biology
letters

Biol. Lett. (2006) **2**, 397–400
doi:10.1098/rsbl.2006.0476
Published online 2 May 2006

Seed size variability: from carob to carats

Lindsay A. Turnbull[1,*], Luis Santamaria[2], Toni Martorell[3], Joan Rallo[3] and Andy Hector[1]

[1]*Institute of Environmental Sciences, University of Zürich, Winterthurerstrasse 190, Zürich 8057, Switzerland*
[2]*Instituto Mediterráneo de Estudios Avanzados (IMEDEA, CSIC-UIB), 07071 Palma de Mallorca, Spain*
[3]*Conselleria d'Agricultura i Pesca, Gobierno Balear, 07190 Esporles, Mallorca, Spain*
**Author for correspondence* (*lindsayt@uwinst.unizh.ch*).

The seeds of various plants were used as weights because their mass reputedly varies so little. Carob (*Ceratonia siliqua*), which has given its name to the carat, is particularly famous in this regard. But are carob seeds unusually constant in weight and, if not, how did the myth arise? The variability of seeds sampled from a collection of carob trees (CV=23%) was close to the average of 63 species reviewed from the literature (CV=25%). However, in a perception experiment observers could discriminate differences in carob seed weight of around 5% by eye demonstrating the potential for humans to greatly reduce natural variation. Interestingly, the variability of pre-metrication carat weight standards is also around 5% suggesting that human rather than natural selection gave rise to the carob myth.

Keywords: seed size; trait variability; carob; *Ceratonia siliqua*; carat; karat

1. INTRODUCTION

Seed weight is generally considered to be one of the least plastic of plant traits (Harper 1970). The optimal seed size is commonly supposed to reflect an underlying trade-off between seed size and seed number, where seedling survival increases asymptotically with increasing seed size but at the cost of decreased seed production (Smith & Fretwell 1974). Under this model any variability around the optimum seed size is seen as maladaptive. However, variability might increase when there is sibling competition for maternal resources (Banuelos & Obeso 2003) or when the parent differentially provisions offspring according to their genetic quality (Bernasconi 2004). In contrast, variability might be particularly low when species can regulate the size of the fruit crop, e.g. through selective abortion of seeds (Rocha & Stephenson 1991) or when additional external selection pressures such as size-selective predation operate (Moles *et al.* 2003; Gomez 2004). Species are, therefore, likely to exhibit different degrees of variability in their seed crops.

It is popularly believed that the carat, the unit of weight for gemstones, is derived from the name of the carob tree (*Ceratonia siliqua* L., Fabaceae, see photo in electronic supplementary material) via an ancient weighing system based on its seeds. Carob was reputedly selected in this regard because the mass of its seeds is unusually constant (Tolansky 1962; Harper 1970; Daniel 1972; Janzen 1979). The idea that species historically used for weighing were specially selected because their seeds do not vary in weight seems to be believed by, and may originate with, people who were using seeds for that purpose (Bauer 1969). In the case of carob, the myth has been widely propagated, despite apparent variation between seeds from a single pod (figure 1) and a variety of published claims which are contradictory, usually based on only a single tree, and make no comparison with other species (Tolansky 1962; Daniel 1972; Janzen 1979). Here, we attempt to unravel the relationship between the carat and the carob and propose an explanation for the myth of constant seed weight.

The electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2006.0476 or via http://www.journals.royalsoc.ac.uk.

There appears to be a long history of a weight carrying a name associated with carob and with a mass close to that of a single carob bean. For example, the ancient Greeks had a small weight, the *kerat*, while the *siliqua* (from the Latin for carob, *siliqua Graeca*) is the smallest subdivision (1/1728) of the Roman pound (Smith 1870). Incidentally, the measure of gold purity—also called the carat (UK English) or karat (US English)—derives from the time of the Emperor Constantine when a new gold coin was struck at 72 to the Roman pound, meaning that each coin weighed 24 siliquae or carats. While the exact modern equivalents of ancient weights are of course unknown, various methods such as weighing ancient coins, give widely accepted values for the *siliqua* in the range 189–192 mg (Smith 1870). According to the *Oxford English Dictionary* (OED 1989) the word carat first appeared in 1555 but its weight varied from place to place prior to its standardization at 200 mg in 1907 (Zhengzhang 1991).

