

Friend or foe? Disparate plant–animal interactions of two congeneric rodents

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Abstract Food and water resources are limiting factors for animals in desert ecosystems. Fleshy fruits are a rare water source in deserts and when available they tend to attract a wide variety of organisms. Here we show that two congeneric rodent species, *Acomys cahirinus* and *A. russatus*, employ different fruit eating strategies that result in either dispersal or predation of the small seeds of the desert plant *Ochradenus baccatus*. The nocturnal *A. cahirinus* leaves intact seeds when consuming *O. baccatus* fruits and thus, acts mainly as a seed disperser; whereas the diurnal *A. russatus* consumes the whole fruit and digests the seeds and thus, acts mainly as a seed predator. *Acomys russatus* is subjected to the toxic products of the glucosinolates-myrosinase system found in *O. baccatus* fruits. *Acomys cahirinus* avoids the toxic compounds by consuming the pulp only, which contains glucosinolates but not the seeds that contain the enzyme that activates them. We suggest that the behavioral responses exhibited by *A. russatus* are the result of physiological adaptations to whole fruit consumption that are absent in *A. cahirinus*. Our results shed new light on the ecological divergence of the two congeneric species.

Keywords Desert · Fruits · Glucosinolates · Rodents · Secondary compounds · Seed dispersal

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Introduction

Seeds and fruits are a valuable food source for many animal species (Kelt et al. 2004). Generally, seeds are of higher nutritional quality compared to the ripe fruit pulp (Norconk et al. 1998). Furthermore, seeds are often available year round in the soil and can be cached for long periods (Brown et al. 1979b; Vander Wall 1990; Maron and Simms 1997; Price and Joyner 1997). Although many plant species possess mechanical and/or chemical protection against seed predation, various animals have developed morphological, behavioral and physiological adaptations that allow them to circumvent these defenses and consume the seeds (Heske et al. 1994; Cipollini and Levey 1997b; Rodgerson 1998; Wang and Chen 2009; Ronel and Lev-Yadun 2012).

Rodents in general, and species in the family Muridae in particular, are granivores (Briani and Guimaraes 2007). Indeed, seed predation by rodents is a wide-spread, well-known phenomenon (Shkolnik 1966; Brown et al. 1979b; Davidson et al. 1980; Howe and Smallwood 1982; Briani and Guimaraes 2007; Wang and Chen 2009; Blendinger and Díaz-Vélez 2010; Velho et al. 2012). Rodents act as pre-dispersal as well as post-dispersal seed predators (Jansen et al. 2004). They excel in locating seeds in the soil (Abramsky 1983; Taraborelli et al. 2009), are good climbers and diggers, have strong jaw musculature and specialized teeth for crushing, are able to firmly hold the seeds using their forelimbs (Ben-Moshe et al. 2001) and some have cheek pouches that allow them to collect and transport seeds (Brown et al. 1979b; Davidson et al. 1980; Leaver and Daly 1998). In fact, seed consumption is so important for rodents that in some cases, they are more effective than ants at finding and harvesting seeds (Davidson et al. 1980; Abramsky 1983). Thus, rodents significantly impact plant reproductive dynamics, distribution, density and diversity (Davidson et al. 1980, 1984; Abramsky 1983; Brown and Heske 1990; Heske et al. 1994; Longland et al. 2001; Briani and Guimaraes 2007; Velho et al. 2012). Conversely, seed abundance can affect rodent population size and dynamics (Brown et al. 1979b; Davidson et al. 1984).

While typically defined as granivores, rodents can also play an important role in seed dispersal (Vander Wall 1990). Scatter-hoarding rodents may disperse seeds via abandonment of seeds in caching places (Sork 1983; Forget and Milleron 1991; Price and Joyner 1997), often in conditions that favor seedling establishment (Vander Wall et al. 2005; Wang and Chen 2009; Beck and Vander Wall 2010). Rodents can also disperse seeds via “sloppy eating” whereby seeds are eliminated intact through a variety of mechanisms (e.g., seeds falling accidentally while eating) (Sork 1983; Gautier-Hion et al. 1985).

Dispersal via scatter-hoarding is a well-studied phenomenon, and is more likely to occur with large seeds (i.e. >2.5 cm in diameter) (Vander Wall 1990, 2010; Moles et al. 2003; Wang and Chen 2009). Seed dispersal by rodents through sloppy eating is common in nutrient rich habitats such as forests (Sork 1983; Gautier-Hion et al. 1985) but is less likely to occur in desert ecosystems where water and food resources are scarce and sporadic both spatially and temporally (Noy-Meir 1973), and where seeds are an especially important source of food and water (Kam and Degen 1991). Thus rodents in arid environments are more likely to negatively impact seed abundance than facilitate dispersal (Vander Wall 1993; Maron and Simms 1997; Price and Joyner 1997; Longland et al. 2001).

