

Science Newsletter

Blister beetle nest parasites cooperate to mimic the sex pheromone of the solitary bee *Habropoda pallida* (Hymenoptera: Apidae)

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The solitary bee *Habropoda pallida*Timberlake is the first native bee to
emerge in the spring on the Kelso Dunes
(Figure 1) in Mojave National Preserve.



Figure 1. Kelso Dunes in the Mojave National Preserve where *Habropoda pallida* nests and depends on the early blooming nectar source of the Borrego milkvetch, *Astragalus lentiginosus* var. *borreganus* (in the foreground), which is also the food plant of the adult blister beetle *Meloe franciscanus* in the winter months. The Mojave Desert ecosystem supports 689 species of bees, which is the highest bee diversity in North America. Image © L. Saul-Gershenz, all rights reserved 2006.

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Its emergence is generally synchronized with the onset of blooming of the Borrego milkvetch Astragalus lentiginosus var. borreganus M. E. Jones. This plant is also the sole host plant of adults of the blister beetle Meloe franciscanus (Coleoptera: Meloidae) Van Dyke, an obligate nest parasite of the bee Habropoda pallida. The adult beetles emerge on the dunes in the winter months and feed exclusively on the



Figure 2. Adult female *Meloe franciscanus* feeding on *Astragalus lentiginosus* var. borreganus foliage at Kelso Dunes, Mojave National Preserve. *Meloe franciscanus* is an obligate nest parasite of the bee *Habropoda pallida*, with beetle larvae completing their entire development inside a bee's nest. Image © L. Saul-Gershenz, all rights reserved 2006.

leaves of *A. lentiginosus*, which leafs out in January (Figure 2). *Astragalus lentiginosus* provides nectar to *H. pallida*, a key pollinator in the Kelso Dunes ecosystem and likely also in other dune systems throughout the greater Mojave Desert ecosystem. It is considered an oligolege (specialist) of creosote (*Larrea tridentata*) (1, 2, 3), but ongoing research in both low and high precipitation years is revealing that *H. pallida* is more plastic in



Figure 3. Meloe franciscanus larval aggregations averaged 549 larvae (ranged from 120 to > 2000 and averaged 6.9 +/- 2.8 mm in diameter (range 2-15 mm n=153) 55% were ≥7mm) (Saul-Gershenz and Millar 2006). Female abdomens' average diameter is 6.9 mm (Hafernik and Saul-Gershenz 2000). Adult female Meloe beetles begin emerging in the winter months and lay their eggs at the bases of grasses. Egg masses laid at the base of Astragalus sometimes become exposed, due to windblown sand movement. Astragalus has a single tap root system making it vulnerable to root exposure from wind action while Pleuraphis rigida (big galleta grass) rhizomes extend radially from the base of the plant enabling it to stabilize blowing sand. An oviposition bout ranged from 4.3 to 7.3 hours. Larvae emerged 19 to 43 days later. Published with permission from PNAS 2006, 103:38 14039-14044.

This Science Newsletter:

The Moiave Desert is internationally known as a place to conduct scientific research on desert ecosystems. In fact Mojave National Preserve was designated in part to "retain and enhance opportunities for scientific research in undisturbed ecosystems" as stated in the California Desert Protection Act of 1994. Much of this research is conducted through the Sweeney Granite Mountains Desert Research Center, part of the University of California Natural Reserve System, and the Desert Studies Center, operated by the California Desert Studies Consortium of California State Universities, Both are located in the Preserve.

The purpose of this newsletter is threefold. First, we would like to highlight some of the research being done by scientists in the Preserve and to distribute this information to management and the scientific community. Second, this periodical will allow us to inform the public and research community about science being done by Preserve staff or funded by the National Park Service. And third, we would like to build collaboration between scientists and resource managers so that scientists are made aware of the needs of managers and top quality science is brought to bear on the problems facing resource managers.

This newsletter is published once per year. Copies are available in print at our Kelso Depot Visitor Center, Barstow Headquarters, Desert Studies Center, Sweeney Granite Mountains Desert Research Center, and electronically as pdf documents on the web¹. Articles range from nontechnical news stories to highly technical research reports. All material in this newsletter has been peer-reviewed by subject-matter experts.