While it seems highly likely that the carat is based on the carob, the question remains whether carob was chosen for the commonly stated reason that the seeds are *unusually* constant in weight. If not, it suggests that human selection played a part in establishing the carob myth. We tested the first question by weighing carob seeds from a large number of trees collected from around Mallorca and comparing their variability to that of 63 other species. We tested the second by conducting a direct test of people's ability to infer differences in the weight of seeds by eye and by comparing the distribution of carob seed sizes with the distribution of carat weight standards around the world prior to 1907.

2. MATERIAL AND METHODS

To assess carob seed variability we sampled 28 trees from a collection at Sa Granja agricultural research station, Mallorca. The trees, half of which were female and half hermaphrodite, differed in size and fell into two distinct age groups: older trees dating from before the establishment of Sa Granja in the 1930s and younger trees added since the 1970s. The collection of younger trees was assembled by collecting branches from a wide variety of individuals from around the island and grafting them onto a standard root stock. We weighed all the seeds from two pods on different branches from each tree ($N=550$) but, consistent with other studies, excluded 59 seeds (10.7%) which were aborted, predated or grossly misshapen. Seed weights reported in the main text are means and their standard errors.

Received 16 January 2006
Accepted 23 March 2006

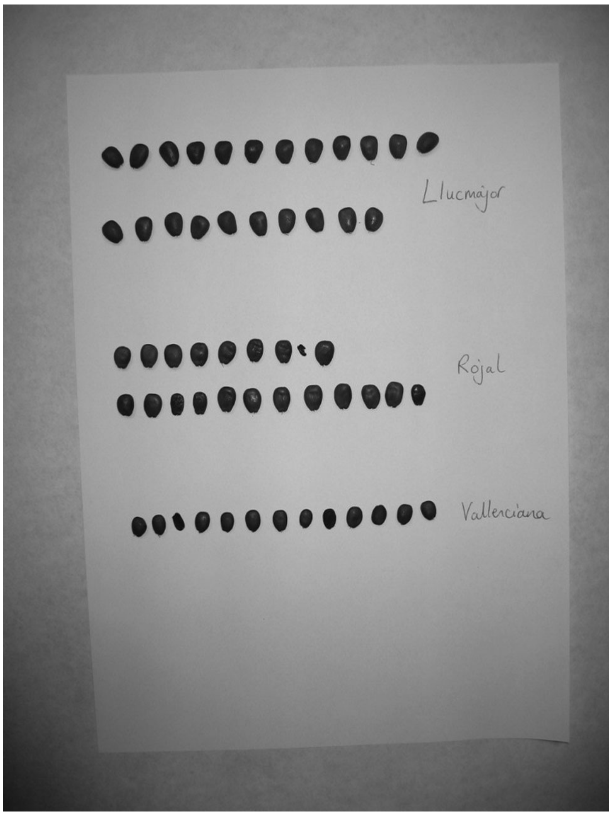

Figure 1. Seeds from five pods (rows) belonging to three different trees (place or origin or variety shown).

We analysed differences in seed weight with mixed-effects ANOVA and variance components analysis using restricted maximum likelihood and implemented with the NLME software for R and S-Plus (Pinheiro & Bates 2000). Age, gender and size of the trees (trunk diameter) were treated as fixed effects, and tree and pod (within tree) were treated as random effects. We analysed variability in seed weight (CVs) within trees and pods to see whether mean seed weight or seed number affected variability. We also tested whether pods containing aborted seeds had lower variability than pods which did not.

The seed size perception study was carried out at IMEDEA. Twenty participants were asked to select the heaviest from each of 12 randomly presented pairs of seeds. They were not allowed to handle the seeds. Each seed pair had the same average mass, 200 mg, but a different CV (0–30%). Data on the weight of the carat in 17 different locations worldwide prior to 1907 were taken from Zhengzhang (1991).

Background information on *C. siliqua* can be found in a comprehensive review of the literature by Batlle & Tous (1997).