Many plants contain fruit secondary compounds in concentrations that are toxic or deterrent to granivores vertebrates (Herrera 1982; Cipollini and Levey 1997b; Tewksbury and Nebhan 2001; Izhaki 2002; Samuni-Blank et al. 2012). Recently, the fruits of the desert plant *Ochradenus baccatus* were shown to harbor a unique compartmentalization of the “mustard oil bomb” (Matile 1980), where the pulp is rich with glucosinolates (GLSs) and the seeds with the activating enzyme myrosinase (Samuni-Blank et al. 2012). Thus,

co-consumption of seeds and pulp generate toxic products. In other plants, the mustard oil bomb was shown to provide effective defense against generalist herbivores (Wittstock and Haliker 2002) while in the fruits of *O. baccatus* it was demonstrated to promote seed dispersal by rodents (Samuni-Blank et al. 2012).

The plant *O. baccatus* and the two congeneric rodents, *Acomys cahirinus* and *A. russatus*, co-occur in arid regions of Israel. The two rodent species inhabit rocky habitats and are very similar in their morphology as well as in their life history. Both species are usually regarded as seed predators (Shkolnik 1966; Jones and Dayan 2000). Nevertheless our previous observations revealed that *A. cahirinus* serves as *O. baccatus* seed disperser (Samuni-Blank et al. 2012). In the present study we tested the following predictions: (1) *A. russatus* is a seed disperser of *O. baccatus*; (2) The eating strategies of the two species when consuming *O. baccatus* fruits are consistent throughout time and space; (3) Fruit handling time will not differ between the two species as their jaw morphology is similar; (4) The mustard oil bomb will negatively affect body mass of both species. We combined field observations, using day and night motion-activated cameras, with laboratory feeding trials, examining fruit eating strategy and its effect on *O. baccatus* seed germination.

Materials and methods

Plant natural history

Ochradenus baccatus (Delile 1813; [Resedaceae]) is a widespread Saharo-Sindian, mostly dioecious shrub, common in Israel's desert zone. Fruiting occurs year-round, with peaks in February–May and September–December (Wolfe and Burns 2001). The fruits are white berries, ~4 mm in diameter each (57 mg fresh mass) containing an average of nine small seeds (average seed fresh mass 0.7 mg) (Samuni-Blank et al. 2012). The pulp is water and nutrient rich (water content: 85.8 ± 2.1 % of wet mass; nitrogen: 0.37 ± 0.09 % wet mass) (Samuni-Blank et al. 2012; Lotan and Izhaki 2013). Indeed, *O. baccatus* is often a focal site for animal activity in arid environments and is probably the single most important food source for many animal species in the Negev desert (Bronstein et al. 2007).

Rodent natural history

The murid rodents *A. cahirinus* (Desmarest 1819; but see Volobouev et al. 2007 for a discussion on the *A. cahirinus-dimidiatus* complex) and *A. russatus* (Wagner, 1840) inhabit the same habitats as *O. baccatus* and are abundant in the Judean and the Negev deserts in Israel. The two *Acomys* population densities are higher in areas where food is abundant (Shkolnik 1966; Kronfeld et al. 1994). While *A. cahirinus* is nocturnal, *A. russatus* is diurnal (Shkolnik 1966). Arthropods, green vegetation, seeds and snails are typical dietary components of the two rodent species (Shkolnik 1966; Kronfeld-Schor and Dayan 1999). Neither of the species have cheek pouches (personal observations).

Fruit eating strategies in situ

We observed wild *A. cahirinus* and *A. russatus* for eight days between September 2010 and March 2011 in two different sites, *A. cahirinus* in Wadi Hever (31°28'N, 35°23'E) and *A. russatus* in Ardon Mountain (31°28'N, 35°23'E). *Ochradenus baccatus* is present

at both sites but is more abundant in Wadi Hever. Although the two are sympatric species, we chose to observe them in separate locations because *A. russatus* individuals in Ardon Mountain are habituated to human presence, allowing us to observe *A. russatus* behavior from a short distance (≤ 50 cm), whereas *A. cahirinus* are more abundant in Wadi Hever. We used a Canon camera (EOS 500D) and three motion-activated day/night DVREye™ video cameras to record foraging behavior (continuous recording). Video recordings were analyzed for fruit collection, consumption strategies and handling times were analyzed for each individual. Individuals were identified by unique scarring patterns resulting from the *Acomys* defense of skin and tail loss (Seifert et al. 2012). In cases where we could not distinguish between individuals we considered them as one individual.

