adaptive radiation. However, we are addressing just the Midwestern Yucca filamentosa and the yucca moth, *Tegeticula yuccasella*, where the story of its coevolution was discovered.

(continued on page 6)

C. V. RILEY

The unusual role of the yucca moth was discovered in 1876 by a Missouri entomologist named C. V. Riley.

Charles Valentine Riley was an enthusiastic naturalist and writer with keen powers of observation in the field. Early in his career he was a writer for the Prairie Farmer, and later started the magazines American Entomologist and Insect Life. He became State Entomologist of Missouri from 1868 to 1877 and issued a series of state reports that were far ahead of his time for accuracy and insight into insects and pest problems. He also helped the French overcome problems with a grapevine insect that was ravaging European vineyards, and headed a Commission to study an outbreak of the Rocky Mountain Locust in Colorado and western Kansas. In those days, Riley lectured often at what are now the University of Missouri–Columbia, and Kansas State University, Kansas. He was appointed national entomologist (technically "Chief in Entomology") in the United States Department of Agriculture in 1878.

In his 13 years as national entomologist, Riley was a controversial man. Described as "restless", "ambitious", and "a great schemer", he built his division into what became a permanent Bureau of Entomology, today's Entomological Research Service. He strove constantly to make his work seem more important, and he made many political enemies both in the U.S.D.A. and in Congress. Yet his stature as a great entomologist was based on major entomological work both pure and applied.

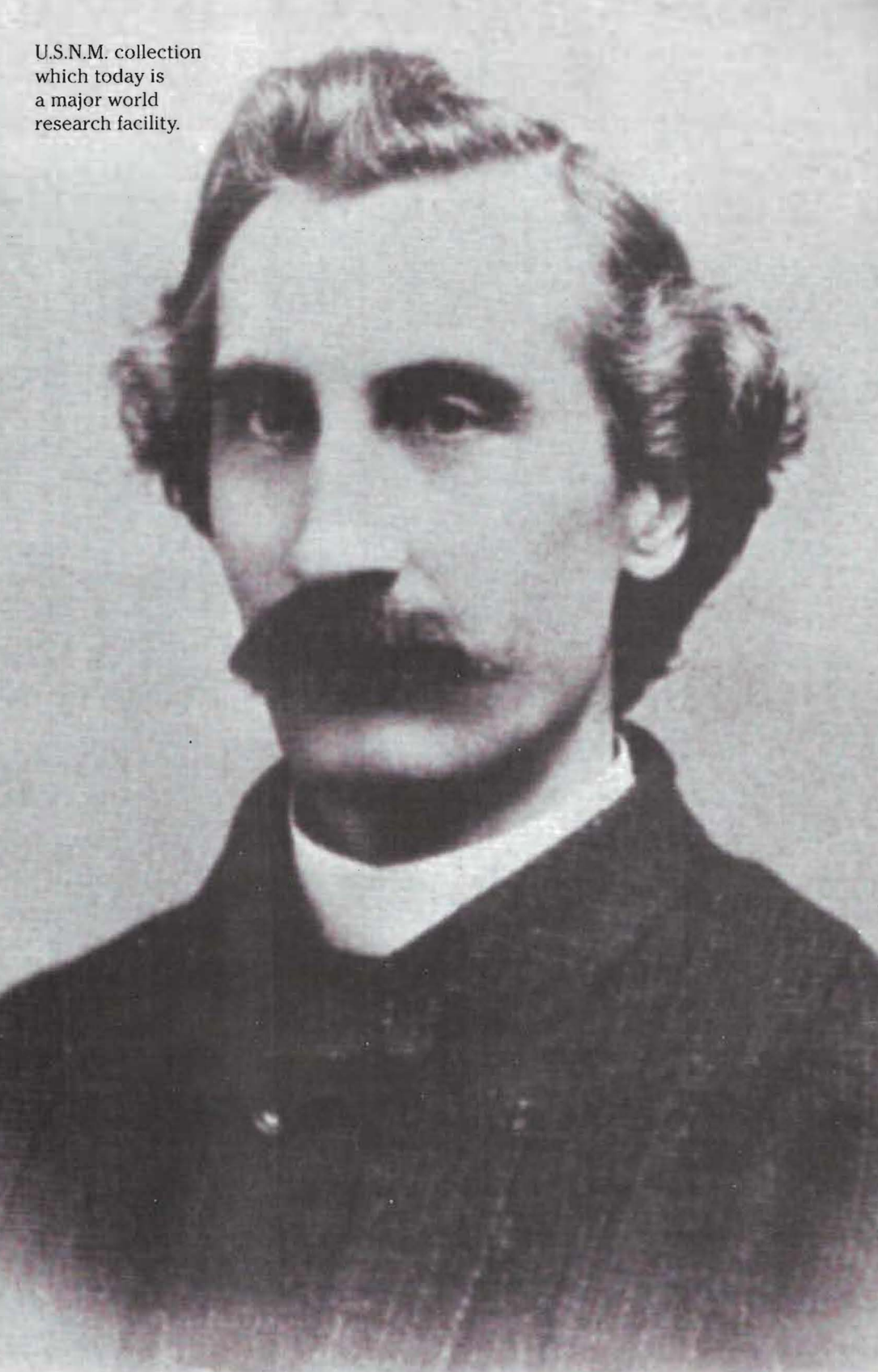
Riley, with the assistance of entomologists Otto Lugger and Theodore Pergande, studied the life cycles of the thirteen and seventeen year cicadas, the life history of blister beetles with unique larval forms, and the strange relationships of figs and fig wasps. Riley very much enjoyed travelling; however, his political enemies were able to curtail official travelling as "extravagance." In 1888, unable to go abroad himself, Riley sent Albert Koebele to an Australian entomological conference. The real mission however was to slip away to collect Australian pests of the cottony-cushion scale, an insect that was devastating citrus crops in California. Koebele brought back the Vedalia beetle which, after being cultured by Coquillet, proved to be an excellent predator and nearly miraculous biological control of the scale.