Debra Hughson, Science Advisor

¹http://www.nps.gov/moja/naturescien ce/sciencenews.htm

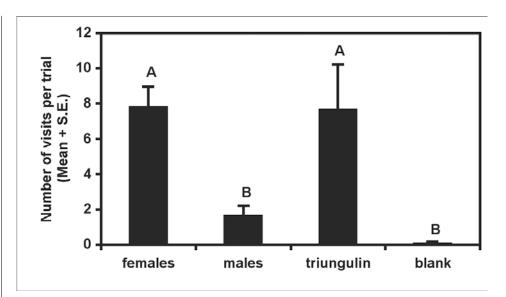


Figure 4. The number of male inspections or "visits" representing attraction of male *H. pallida* bee to hydrocarbon blends mimicking the alkene fractions of female bees, male bees, or triungulins (as per fig. 7) and a control (n=12). Bars marked by the same letter are not significantly different (Student-Newman-Keuls procedure, alpha= 0.05). Control (blank) consisted of hexane. Published with permission from PNAS 2006, 103:38 14039-14044.



Figure 5. *Habropoda pallida* male bee inspecting a *M. franciscanus* triungulin aggregation emitting a blend of female mimicking sex pheromone. Published with permission from PNAS 2006, 103:38 14039-14044.

its host plant preferences than previously thought. This relationship is mirrored at the Eureka Dunes in Death Valley with *A. lentiginosus* var. *micans* and at Panamint Dunes with *A. lentiginosus* var. *variabilis*. The triungulins (first instar larvae) of the blister beetle, *M. franciscanus* are faced with a formidable task: after they emerge, they must find some way of getting to the nests of their host bees. Different species

of parasitic meloid beetles have different strategies for locating the nests of their hosts. Some species climb up on flowers to await bees when they make a nectar visit, grabbing onto the bee and being carried back to the nest (4). In some meloid species, the beetle larvae crawl around on the ground in search of bees' nests, whereas in others the female meloid lays her eggs near the entrance of



Figure 6. Habropoda pallida male immediately after an encounter with an aggregation of Meloe franciscanus larvae feeding on nectar from Astragalus lentiginosus var. borreganus. Image © L. Saul-Gershenz, all rights reserved 2004.

a bee's nest, so the newly hatched larvae just have to crawl into the nest.

However, M. franciscanus employs a completely different approach. Meloe franciscanus eggs from a single large egg mass all hatch together, emerge from the sand, and climb up grasses where there are no flowers with nectar to attract bees (Figure 3). At or close to the top of the stem, the beetle larvae form a tight mass (5). This was the unusual behavior that initially caught my (LSG) attention. The larvae aggregate and they cooperate to stay aggregated for up to fifteen days without feeding (mean 5.4 days, range 1-15 days, n=36) (5). They move together up and down on big galetta grass (Pleuraphis rigida) or on other species of dune grasses, but remain aggregated. Also, their emergence is timed to coincide with the emergence of male H. pallida, which appear before the females.

In experiments conducted over several

field seasons, we determined that the aggregations of beetle larvae are collectively producing a scent that mimics the volatile sex pheromone utilized by female bees to attract males for mating. In particular, we found that whole body extracts from either the female bees or the beetle larvae contained the attractive blend of compounds (Figure 4) (6).

Thus, to get to the nest of a host bee, the newly hatched M. franciscanus triungulins aggregate and cooperate to mimic the sex pheromone of the female bee (Figure 5). When male bees are attracted and approach the aggregations, the whole mass of several hundred beetle larvae attaches to the male in a fraction of a second (Figure 6) (5, 6). The male, with all his larvae passengers, then flies off to find a female bee. During mating or mating attempts, the beetle larvae transfer to the female bee, and she carries them back to her nest, where they feed on the pollen and nectar that she has used to provision the nest, and

her egg. The nest is 1.5 to 2 m deep in the sand dunes and the next generation of adult blister beetles emerges the following January. The male bees are even attractive to other males when covered with *Meloe* larvae because they smell like a female bee.