Fresh ripe *O. baccatus* fruits were collected daily at the vicinity of the observation site. Fruits from two fruit clusters were placed at each of seven sites between the rocks where *Acomys* typically feed. We measured the number of fruits consumed during the first continuous minute of fruit consumption (live and/or video). Mean handling time and mean percentage of fruits eaten whole were calculated for each individual and then we calculated the mean of each species as the mean of the individual means. We calculated the percentage of fruits eaten whole (no spitting of pulp and/or seeds) out of the total number of consumed fruits. We used jaw movement as an indication for fruit consumption.

Fruit eating strategies ex situ

The field observations were reinforced by controlled laboratory experiments. Experimental protocols were approved by the University of Haifa's Committee of Animal Experimentation (Permit 096/08). We used animals from captive breeding colonies of *A. cahirinus* (body mass = 50.9 ± 1.2 g SE; $n = 117$) and of *A. russatus* (body mass = 53.8 ± 1.1 g SE; $n = 110$) maintained at the Department of Biology and Environment at the University of Haifa, Oranim. During the experiments, animals were housed individually in standard mouse cages (21 cm \times 31 cm \times 13 cm) in a temperature-controlled room (25 ± 2 °C) under a 12:12 h light–dark cycle. All animals were weighed prior to the experiments on an electronic balance (Percisa, XB 620C, ± 0.1 g). Ripe *O. baccatus* fruits were collected from a wild population near the Dead Sea (31°80'N, 35°45'E), stored at -20 °C and thawed a few hours before use.

Fruit eating strategies of individual mice were categorized to one of the three following types: “Whole fruit”—eating pulp and seeds simultaneously; “Pulp”—eating the pulp and spitting the seeds; “Seed”—spitting the pulp and eating the seeds. Captive adult males of *A. russatus* ($n = 43$) and *A. cahirinus* ($n = 43$), all naïve to *O. baccatus*, were given a single whole fruit of *O. baccatus* and their eating strategy was determined during 60 min focal-animal sampling. Fruit handling time was measured by introducing three whole fruits, one at a time, to each individual of *A. russatus* or *A. cahirinus* ($n = 7$ per species). The time taken for each individual to consume the fruit was measured from the moment the mouse started eating until jaw movement stopped or until the rodent dropped the fruit and left it for more than 10 s. Mean handling time was calculated for each individual.

To examine fruit eating strategy over time, we performed a feeding trial, on another group of naïve animals. Adult males and females of *A. cahirinus* ($n = 8$) and *A. russatus* ($n = 8$) were given *ad libitum* rodent chow (Koffolk serial no. 19510) and 30 fruits (per individual

per day) as a sole source of free water. We documented fruit intake and the number of intact seeds that had been removed from the fruit for 4 days, sampling once every 24 h.

Seed viability

Captive male and female *A. russatus* ($n = 11$) that had never experienced (naïve) *O. baccatus* were given whole fruits. Prior to feeding, the fruits were gently opened, the number of seeds inside each fruit was counted (9.4 ± 0.5 SE) and returned, and the fruits were closed. Feces of the above animals were collected and examined for the presence of intact seeds within 24 h post fruit consumption (estimated digestive transit time is <8 h; M. Samuni-Blank, unpublished data). We recorded the number of intact seeds on the cage floor as well as the number intact defecated seeds. Both types of intact seeds were collected and germinated in stable conditions previously determined as favourable for *O. baccatus* (Samuni-Blank et al. 2012). We define the “germination index” as the (number of germinated seeds/original number of seeds in the whole fruit) $\times 100$ %. The germination index depends on both the portion of seeds left intact (excluding seeds found in the feces) and their vitality.