Riley's insight into the yucca moth as a pollinator required tedious field work, including much nighttime observation. This was conducted during his earlier days in Missouri, and mostly on the cultivated yuccas. Everyone knew bees pollinated many flowers, but the role of the small white moths sometimes found in the yucca flower was by no means obvious.

When Riley published the details of the yucca moth-yucca plant relationship in 1892, he had worked out its basic life history. He had answered the questions that could be asked at that time. Evolution by natural selection had been elaborated by Charles Darwin and the explanatory power of this theory was of great use in understanding insect diversity. Riley was an avid advocate of evolution and travelled to England to meet Darwin. Darwin was particularly interested in Riley's understanding of insect mimicry, a biological phenomenon only understood in the light of evolution. Riley also corresponded with Alfred Russell Wallace (co-discoverer of evolution by natural selection), Henry Bates (of Batesian mimicry), and Herbert Spencer.

However, the work of Gregor Mendel had not yet been recognized, and it would be over a half century before the fields of genetics and evolution developed to where additional questions in population genetics and population ecology could be asked. Riley's account of the yucca moth and yucca plant was so complete that further research only began again in the 1980s.

On September 14, 1895, three years after publishing the yucca moth relationship, C.V. Riley was speeding along on his bicycle when he hit a granite paving block that had fallen from a wagon. He broke his skull against the pavement and never recovered. He died at the age of 52, leaving behind his widow and five children. He had been a curator of insects at the United States Museum of Natural History. His 115,000 mounted insects formed the core of the



U.S.N.M. collection which today is a major world research facility.

YUCCA FLOWERS

Flowers are produced on a vertical stalk, called a raceme inflorescence. The flowers are similar to related lilies and have three sepals, three petals, six stamens (the male structures bearing pollen) and one pistil (the female structure containing the plant eggs in a ovary). The sepals and petals are greenish white and very similar in structure, so they are called "tepals."