The compositions of the sex pheromone of the female bee and the mimicking *M*. franciscanus larvae were identified by gas chromatography coupled to mass spectrometry. The sex pheromone is a blend of long-chain cuticular hydrocarbons and is comparatively long lasting (Figure 8) (6). The sex pheromones are produced in the cephalic glands of the female bee. Interestingly, Meloe franciscanus only mimics a subset of the female H. pallida sex pheromone because apparently this subset of compounds is sufficiently attractive to be effective (Figure 4) (6). Thus, these beetles have evolved a very clever way of getting to the scarce resource (a bee's nest) that they must find in order to survive in the harsh environment in which they live. Instead of searching for a host nest, they attract the host to them, and then have the host carry them to a nest.

The Mojave Desert ecosystem is a hotspot of native bee diversity with 689 species, the highest bee diversity in North America, based on an inventory conducted in 2004 and 2005 (7). This is concordant with the immense botanical diversity found in the Mojave, as shown by an inventory of the Mojave National Preserve that identified 928 plant species (8). It is then not surprising to find some of the most remarkable examples of natural selection in this environment where species diversity is high and organisms live at the edge of ecological and physiological tolerances and will likely be under pressure as global climate shifts.

We have determined that *M. franciscanus* also parasitizes several other sister species of solitary bees in the genera

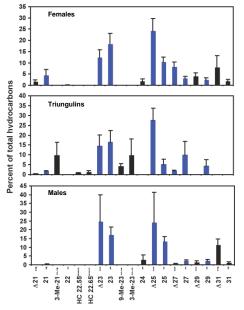


Figure 7. Composition of the extracts of female and male *H. pallida* heads (~n=12) and *Meloe franciscanus* triungulin aggregations (n=6), Numbers equal hydrocarbon chain length. Published with permission from PNAS 2006. 103:38 14039-14044.

Habropoda and Anthophora that are found throughout the southern deserts of California. The focus of our current research is the elucidation of the mechanisms of how this sex pheromone mimicry system bridges species and genus boundaries and enables this nest parasite to use multiple bee species as hosts across its extensive range.

In addition, long-term mapping of bee nesting sites in the Mojave National Preserve (LSG) and desert bee biodiversity surveys have yielded two major nesting populations of the bee Calliopsis puellae, which is a specialist pollinator of desert dandelion Malacothrix glabrata in the Preserve, a plant documented as an occasional food plant of juvenile desert tortoises (9). New natural history information has been gathered that will aid in the sustainable management of these pollinators for the future health of the Mojave Desert ecosystem.

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Acknowledgements

We are deeply indebted to Debra Hughson, Science Advisor for the Mojave National Preserve for her support and assistance during all aspects of this research as well as Rob Fulton of the Desert Studies Center, (CSU). This research is supported by the Disney Worldwide Conservation Fund, MacBeth Memorial Scholarship grants, and SaveNature.Org. Thanks to Jim Andre and Tasha La Doux for use of the facilities at Sweeney Granite Mountain Research Center (UC NRS). A special thanks to Norman Gershenz for field assistance and support and to John Pinto for his support and continued collaboration and to Rick Westcott. We also thank Peggy Fiedler, John Ascher, Robbin Thorp, Jim Cane and Neal Williams for their shared expertise and support during this project.

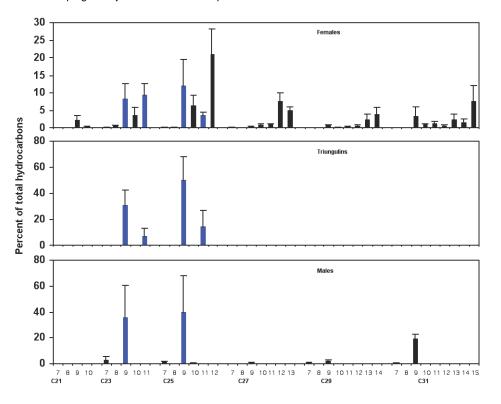


Figure 8. GC-MS analysis and isomeric composition (+/- SD) of the alkene fractions of the extracts of the heads of the female and male H. pallida and *M. franciscanus* larvae revealed that *M. franciscanus* larvae mimic a subset of the female sex pheromone. Published with permission from PNAS 2006, 103:38 14039-14044.

