



Histograms comparing the numbers of *T. maculata* eggs contained in 26 pairs of aborting (pink bars) and maturing (green bars) fruits. Aborting fruits contained more eggs (Wilcoxon's signed-ranks test,  $P < 0.001$ ). Fruits were collected from 26 plants. Fruits within a pair were located directly opposite each other on the same branch. Pairs in which one was aborting and one was not were collected, then dissected to determine the number of moth eggs. The proximity of the fruits on the branch indicates that they were produced and exposed to oviposition at the same time.

per flower, and number of seeds destroyed per larva, we estimate that with random abortion, *Y. w. typica* would mature 167 seeds per fruit, whereas differential abortion resulted in an average of 174 seeds — a 4% increase. By contrast, the impact of differential abortion on moth reproductive success is severe. On average, 0.83 eggs were deposited per fertilized fruit. Of these, 0.40 would survive if abortion were random, but only 0.19 actually survived under differential abortion — a decrease of more than 50%. Thus, the plant shifts a small amount of its cost in this mutualism back onto the pollinator in the form of egg mortality. Although the moth may mitigate this cost shift by depositing fewer eggs per flower, this mitigation must be balanced against the added expense of visiting more flowers to deposit the full complement of eggs.

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PELLMYR AND HUTH REPLY — We disagree with Richter and Weis's suggestion that over exploitation cannot explain the maintenance of differential abortion, on the notion that random abortion would cause only a slight decrease in mean number of intact ripe seeds. First, intact seed gain attributable to selective abortion was 9% in our original data<sup>1</sup>, a fitness difference that (if fixed) would translate into considerable selection for

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differential abortion. The difference in terms of eaten seeds is likely to be a function of pollinator density, rather than a fixed number. A given plant will be able to retain a certain number of flowers to ripe fruit, so that in years of high pollinator density it can retain a subset of flowers with far lower moth density than the average flower. With the Poisson-like egg distribution found in *Yucca filamentosa*, the selection differential will be positively correlated with pollinator density. *Tegeticula* density is highly variable between years and sites<sup>6,7</sup>, so long-term data for pollinator density variation are needed to obtain a robust measure of variation in selection differential between random and selective fruit abortion in yuccas.

Richter and Weis's conclusion that selective abortion is a "general adaptation" agrees with our conclusion that it is a symplesiomorphy within the Agavaceae, and thus a preadaptation within the yuccas. In fact, it was the basis for our proposed model as to why selection could act on colonizing yucca moths to provide high-quality pollination. Our present experiments show strong positive effects on fruit retention of increased pollen load, outcrossing and genotype diversity in *Y. filamentosa*; this effect extends beyond pollen loads needed for complete seed set by a factor of at least ten, confirming the inferred positive effect of multiple moth pollinations suggested by our original dataset.

Why, then, do flowers with many moth pollinations suffer increased risk of abortion? The rapid death of ovules at the point of egg insertion could be a plausible proximal cause as to why flowers with many eggs fail in competition (despite high pollen loads), because they constitute a lesser sink relative to simultaneously developing fruit with more developing ovules. In this scheme, the moths carry the seed of their own demise in the form of an egg-linked factor triggering ovule death — perhaps a preadaptation in a lineage of moths whose more basal taxa oviposit into the flowers of host species without abortion of pollinated flowers<sup>8,9</sup>.

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**Age of early hominids**

SIR — We read the announcement of the discovery and naming of *Australopithecus ramidus*<sup>1</sup> or *Ardirpithecus ramidus*<sup>2</sup> by White *et al.* with great interest, but take issue with its age as reported by WoldeGabriel *et al.*<sup>3</sup> and especially their interpretation of the results from their paleomagnetic sampling.

As noted by WoldeGabriel *et al.*<sup>3</sup>, the geological section at Aramis has several volcanic tuffs present throughout its exposures, but only the Gåala Vitric Tuff Complex which is found at a stratigraphic level below the hominid fossils has been shown to be datable. This tuff, although contaminated, shows one feldspar population having a mean age of  $4.387 \pm 0.031$  Myr which is taken as the maximum age for the fossil hominids<sup>3</sup>. Other tuffs found immediately above the hominid fossil localities were shown to be contaminated and undatable<sup>3</sup>.

In an attempt to further constrain the age of the fossils, WoldeGabriel *et al.*<sup>3</sup> sampled for palaeomagnetic reversal stratigraphy and collected two samples, one of which yielded uninterpretable results. The second palaeomagnetic sample is reported to be of reversed polarity and was collected from a level slightly below the undated Daam-Aatu Basaltic Tuff, both of which are from within the stratigraphic interval of the fossil localities. Although WoldeGabriel *et al.*<sup>3</sup> argue that this single reversed sample constrains the *A. ramidus* material to subchron C3n.1r, this is not the case. Until other older and dated tuffs such as the Sibabi Marker Tuff<sup>3</sup> can be correlated into the section at Aramis either physically or by chemical composition, or other tuffs at Aramis are dated, the only clearly available capping age for the fossils is that of  $3.89 \pm 0.02$  Myr for tuff VT-1 (= Moiti Tuff)<sup>3,4</sup>. The age range for the fossils should be given as 3.89–4.39 Myr, and the reversely magnetized rock sample reported could be from either the younger reversed interval of chron C2Ar (3.58–4.18 Myr) or the older reversed interval of subchron C3n.1r (4.29–4.48 Myr)<sup>5,6</sup>.

Although future work at Aramis may provide more convincing support for an age assignment of *A. ramidus* to subchron C3n.1r, this determination will require either a clear identification of C3n.1n in the sediments that overlie the fossils, or an age determination of greater than 4.18 Myr for one of the tuffs found above the site of the single palaeomagnetic sample reported from Aramis. Until then, the age of *A. ramidus* should be reported as ranging between 3.89 and 4.39 Myr, rather than as "... around 4.4 million years of age" (ref. 1, p. 306; ref. 3, p. 330).

Interestingly, this age range shows near temporal overlap with a variety of specimens attributed to or suggested to show