The white yucca flower is a perfect place for a white yucca moth to hide in the daytime. Indeed, the yucca moths are so secure inside the flowers that a researcher has to batter a flower considerably to encourage the moth to leave. The moths are so cued to fly into white flowers that they readily enter a small white insect net made from the scoop from lemonade mix-they see it as another flower! Like many other moths, they are not attracted at all to lights at night.

The yucca pollen is on the anthers at the tips of the stamens; the pollen is sticky and remains so throughout the flowering season–a fact first observed by Riley. The yucca stamens bend away from the female stigma, and reach only two-thirds the length of the pistil. Through evolution, the flower is "doing" all it can to favor the moth and prevent self-fertilization.

YUCCA PRODUCTS

Indians used the yucca plant for many products. The strong fibers from the plant made cord, cloth, baskets and sandals. Raw flowers were eaten in salads, or boiled as vegetables. The immature pods were roasted and peeled before eating. Dried pods and seeds were ground into flour. The roots form a frothy soap (hence the name "soapweed) that was both a cleansing agent and a skin cream used for treating rashes. Leaves and roots were also used as a tea for treatment of headaches, arthritis and gonorrhea.

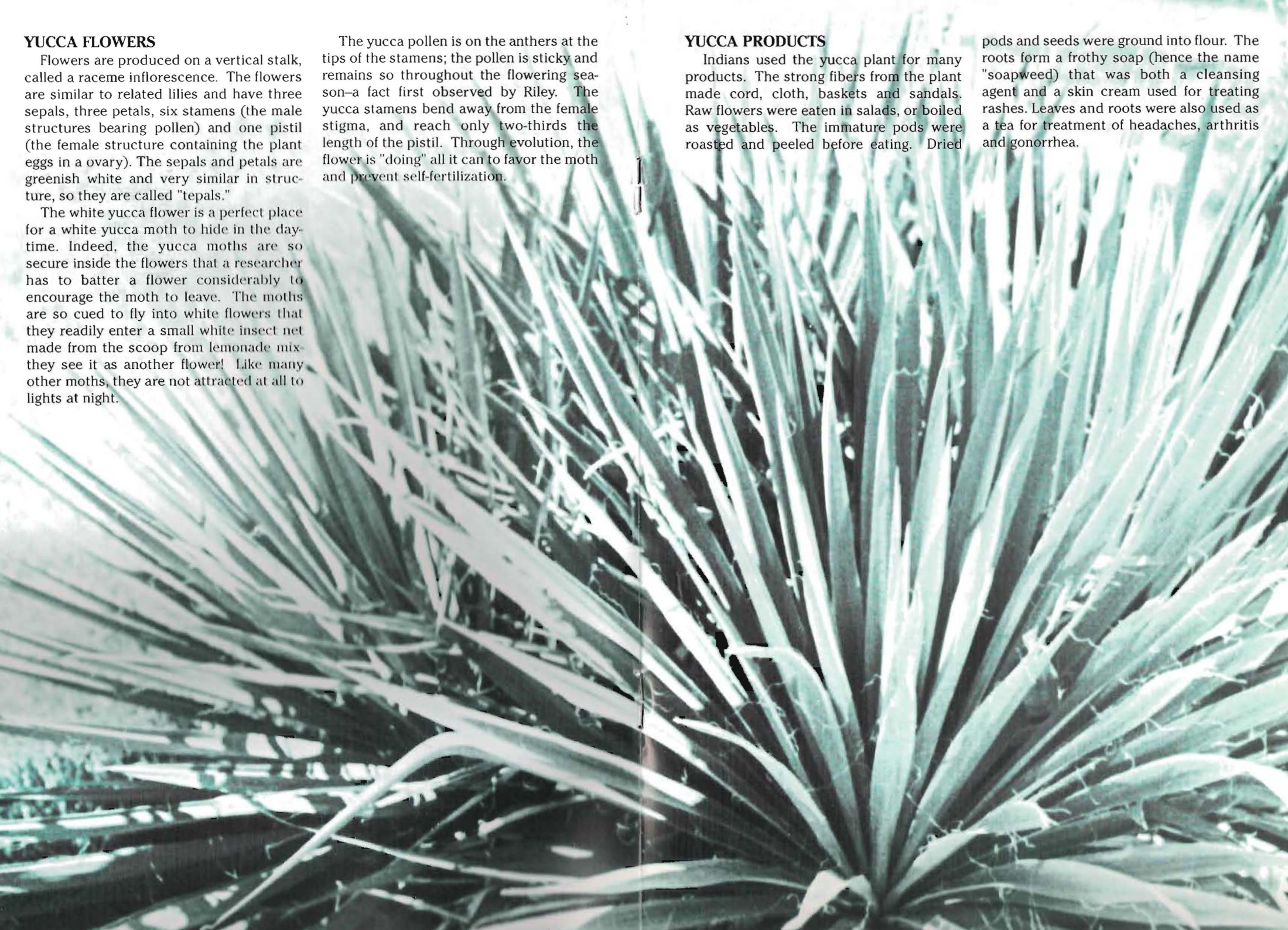


Figure 3. Yucca moth caterpillars found eating the seeds inside yucca pods during the summer. Each larva is over a centimeter long.

YUCCA PODS AND LARVAL MOTHS

By mid-June, the white yucca flowers have all dropped away. Many yucca stalks are barren, indicating that there were no yucca moths to present in the locality. But green yucca pods during the summer are a sure sign the moths were busy in the flowers, and most pods will contain a few of their larvae.

Six stacks of black coin-like seeds form rows inside the pods. You can split the green pods into thirds, each carpel holding two rows or locules of seeds. The small gray-to pinkish yucca moth caterpillars may be feeding anywhere in the core of the seed rows. If they burrow toward the end and run out of food, they bore sideways into another locule or across a carpal wall. Often an outside constriction in the pod reveals their internal consumption of seeds.

Germination of yucca seeds reveals that nearly 100 percent are viable, so every seed eaten or left intact was/is a potential yucca plant. Figure x shows that while most pods hold two or three larvae, it is possible to find no larvae at all, or as many as six to twelve! Since there must be pollination to produce a pod, it is possible that egg laying was disturbed by storms, etc. or that some eggs fail to hatch and young larvae die. But the higher numbers of larvae also suggest that the moth has the potential to eat a larger share of the seeds without some control by the plant.