Functional Ecology Measures: Evaluation of Springs in Mojave National Preserve

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Within each type of ecosystem there exist limiting factors that regulate maximum primary productivity, species diversity, and control an ecosystem's food web structure. Water availability is a limiting factor for wetland dependent species in desert ecosystems. Deserts are characterized by the limited amount of rainfall they receive (1), yet numerous small springs and seeps occur in the mountainous desert areas and are focal points of biodiversity. These small wetlands have been historically impacted by cattle grazing and feral burros. Grazing has been retired over much of the Preserve but cattle continue to utilize springs on two active permits in the Preserve, while feral burro management is an ongoing priority. We investigated the use of arthropods (insects) for monitoring selected springs within Mojave National Preserve, hypothesizing that species and numbers present may be correlated with cattle or burro use and observable ecosystem impacts (e.g. water quality degradation).

Cattle grazing near water sources may impact species diversity, disrupt nutrient cycling, and alter plant succession characteristics (2, 3). Our preliminary work focused on identifying a range of naturally occurring arthropod taxa and population density relationships above and below which detrimental ecological impacts could be inferred in a spring ecosystem by comparing cattle impacted to non-impacted water sources in Mojave National Preserve. Terrestrial and aquatic arthropods, observations of physical conditions, and water quality parameters will later be combined in a functional ecology framework (4, 5) to characterize the status and level of disturbance of spring ecosystems.

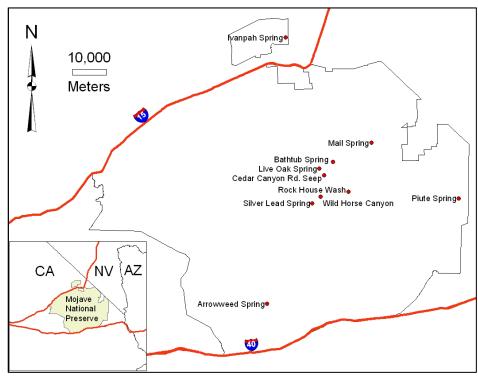


Figure 1. Locations of springs evaluated in this study are shown with respect to Interstate 15, Interstate 40, and the boundary of Mojave National Preserve.

We sampled arthropods and estimated vegetation cover at ten springs (Figure 1, Table 1) in Mojave National Preserve. Beginning in 2008, we placed ten commercially available yellow sticky traps at each of the spring locations (Table 1) within or near the watercourse for three two-day intervals in August and July. Observations were made of vegetation cover, cattle presence, and existence of an exclosure fence around the water source. Yellow sticky traps were placed at the same locations in May, 2009, along with pan traps filled with a water and propylene glycol solution, in order to obtain a broader range of specimens in better condition for improved identification. Both pan traps and sticky traps were placed in transects at the four locations with highest biodiversity, based on results from previous sampling, during the second week of April, 2010, and collected four days later. The period of

early April in Mojave National Preserve is a peak of diurnal activity and seasonal occurrence of arthropods corresponding to at a heat unit accumulation of 250 DD₅₀ °F (degree-days Fahrenheit). We used various pheromone and kairomone odor attractants to lure specific insect species to the traps. The traps were placed as inconspicuously as possible, taking into consideration terrain, plant height, and proximity to well-traveled human routes in order to minimize contact and disturbance by animals and humans. These techniques of arthropod trapping are minimally disruptive and limit potential confounding factors related to human presence.

Typical species collected by the sticky traps and water pan traps included *Halictus ligatus* (bees), *Acanalonia* spp. (plant hoppers), *Ammophila* spp. (threadwaisted wasps), and various members of

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Chrysididae (cuckoo wasps) (Figure 2). Preliminary identification based on field observations and comparison to known arthropod species from taxonomic records has indicated that in excess of 300 arthropod species were collected near these water sources. A complete list of taxa is pending further identification by specialists in Hymenoptera and dipterans.