Physiological effects of the fruit diet

To examine the physiological effects of consumption of different parts of the fruit on *A. cahirinus* and *A. russatus*, we performed feeding trials ($n = 8$ individuals per treatment). The diets consisted of rodent chow combined with water, *O. baccatus* pulp and seeds with a pulp/seed ratio similar to the proportion in the whole fruit. We manipulated the toxicity of the diets by crushing together pulp and seeds to activate toxins (AMash) or crushing the pulp with pre-autoclaved seeds (DMash) where the myrosinase enzyme was inactivated (Samuni-Blank et al. 2012). AMash contained all the necessary components to generate the mustard oil bomb, whereas the DMash contained only the GLSs. These diets were prepared as follows. On day one the composition of both diet treatments contained 50 % rodent chow, 25 % water, 23 % pulp and 2 % seeds (fresh or autoclaved). The diets on days 2–4 contained 50 % rodent chow homogenized with 46 % pulp and 4 % seeds (fresh or autoclaved). The chow, pulp and seeds were mashed to powder and homogenized. Wet pellets were made from the mashed food and immediately (less than an hour) given to the rodents. We monitored body mass of rodents fed for four days with the different diets.

Statistical analyses

We used a Mann–Whitney U test to compare the mean percentage of fruits eaten whole that were calculated for each individual between the two rodent species in the field. To test for differences between the fruit eating strategies with respect to number of intact seeds in the feces of the two species, we used the two proportions Z test. To test for differences between the two species in fruit consumption with respect to intact seeds over the four day feeding trail, we used repeated measures ANOVA. Because there were no differences among days within each species, we averaged daily fruit consumption and used it as the dependent variable in ANCOVA (with body mass as covariate). In addition, we averaged number of intact seeds left each day and analyzed for the difference between the two species by t test. To test for differences in seed vitality after fruit handling between the two species, we arcsin transformed the proportion of germinated seeds and performed a t -test.

T-test was also used to test for differences in fruit handling time and fruit consumption rates between the two species. We used two-way ANOVA to test for differences of change in body mass (%) between the two species, between treatments and their interaction. The data were tested for normality prior to statistical comparisons; non-normal data were transformed as stated. In all cases, a minimum $P < 0.05$ was considered significant. All data are reported as mean \pm standard error (SE).

Results

Fruit eating strategies

In situ, we observed (directly and by video analysis) consumption of *O. baccatus* fruits by both *A. russatus* (10 individuals; seven adults and three juveniles) and *A. cahirinus* (eight individuals; all adults). A significantly greater percentage of adult *A. russatus* ($91.4 \pm 8.6\%$) consumed the fruits as whole (confronting the fruits secondary compounds; movie available at: <http://y2u.be/X3zdqRwWdA4>) than adult *A. cahirinus* ($11.5 \pm 5.7\%$) (Mann–Whitney $U = 28$, $P < 0.001$). Interestingly, all three juvenile *A. russatus* used the pulp strategy exclusively (movie available at: <http://y2u.be/ETraLILE2Ws>).

Fruit eating strategies ex situ were also different between the two species (Fig. 1). Overall, the results mirrored the results of the animals under natural conditions. *Acomys russatus* significantly preferred the whole fruit strategy over the pulp strategy ($Z = 7.1$, $n = 43$, $P < 0.001$; movie available at: <http://y2u.be/RcLDPst87vs>) whereas *A. cahirinus* significantly used the pulp over the whole fruit strategy ($Z = 5.6$, $n = 43$, $P < 0.001$; Fig. 1; movie available at: http://y2u.be/25XI_mtg1PU). More specifically, *A. russatus* inserted the entire fruit in its mouth and chewed it extensively (pulp and seeds), whereas *A. cahirinus* held the fruit between its forepaws and rotated it across the distal portion of its mouth and expelled the seeds.

There was no daily variation in fruit intake within a species (DM; *A. cahirinus*: repeated measures ANOVA: $F_{3,21} = 2.2$, N.S.; *A. russatus*: repeated measures ANOVA: $F_{3,21} = 0.3$, N.S.). The same was true for the number of seeds left intact each day (repeated measures ANOVA with a Greenhouse–Geisser correction; *A. cahirinus* $F_{1.5,10.2} = 1.3$, N.S.; *A. russatus* $F_{1.9,13.4} = 0.7$, N.S.). Therefore, in further statistical analyses, we used the mean mass of fruits consumed (g DM) and mean number of seeds left per day by each individual of each species. The mean fruit intake per day by *A. russatus* was significantly higher than that of *A. cahirinus* (ANCOVA: $F_{1,13} = 5.1$, $P < 0.05$) even when controlling for body mass as covariate (ANCOVA: $F_{1,13} = 6.7$, $P < 0.05$). *Acomys russatus* consumed twice as much fruit per day as *A. cahirinus*. *Acomys russatus* ingested 0.28 ± 0.01 g fruit (DM; about 25 whole fruits) per day while *A. cahirinus* ate only 0.15 ± 0.02 g fruit (DM; about 13 whole fruits) per day. The mean number of seeds left intact per day by *A. cahirinus* was more than five times greater than that left by *A. russatus* ($t_{14} = 2.47$, $P < 0.05$). *Acomys cahirinus* left an average of 27.5 ± 6.1 intact seeds per day (highest number of seeds left was 183 intact seeds per day) while *A. russatus* left only 5.8 ± 1.1 intact seeds per day (highest number left was 41 intact seeds per day).