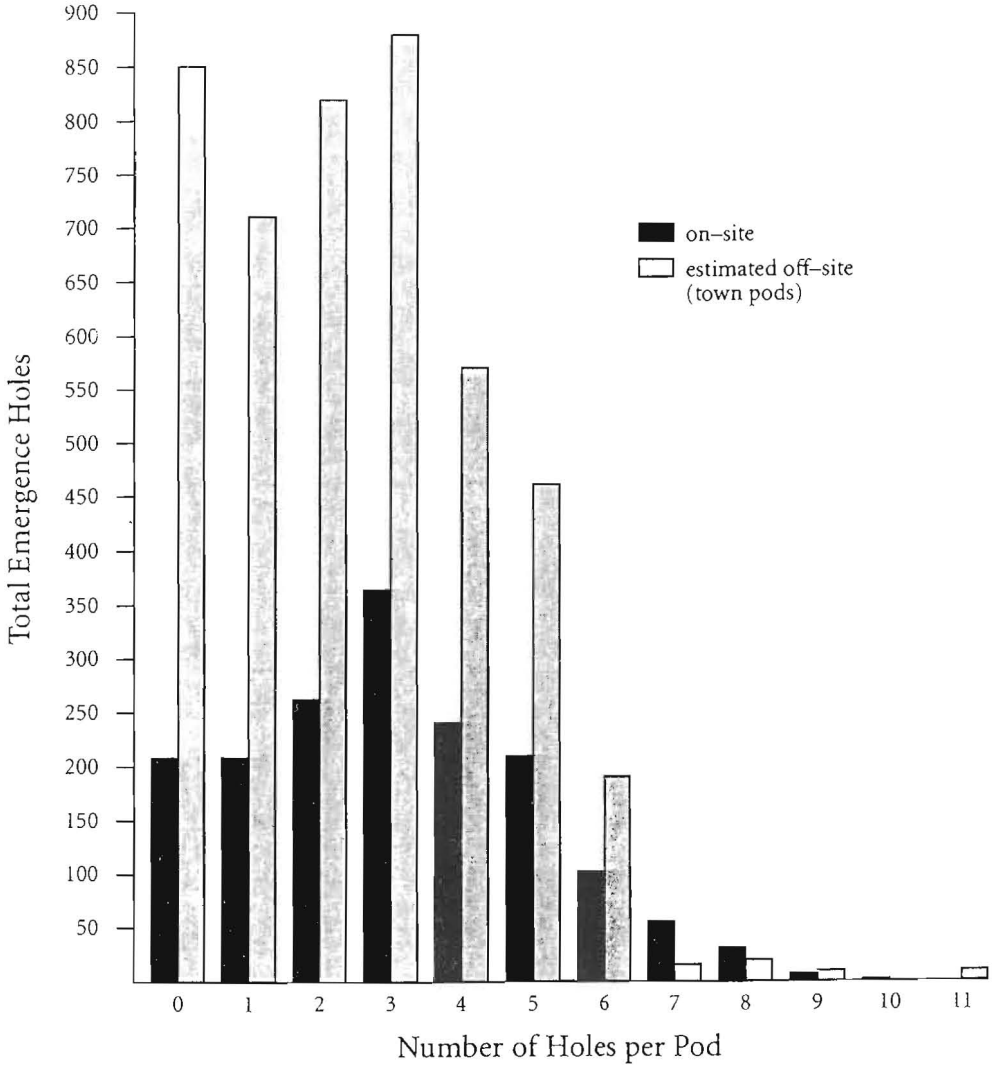


Figure 4. Total number of emergence holes according to the number of holes per pod sampled (from Ramsay).

BAILING OUT OF THE PODS

When the larvae are mature, they excavate an exit burrow to the surface of the pod, although they may continue feeding for a time. When they completely chew through the surface, they leave an exit hole or scar. Riley describes the larvae as descending to the surface on a silken thread, a common ability for many caterpillars. Davis reports that they just drop to the ground. In either case, the larvae begin crawling for some time and eventually burrow into the soil to form a cocoon and eventually pupate. It is assumed that they emerge the next year but Riley observed one larvae unchanged and still living in a cocoon after two and a half years.

OLD PODS

By August, the green pods begin to blacken and dry out. The caterpillars have long since left and the pods continue to dry and split. Over the next year, the shells act as "pepper shakers," rustling and sporadically scattering the black seeds. The wind that dislodges the seeds also increases the chances the flattened discs are carried some distance.

Figure 5. Yucca pods at end of summer.

WHAT PREVENTS A CHEATER?

The most puzzling aspect of the yucca and moth relationship is what prevents a "cheater"?

A cheater is a female moth that lays two or three times the number of eggs per flower, thus producing so many larvae that all of the seeds in the pod are consumed. While this would result in two to three times the number of moth offspring in the next generation, it would also decimate the seed production of the local yucca plants. Over time, if the yucca plants failed to produce variation needed to survive changing conditions or disperse to better areas via seeds, the local population–and the cheating yucca moth–would die off. This theory for controlling greedy moths is called "group selection" because the whole group is "selected against." Yet most biologists do not believe in group selection, in part because we do not see whole communities die out from heating organisms and because other factors directly limit "cheating."

From Figure 4, it is obvious that some pods do indeed carry more than two or three larvae. It is not known whether this is due to one cheating moth laying many more eggs, or from a failure to deposit a chemical signal that eggs have been laid, and other moths each lay a few more additionally. But on average, over two-thirds of the seeds escape being eaten by larvae.