3. RESULTS

The average mass of seeds from female trees (200.5 ± 2.47 mg) was very close to the metric carat (200 mg) while seeds from hermaphrodite trees were lighter (175.8 ± 7.1 mg) possibly reflecting the cost of pollen production (figure 2*a*). However, average seed mass was unaffected by the age or size of the trees (mixed effects ANOVA; age: $F_{1,26}=0.7$, $p=0.406$; size: $F_{1,26}=0.1$, $p=0.704$). There were, however, significant differences between individual trees and pods within trees (likelihood ratio tests for individual trees: $\chi_1^2=11.6$, $p=0.0007$; pods within trees: $\chi_1^2=19.9$, $p<0.0001$). Variance components analysis showed that approximately one-third (30.4%) of the variation in seed mass occurred between trees and two-thirds within trees (13.4% between pods within trees and 56.2% between seeds within pods).

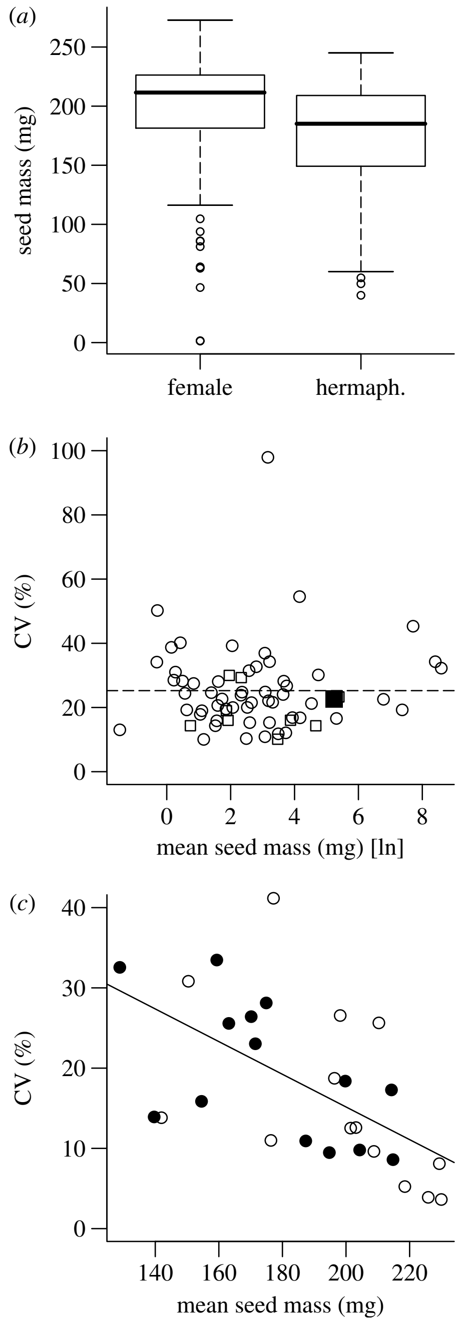

Figure 2. (*a*) Seeds from hermaphrodite (hermaph.) carobs are lighter than those from females (ANOVA: $F_{1,26}=5.5$, $p=0.027$) but have similar variability (box plot shows median, 1 and 1.5 times the interquartile range, and extremes); (*b*) Coefficients of variation for 63 species collected from the literature with the overall mean (dotted line), filled square, carob; open squares, other Fabaceae; open circles, non-Fabaceae species; (*c*) CVs of individual carobs decline with mean seed mass (regression: $F_{1,26}=15.9$, $p=0.0005$, $R^2=0.34$), filled, hermaphrodite; open, female.

Carob did not have unusually low variability when compared with 63 other species including nine other Fabaceae (see table, electronic supplementary material; figure 2*b*): the CV for carob was 22.7% (females = 19.3%, hermaphrodites = 24.4%), for other Fabaceae 19% and across all species 25%. Carobs producing larger seeds had lower variability (figure 2*c*) but despite this effect, trees with an average seed mass equivalent to the metric carat (200 mg) still had a CV of 14.7%. The relationship