Fruit consumption and handling time

Acomys russatus was documented collecting several fruits in its mouth (movie available at: <http://y2u.be/2qImxjeQcYs>). When the fruit were consumed on site, there was no

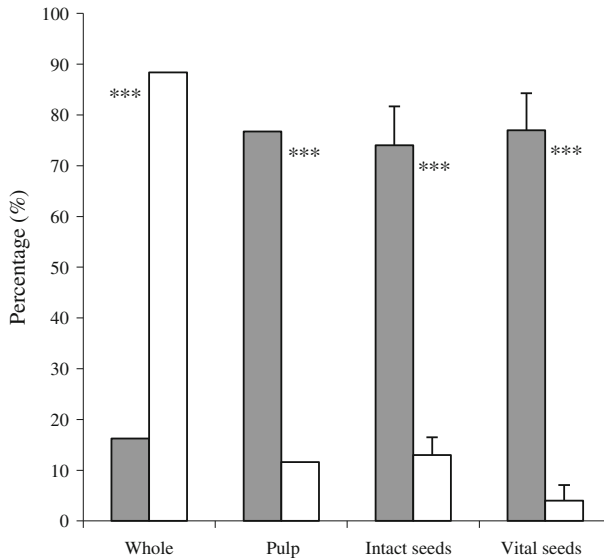


Fig. 1 Plant-rodent interactions ex situ. The percentage of individuals exhibiting “Whole” and “Pulp” strategies and the mean (+SE) percentage of intact and vital seeds. *Acomys cahirinus* (gray bars; $n = 10\text{--}43$) and *A. russatus* (white bars; $n = 11\text{--}43$; Two proportions Z Test, $Z > 2.6$ for all four comparisons). Each individual was given a whole fruit and its behavior was recorded. The main behaviors were: “Whole”—ingestion of the whole fruit (seed and pulp together) and “Pulp” (seeds spitting). The seeds that were left untouched were counted and tested for viability. *** $P < 0.0001$

significant difference in the number of fruits consumed per minute by wild *A. cahirinus* (6.2 ± 1.1) and wild *A. russatus* (6.2 ± 0.7 ; $t_{10} = 0.0$, N.S.), or in fruit handling time (10.0 ± 1.3 s and 8.4 ± 1.7 s respectively; $t_{10} = 1.2$, N.S.). Interestingly, fruit handling time by naïve captive *A. cahirinus* (44.4 ± 11.4 s) was more than three times longer than fruit handling time by naïve captive *A. russatus* (12.8 ± 2.0 s; $t_{12} = 2.6$, $P < 0.05$). Furthermore, fruit handling time did not differ between captive and wild *A. russatus* ($t_{10} = 2.8$, N.S.), but did significantly differ between captive and wild *A. cahirinus* ($t_{12} = 5.5$, $P < 0.001$).

Seed viability

Seed germination index [(number of germinated seeds/original number of seeds in the whole fruit) $\times 100$ %] was almost 20 times greater for captive *A. cahirinus* (74.4 ± 9.0 %) than for captive *A. russatus* (4.0 ± 3.1 %; $t_{19} = 7.6$, $P < 0.001$). Furthermore, intact seeds were rarely found in the feces of either rodent species and there was no significant difference between the two species in fraction of seeds that appeared in the feces (*A. russatus*: 0.13 ± 0.10 %; $n = 11$ and *A. cahirinus*: 0.05 ± 0.05 %; $n = 10$; $Z = 0.4$, N.S.). However, the majority of the intact seeds present in the feces germinated (65 % for both species).