What might be discouraging moths from laying more eggs per flower? Kingsolver suggests that the yucca plant produces a huge array of flowers and then drops (or "dehisces") a large number of the flowers

WHAT WE DO NOT KNOW

In the fall when the larvae emerge from the pods and drop to the ground, where do the larvae go to pupate (change into an adult moth)? Do they pupate in the rosette of yucca leaves or away from the yucca plant? Do moths emerge the very next spring or do they emerge after two winters?

How does a female moth know if she is revisiting a flower she has already pollinated, or if it has been pollinated by another moth? When she lays eggs, is she leaving a pheromone, a scent that signals other moths that this flower has been "taken"?

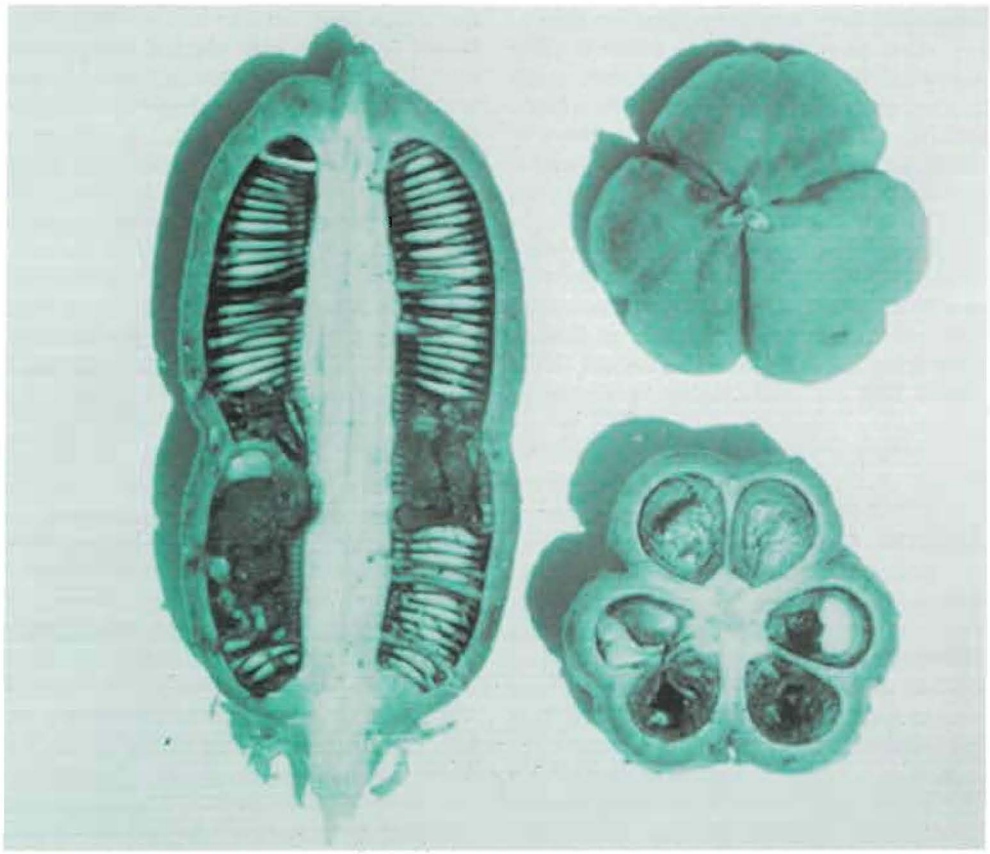


Figure 6. Interior of yucca pods showing damage by yucca moths. Plenty of black disc-like seeds remain to produce future yucca plants..

including many that have been pollinated. This establishes a "lottery": if the moth gambles on a few big bets–laying lots of eggs at a few flowers–they may all be dropped and she produces no young. If the moth places smaller bets (fewer eggs) on many more flowers, there is a greater chance that a few will be among the flowers that are not dropped, and will produce some more moths. In this way, a plant might force moths to lay eggs "thin and wide."