Analyses are as yet incomplete and it is unknown what proportion of biodiversity and what species were missed by limited sampling. Our sampling did, however, suggest there may be a higher arthropod diversity at the sites without grazing presence as compared to sites with evidence of cattle impacts, which corresponded to observations of greater vegetation cover, lower water turbidity, and less evidence of trampling at sites without cattle. Existing exclosure fences had been successful at preventing cattle ingress to the water source at the two sampling sites we observed with fences. Greater numbers of pollinator insects and natural enemy insects (i.e. those which tend to reduce the reproductive success of other insects) were noted in the undisturbed zones inside the fenced exclosures. Higher levels of natural enemy insects may reduce pestiferous populations such as biting flies and mosquitoes in the vicinity of springs. Fewer species overall were sampled at water sources utilized by cattle and the spring source areas tended to show more signs of cattle trampling. Most of the water sources utilized by cattle have pipes and troughs that divert water for livestock. These diversions appear to reduce flow in the small wetland zones around spring water sources. Samples from sites with cattle tended to have higher levels of biting flies, fecal feeders, and gnats compared to sites enclosed by fences and those without cattle. These initial results, however, represent preliminary indications and are inconclusive pending additional sampling and complete analysis of the data.



Figure 2. Examples of insect specimens recovered from the water and sticky traps deployed around Mojave National Preserve springs: *Halictus ligatus* (top left), plant hopper [Acanaloniidae] *Acanalonia* (top right), [Chrysididae] (bottom left) and *Ammophila* (bottom right).

A surprising and significant finding of this study was the first detection record in Mojave National Preserve of spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), an invasive species from Asia (Figure 3) that has been destructive in fruit orchards in

western California. After its recent introduction into the U.S., spotted wing drosophila has been tracked across California, Oregon, Washington, Florida, North Carolina, and Michigan. Six specimens of spotted wing drosophila were collected at the Arrowweed Spring

					Vegetation Cover (%)		
Name of water source	Date	Elev.	Excl.	Cattle	Water	Bank	Overall
		(m)			Course		
Arrowweed Spring	1-5	1207	Yes	No	90	60	75
Bathtub Spring	1-4	1772	No	No	20	40	30
Cedar Canyon Rd. Seep	1-4	1558	No	Yes			5
Ivanpah Spring	1-4	1295	No	Yes	15	60	30
Live Oak Spring	1-4	1512	No	No	80	50	70
Mail Spring	1-5	1527	Yes	No	40	60	50
Piute Spring	1-4	829	No	No	90	45	80
Rock House Wash	1-4	1550	No	Yes	10	25	15
Silver Lead Spring	1-5	1623	No	Yes	10	20	15
Wild Horse Canyon Rd.	1-5	1661	No	Yes	30	40	35

Table 1. Arthropods were collected at 10 water sources in Mojave National Preserve on sample dates: 1 (July 21-22, 2008), 2 (July 28-29, 2008), 3 (Aug. 4-5, 2008), 4 (May 22-23, 2009), and 5 (Apr. 17, 2010). Vegetation cover was estimated within the wet area of the water course, along the riparian bank, and for the spring site overall. Presence of cattle and a fenced exclosure were noted.

sample site (Figure 4) on two of six yellow sticky traps deployed in May, 2010. No spotted wing drosophila were found at Arrowweed spring during the subsequent sampling the following year, but three more specimens were collected in vinegar traps placed at Kelso Depot near a waste container at the visitor parking lot. At the Arrowweed Spring site, where the spotted wing drosophila specimens were initially found, several large trash bags of litter had been left behind by park visitors. Spring flow and vegetation cover at Arrowweed Spring (Figure 4) have increased since retirement of grazing in 1998 and it had one of the higher levels of arthropod biodiversity found during this sampling. Although it is unknown how the spotted wing drosophila arrived in the Preserve, its correlation with trash—especially discarded fruit—was noted. Previously infested fruit could account for the presence of spotted wing drosophila, although none were found in the garbage left at the site.

Management of high desert springs in Mojave National Preserve to conserve biologic diversity and ecosystem function must take into account potential impacts from visitor use as well as cattle grazing on permitted grazing allotments and feral burros. Periodic inspections of popular locations, such as Arrowweed Spring, for removal of garbage, and monitoring for pestilent insect invasion are recommended. Exclosure fencing appears to function as intended to protect the spring sources area and should continue to be maintained.