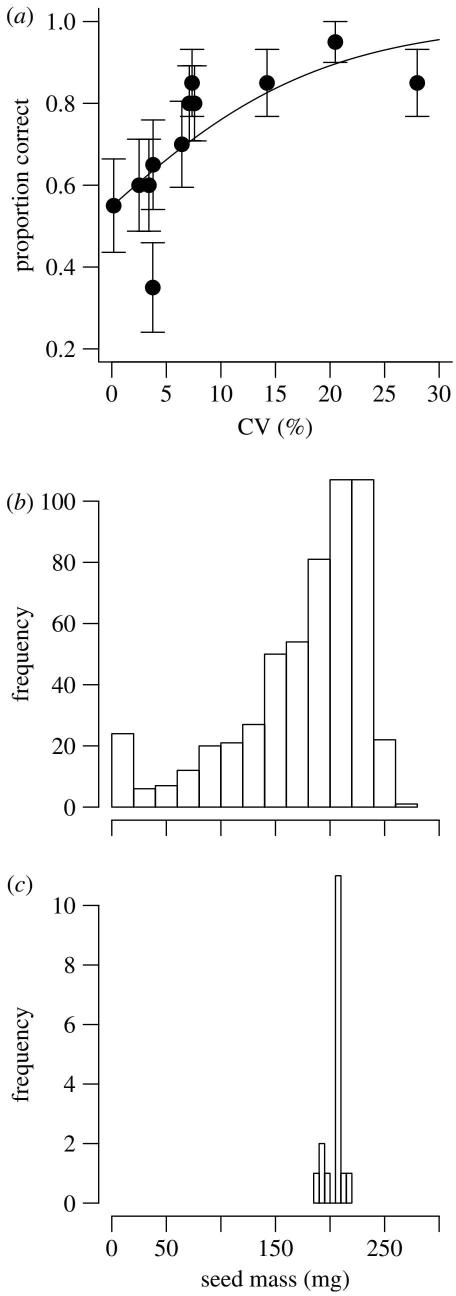

Figure 3. (*a*) Proportion of observers who correctly identified the heavier of a pair of seeds as a function of their CV (logistic regression: $\chi_1^2 = 19.7$, $p<0.0001$). (*b*) The distribution of seed weights in the total sample. (*c*) The distribution of carat weight standards worldwide prior to 1907 (when the metric carat was adopted).

between mean seed weight and variability was the same for both female and hermaphrodite trees (gender: $F_{1,24}=0.1$, $p=0.83$; gender×mean seed weight: $F_{1,24}=0.1$, $p=0.82$). Coefficients of variation for seed weights within pods ranged from 3 to 51%. The relationship between the CV of seeds within pods and mean seed weight per pod was also highly significant ($F_{1,25}=27.8325$; $p<0.0001$) so that pods with large seeds were less variable, but variability was unaffected by both seed number per pod ($F_{1,25}=3.0922$; $p=0.091$) and the presence of aborted seeds ($F_{1,25}=2.1945$; $p=0.151$).

When asked to identify the heaviest from a pair of seeds, people did better than chance for almost all pairs (figure 3*a*), e.g. more than 70% of people could correctly identify the heavier seed when the CV was just 10%. We assume people inferred differences in carob seed mass from differences in size since the relationship between carob seed mass and volume is known to be linear ($R^2=0.71$; Zhengzhang 1991). This ability to accurately discriminate such small differences in weight would allow a carefully selected sample of seeds to have greatly reduced variability, undoubtedly far lower than in a random sample. Indeed, the distribution of carat weight standards around the world prior to metrication in 1907 has a coefficient of variation of 3.6% in contrast to that of 34% for our seed sample (including all aborted and misshapen seeds; figure 3*b* versus *c*). Interestingly, human selection has penalized against both extremes, 44% of our seeds are smaller than the range of carat weights and 27% are larger.

4. DISCUSSION

The etymology and mass of the carat support its direct descent from the carob bean via the ancient Roman *siliqua*. However, our analysis shows that carob is not unusually invariant in seed mass when compared to 63 other species. The variability of carob seeds within individual pods and trees declines with increasing seed mass, most likely because the variance remains constant, giving some pods with large seeds very low CVs. This new observation provides one possible explanation for the carob myth; however, it seems more likely that the myth arose from consideration of collections of seeds used for weighing, which had already been subjected to strong human selection. Our study shows that people are remarkably good at selecting seeds by eye, and can discriminate differences in weight of around 5%. In this instance, human selection seems, unusually, to have been stabilizing rather than directional leading to a distribution of carat weights around the mean weight of carob seeds rather than at the higher end of the distribution. This might reflect the conflicting interests of buyers and sellers, one of whom would always prefer bigger seeds and one of whom would always prefer smaller. Carob was perhaps chosen for use as a weight simply because of its ready availability—it spread widely around the Mediterranean in Classical times from its centre of origin in the Horn of Africa and southern Arabia (Ramón-Laca & Mabberly 2004)—and perhaps owing to its useful size. It is likely that one-carat diamonds were traded in ancient times even in Europe: the marks of diamond drills have been found on Roman antiquities (Gorelick & Gwinnett 1988) and even on beads in Yemen dated to the fourth century BC (Gwinnett & Gorelick 1991), raising the possibility of a truly ancient association between diamond and carob.