HOW DID THE YUCCA AND YUCCA MOTH RELATIONSHIP EVOLVE?

The first fossil flowering plants appear in rocks formed 90-120 million years ago. Flowers improved a plant's ability to reproduce with variation. There were no pollinating bees and wasps, moths or butterflies prior to flowering plants, and the first pollinators were beetles. The gradual improvement in flowers' ability to attract insects, and the modification of insects to better pollinate flowers resulted in an evolutionary explosion in flowering plants and pollinating insects. North America, at that time, was a major site of
flower evolution and the coevolution of the yucca and yucca moth began in southwestern North America.

The beneficial relationship has probably evolved recently in geological time. The primitive yucca plants most likely relied on wind to distribute pollen, fertilize flowers and produce seed. Today, only the moth can do this job.

There are close relatives of the yucca moth that mine the vegetative tissues of the plant; they are yucca "pests" and provide no benefits to the plants. The ancestors of the yucca moth almost certainly began as harmful feeders on yucca tissues but converted to feeding on seeds and

eventually took over the pollination duties.

One possible scenario follows. The ancestral yuccas were plagued with small moth caterpillars that fed inside plants shoots. As with modern moths, there is some variation in each generation, and a few eggs are laid beyond the stems on blades and flower parts. Eggs laid in fertilized flowers discovered an untapped developing supply of seeds rich in protein, and their young survived in high numbers and reinforced this population of flower-inhabiting larval moths. The variant larval moths that ate seeds added a burden to the plant, but moths that moved from flower to flower also carried pollen with more accuracy than casting pollen to the wind. Such a tradeoff, perhaps only slightly in the plant's favor at first, became even greater as moth variants became more skillful at transfer of pollen, especially by selection for palps and behavior to comb the yucca pollen from anthers. Meanwhile, the yucca could save much energy by forming pollen that is gummy rather than fine and wind dispersed. To evolutionary biologists, confirming this sequence remains an exciting problem.

SOLVING PROBLEMS

A. C.V. Riley correctly determined that the yucca plant is not wind pollinated, but requires the yucca moth to fertilize flowers and produce the seed pods. Since you cannot watch flowers 24-hours a day, how would you design an experiment that proved yucca is not wind pollinated?

B. Some of the pods collected in Figure 4 did not contain moth larvae. Does this prove that pods can develop without pollination by a moth? What are some possible reasons such pods might develop without any larvae?

C. Yuccas are commonly planted to beautify front yards. After the stalk of flowers has withered in June, some homeowners prefer to cut down the "ugly" stalk with pods that remains. What effect will this have on yuccas flowering the next year? Will they set pods again?

D. Yucca plants can be purchased at nurseries and carried home with a ball of soil around their roots, to be planted. Some of these yuccas soon have yucca moths but there are no other yucca plants in the county. Where could the moths come from?

E. You ink-stamp the hands of 50 students entering the stadium to watch a ballgame. Inside, you pick a sample and count that only one out of ten have hand-stamps. How many students are attending the game? How would this estimate be affected if some left early (equal to some dying)? How would this be affected by a migration in of a busload of fans? You can further explore the Lincoln Index in an ecology book.

F. Some of the pods collected in Figure x show six to twelve larvae, enough to decimate all the seeds. If yucca moths "should" only consume a portion of the seeds, what might have "gone wrong" to permit more larvae to develop?

G. You have a cluster of yucca plants that had moths and produced pods, but you accidentally cut and destroyed the stalks and pods before the moths emerged. Since there are no other yuccas in you region, and the moths do not fly far, you do not expect to have any moths or pods next year. Yet, next year both moths and pods appear. Give a possible explanation that does not contradict the above facts.

H. Although it is not possible to go back in time and "rerun evolution", biologists can piece together snapshots of evolution by finding intermediate forms that have survived through to today. What "intermediate forms" would help us understand how the yucca and yucca moth relationship evolved?

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