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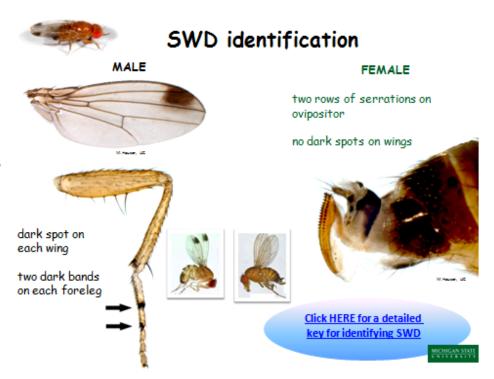


Figure 3- Spotted winged drosophila (SWD) taxonomic characteristics suitable for species identification. *Drosophila suzukii*, commonly called the spotted-wing drosophila, is a vinegar fly—closely related to *Drosophila melanogaster* (the common vinegar fly).



Figure 4. Arrowweed Spring in Mojave National Preserve.

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Endemic Kelso Dunes Insects:

a Hotspot of Biodiversity

Doug Yanega¹



Polyphylla aeolus, Kelso Dunes endemic (photo by Greg R. Ballmer).

As is true of nearly all of the dune systems in the US, the Kelso Dunes contain a large variety of insects that are known only from that area. Compiling a complete list of endemic insects would be a difficult task given that the various species can be in virtually any order, and especially difficult because a fairly large number have yet to be described or even discovered. The number of practicing insect taxonomists studying the fauna of the Kelso Dunes is very small (and always has been), so only the proverbial tip of the iceberg has been scrutinized, and what *is* known is scattered through the literature, rather than compiled in any single resource. Obviously, the knowledge of each group of insects reflects the taxonomic expertise of those few workers who have studied the fauna. and each component has been worked on in isolation. The crickets, for example, received a fair bit of attention many years ago, resulting in the description of many endemic taxa such as Ammopelmatus kelsoensis, Eremopedes kelsoensis, and Macrobaenetes kelsoensis. A quick review also reveals that many of the endemic species have only been described since 1975, (e.g., the fly Rhaphiomidas tarsalis, the scarabs Polyphylla aeolus and Aegialia kelsoi, a



Rhaphiomidas tarsalis, Kelso Dunes endemic (photo by Greg R. Ballmer).

couple of species of weevils including *Trigonoscuta kelsoensis*, and the aphid wasp *Spilomena kelso*), suggesting that we are only just beginning to develop an idea of the endemic species that inhabit the Kelso Dunes.

There are some species which are presently thought not to be endemic, but which will certainly prove to be so when detailed work is finally complete (e.g., a flightless darkling beetle in the genus Lariversius, a newly-described bee in the genus Hesperapis, and a newlydescribed pollen wasp in the genus Euparagia, all of which are believed to occur elsewhere, though the populations at Kelso Dunes are morphologically different from those elsewhere, and may only need some genetic work to be shown as distinct). There are many species known to be new, but still awaiting formal description, including a few species of bees in the genus Perdita, and wasps in the genera Belomicrus and Plenoculus. Most important, though, is that there are undoubtedly dozens of species still undiscovered, either residing as specimens in museums, or not yet having been collected; one can only guess at how many taxa remain to be found. As such, existing collections of specimens from this area, and future collections, will be of crucial importance if we are ever to even approach some sort of definitive list of endemic species.

Diversity of several Hymenoptera taxa is concentrated in the North American deserts, with the eastern Mojave Desert their apparent origin and center of diversity, including large bee genera such as *Ashmeadiella*, *Hesperapis*, and most notably *Perdita* (1).

Reference

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This Science Newsletter is a publication of Mojave National Preserve, 2701 Barstow Road, Barstow, CA 92311.

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The Mojave National Preserve Science Newsletter accepts contributions from qualified researchers on scientific work in progress or completed in Mojave National Preserve. Articles can range from general interest stories intended for a broad audience to technical research reports. If you are interested in publishing in this Science Newsletter, please contact the editor. Manuscripts, including figures, photographs, maps, references, and acknowledgements, should be less than 5,000 words. References and notes should be in the *Science* reference style¹.

¹http://www.sciencemag.org/about/author s/prep/res/refs.dtl

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