We thank: Joan Tous for putting us in contact with each other; Karl Petruso for encouragement; Maja Weilenmann, Gwilym Lewis and the American Museum of Natural History for help with literature; Marc Hall, Rowan Hooper, Jasmin Joshi, Petra Lindemann-Matthies, Christine Müller, Glen Reynolds, Bernhard Schmid, Andy Wilby and two anonymous reviewers for comments.

Banuelos, M. J. & Obeso, J. R. 2003 Maternal provisioning, sibling rivalry and seed mass variability in the dioecious shrub *Rhamnus alpinus*. *Evol. Ecol.* **17**, 19–31. (doi:10.1023/A:1022430302689)

Batlle, I. & Tous, J. 1997 *Carob tree. Ceratonia siliqua* L. Promoting the conservation and use of underutilized and neglected crops. 17. Gatersleben, Germany & Rome, Italy: Institute of Plant Genetics and Crop Plant Research & International Plant Genetic Resources Institute.

Bauer, M. 1969 *Precious stones*. New York, NY: Dover Publications Inc. cited in Zhengzhang (1991).

Bernasconi, G. 2004 Seed paternity in flowering plants: an evolutionary perspective. *Perspect. Plant Ecol. Evol. Syst.* **6**, 149–158. (doi:10.1078/1433-8319-00075)

Daniel, P. 1972 The carat—its origin as a unit of weight for diamond. *Phys. Educ.* **7**, 454–455. (doi:10.1088/0031-9120/7/7/317)

Gomez, J. M. 2004 Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution* **58**, 71–80.

Gorelick, L. & Gwinnett, A. J. 1988 Diamonds from India to Rome and beyond. *Am. J Archaeol.* **92**, 547–552.

Gwinnett, A. J. & Gorelick, L. 1991 Bead manufacture at Hajar Ar-Rayhani. Yemen. *The Bib. Archaeol.* **54**, 186–196.

Harper, J. L. 1970 The shapes and sizes of seeds. *Annu. Rev. Ecol. Syst.* **1**, 327–356. (doi:10.1146/annurev.es.01.110170.001551)

Janzen, D. H. 1979 How accurate was the carat? *Nature* **280**, 10. (doi:10.1038/280010a0) (correspondence).

Moles, A. T., Warton, D. I. & Westoby, M. 2003 Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology* **84**, 3148–3161.

OED 1989 *The Oxford English Dictionary*. Oxford, UK: Oxford University Press.

Pinheiro, J. C. & Bates, D. M. 2000 *Mixed-effects models in S and S-Plus. Statistics and computing*. Berlin, Germany: Springer.

Ramón-Laca, L. & Mabberly, D. J. 2004 The ecological status of the carob-tree (*Ceratonia siliqua* Leguminosae) in the Mediterranean. *Bot. J. Linn. Soc.* **144**, 431–436. (doi:10.1111/j.1095-8339.2003.00254.x)

Rocha, O. J. & Stephenson, A. G. 1991 Effects of non-random seed abortion on progeny performance in *Phaseolus coccineus* L. *Evolution* **45**, 1198–1208.

Smith, W. 1870 *Dictionary of Greek and Roman antiquities*. Boston, MA: Little & Brown.

Smith, C. C. & Fretwell, S. D. 1974 Optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506. (doi:10.1086/282929)

Tolansky, S. 1962 *The history and use of diamond*. London, UK: Methuen.

Zhengzhang, T. 1991 On the origin of the carat as the unit of weight for gemstones. *Chin. J. Geochem.* **10**, 288–294.