Physiological effects of fruit diet

We tested the ability of both species of *Acomys* to maintain body mass on diets comprised of *O. baccatus* activated mash (AMash; pulp mashed with seeds) or deactivated mash

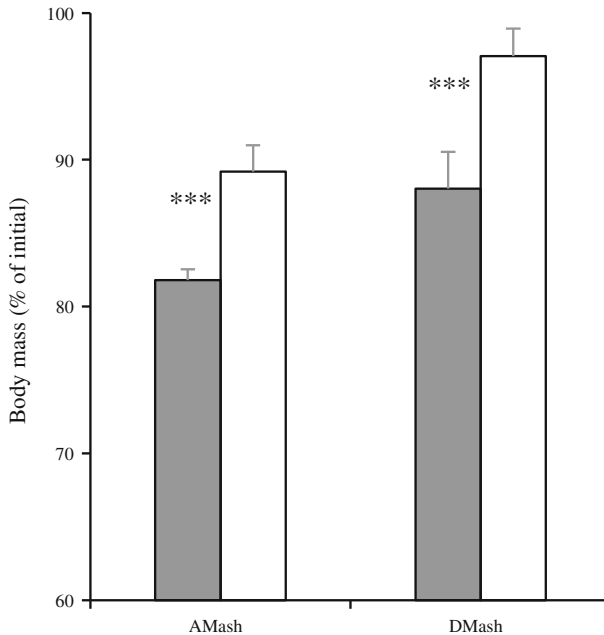


Fig. 2 Body mass after four days on *O. baccatus* diets AMash (pulp mashed with seeds) and DMash (pulp mashed with seeds treated for myrosinase deactivation) of *A. cahirinus* (gray bars) and *A. russatus* (white bars; $n = 8$ for each diet within each species; two-way ANOVA). *** $P < 0.0001$. Data are presented as means + SE

(DMash; pulp mashed with seeds treated for myrosinase deactivation). On each of the diets, *A. cahirinus* lost about ten percent of its initial body mass more than *A. russatus* (two-way ANOVA: Species: $F_{1,28} = 22.8$, $P < 0.0001$; Fig. 2) and both species lost significantly more mass on AMash than DMash (Diet— $F_{1,28} = 16.9$, $P < 0.0001$; Diet*Species interaction: $F_{1,28} = 0.2$, N.S; Fig. 2).

Discussion

It is unusual for sympatric congeners to exhibit such fundamental differences in their fruit eating strategies. The interactions between spiny mice and *O. baccatus* are intricate; the diurnal *A. russatus* crushes seeds of *O. baccatus* in its mouth and thus acts mainly as a seed predator whereas the nocturnal *A. cahirinus* consumes the fruit pulp, leaving the seeds intact in the process. These observations are in addition to our previously published data that *A. cahirinus* carries fruit away from the parent plant and spits the seeds at locations suitable for germination, demonstrate that *A. cahirinus* is behaving as a legitimate seed disperser (Samuni-Blank et al. 2012).

The fruit eating strategy of each species was consistent throughout the four-day feeding trial. Interestingly, even within the restrictions of a cage, *A. cahirinus* left a significant number of seeds intact and is likely to leave even more seeds intact when under natural conditions. Eating the fruits and leaving the seeds undamaged is particularly interesting because the seeds of *O. baccatus* are small, and small seeds are more likely to be consumed

by rodents compared to large seeds that are more likely to be dispersed by them (Vander Wall 2010).

For *A. cahirinus*, the handling time of fruit was four times longer in the naïve, laboratory mice than in those in the field. This may be due to wild individuals having prior experience in consuming these fruits, resulting in shorter handling time. In addition, differences in the perceived risk of predation in nature versus the laboratory could explain the difference in handling time. The availability of food and water resources in addition to the lack of predators in the laboratory environment may have permitted longer fruit handling time in captivity. Indeed, fruit handling time of wild *A. cahirinus* was much shorter and similar to that of *A. russatus*, which faces a simpler task of consuming the fruit in its entirety. Naïve, captive, *A. russatus* had fruit handling times similar to those of wild individuals, without practicing any unique feeding skills. Moreover, the diurnal *A. russatus* is adapted to limited foraging time (Haim et al. 1994) that may result in decrease in the amount of time dedicated to food consumption.

Being diurnal, *A. russatus* faces higher solar radiation, higher ambient temperature and fewer feeding opportunities across time and space compared to the nocturnal *A. cahirinus* (Haim et al. 1994; Vonshak et al. 2009). Indeed *A. russatus* has several adaptations to survive daily activity in hot arid environments (Shkolnik and Borut 1969; Haim et al. 1994). Thus, consuming the whole fruit may be the result of the intense competition over resources, especially seeds, in the desert ecosystem (Brown and Davidson 1977; Brown et al. 1979a). Upon fruiting, competition for fruits increases and indeed, *A. russatus* was documented collecting several fruits in its mouth before leaving the feeding site.

The compartmentalization of the GLSs and myrosinase in *O. baccatus* fruits is probably the main factor shaping the interaction between *O. baccatus* and its fruit consuming rodents. For example, although *A. russatus* and *A. cahirinus* are congeneric species that possess the mechanical ability to crush the seeds of *O. baccatus*, only *A. russatus* consistently consumes the whole fruit. We propose that physiological differences in their ability to metabolize GLSs may be the underlying reason for the significant differences in fruit eating strategies.

The concentration of many plant secondary compounds increases in response to water stress, which is the case in the desert ecosystem (Bronstein et al. 2007). Thus, species that inhabit arid ecosystems face not only the dry and hot environment, but also higher concentrations of secondary compounds. Physiologically, *A. russatus* is known (Haim and Borut 1981; Haim et al. 1994, 2005; Ehrhardt et al. 2005; Levy et al. 2011) for its unique adaptive mechanisms for desert survival which includes: (1) significantly lower than predicted resting metabolic rate and daily energy expenditure; (2) the use of torpor to adapt to low availability of resources; (3) effective regulation of body temperature at high ambient temperatures; (4) high urine concentrating capacity. Some of these adaptations are absent in *A. cahirinus*, which is less desert-adapted than *A. russatus* (Shkolnik 1966; Shkolnik and Borut 1969; Kam and Degen 1993; Kronfeld et al. 1994). Furthermore, of the two species, *A. russatus* was significantly more adapted to *O. baccatus* diets in terms of defending body mass (Fig. 2). After 4 days on the AMash diet (pulp mashed with seeds), *A. russatus* maintained ~90 % of its initial body mass while *A. cahirinus* maintained only ~80 %. This is in line with other studies demonstrating the ability of *A. russatus* to maintain body mass under various conditions (Shkolnik and Borut 1969; Kam and Degen 1993; Gutman et al. 2006).

The present findings demonstrate that *A. russatus* is not deterred from seed predation in the presence of fruit secondary compounds (e.g., eating the whole fruit, pulp and seeds together). However, whole fruit consumption does not come without cost as there were

significant negative effects (e.g., body mass loss). As with most plant or fruit secondary compounds, the outcome is a function of the dose (Dearing et al. 2005; Torregrossa and Dearing 2009). With respect to the directed-deterrence hypothesis, which states that fruit secondary compounds deter seed predators but have little or no effect on seed dispersers (Cipollini and Levey 1997a), these findings offer both supportive evidence (negative physiological consequences of eating the whole fruits), but also contradicting evidence (seed predators are not deterred from consuming the whole fruit).

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References

- Abramsky Z (1983) Experiments on seed predation by rodents and ants in the Israeli desert. *Oecologia* 57:328–332
- Beck MJ, Vander Wall SB (2010) Seed dispersal by scatter-hoarding rodents in arid environments. *Ecology* 98:1300–1309
- Ben-Moshe A, Dayan T, Simberloff D (2001) Convergence in morphological patterns and community organization between Old and New World rodent guilds. *Am Nat* 158:484–495
- Blendinger PG, Díaz-Vélez MC (2010) Experimental field test of spatial variation in rodent predation of nuts relative to distance and seed density. *Oecologia* 163:415–423
- Briani DC, Guimaraes PR (2007) Seed predation and fruit damage of *Solanum lycocarpum* (Solanaceae) by rodents in the cerrado of central Brazil. *Acta Oecol* 31:8–12
- Bronstein JL, Izhaki I, Nathan R, Tewksbury JJ, Spiegel O, Lotan A, Altstein O, Dennis AJ, Schupp EW, Green RJ (2007) Fleshy-fruited plants and frugivores in desert ecosystems. In: Dennis AJ, Schupp EW, Green RJ, Westcott DW (eds). *Seed dispersal: theory and its application in a changing world*. Cab International, Wallingford, pp 148–177
- Brown JH, Davidson DW (1977) Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196:880–882
- Brown JH, Heske EJ (1990) Control of a desert-grassland transition by a keystone rodent guild. *Science* 250:1705–1707
- Brown JH, Davidson DW, Reichman OJ (1979a) An experimental study of competition between seed-eating desert rodents and ants. *Am Zool* 19:1129–1143
- Brown JH, Reichman OJ, Davidson DW (1979b) Granivory in desert ecosystems. *Annu Rev Ecol Syst* 10:201–227
- Cipollini ML, Levey DJ (1997a) Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *Am Nat* 150:346–372
- Cipollini ML, Levey DJ (1997b) Why are some fruits toxic? Glycoalkaloids in *Solanum* and fruit choice by vertebrates. *Ecology* 78:782–798
- Davidson DW, Brown JH, Inouye RS (1980) Competition and the structure of granivore communities. *Bioscience* 30:233–238
- Davidson DW, Inouye RS, Brown JH (1984) Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology* 65:1780–1786
- Dearing MD, Foley WJ, McLean S (2005) The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annu Rev Ecol Syst* 36:169–189
- Ehrhardt N, Heldmaier G, Exner C (2005) Adaptive mechanisms during food restriction in *Acomys russatus*: the use of torpor for desert survival. *J Comp Physiol B* 175:193–200
- Forget PM, Milleron T (1991) Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87:596–599
- Gautier-Hion A, Duplantier JM, Quris R, Feer F, Sourd C, Decoux JP, Dubost G, Emmons L, Erard C, Hecketsweiler P (1985) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65:324–337

- Gutman R, Choshniak I, Kronfeld-Schor N (2006) Defending body mass during food restriction in *Acomys russatus*: a desert rodent that does not store food. *Am J Physiol* 290:881–891
- Haim A, Borut A (1981) Heat production and dissipation in golden spiny mice, *Acomys russatus*, from two extreme habitats. *J Comp Physiol* 142:445–450
- Haim A, Yedidia I, Haim D, Zisapel N (1994) Photoperiodicity in daily rhythms of body temperature, food and energy intake of the golden spiny mouse (*Acomys russatus*). *Isr J Zool* 40:145–150
- Haim A, Alma A, Neuman A (2005) Body mass is a thermoregulatory adaptation of diurnal rodents to the desert environment. *J Therm Biol* 31:168–171
- Herrera CM (1982) Defense of ripe fruit from pests: its significance in relation to plant-disperser interactions. *Am Nat* 120:218–241
- Heske EJ, Brown JH, Mistry S (1994) Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. *Ecology* 75:438–445
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annu Rev Ecol Syst* 13:201–228
- Izhaki I (2002) Emodin—a secondary metabolite with multiple ecological functions in higher plants (a review). *New Phytol* 155:205–217
- Jansen PA, Bongers F, Hemerik L (2004) Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecol Monogr* 74:569–589
- Jones M, Dayan T (2000) Foraging behavior and microhabitat use by spiny mice, *Acomys cahirinus* and *A. russatus*, in the presence of Blanford's fox (*Vulpes cana*) odor. *J Chem Ecol* 26:455–469
- Kam M, Degen A (1991) Diet selection and energy and water budgets of the common spiny mouse *Acomys cahirinus*. *J Zool* 225:285–292
- Kam M, Degen AA (1993) Effect of dietary preformed water on energy and water budgets of two sympatric desert rodents, *Acomys russatus* and *Acomys cahirinus*. *J Zool* 231:51–59
- Kelt DA, Meserve PL, Gutiérrez JR (2004) Seed removal by small mammals, birds and ants in semi-arid Chile, and comparison with other systems. *J Biogeogr* 31:931–942
- Kronfeld N, Dayan T, Zisapel N, Haim A (1994) Coexisting population of *Acomys cahirinus* and *A. russatus*: a preliminary report. *Isr J Zool* 40:177–183
- Kronfeld-Schor N, Dayan T (1999) The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species. *Oecologia* 121:123–128
- Leaver L, Daly M (1998) Effects of food preference on scatter-hoarding by kangaroo rats (*Dipodomys merriami*). *Behaviour* 135:823–832
- Levy O, Dayan T, Kronfeld-Schor N (2011) Interspecific competition and torpor in golden spiny mice: two sides of the energy-acquisition coin. *Integr Comp Biol* 51:441–448
- Longland WS, Jenkins SH, Vander Wall SB, Veech JA, Pyare SS (2001) Seedling recruitment in *Oryzopsis hymenoides*: are desert granivores mutualists or predators? *Ecology* 82:3131–3148
- Lotan A, Izhaki I (2013) Could abiotic environment shape fleshy fruit traits? A field study of the desert shrub *Ochradenus baccatus*. *J Arid Environ* 92:34–41
- Maron JL, Simms EL (1997) Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*). *Oecologia* 111:76–83
- Matile PH (1980) The mustard oil bomb. Compartmentation of the myrosinase system. *Biochem Physiol Pflanz* 175:722–731
- Moles AT, Warton DI, Westoby M (2003) Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology* 84:3148–3161
- Norconk MA, Grafton BW, Conklin-Brittain NL (1998) Seed dispersal by neotropical seed predators. *Am J Primatol* 45:103–126
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 4:25–51
- Price MV, Joyner JW (1997) What resources are available to desert granivores: seed rain or soil seed bank? *Ecology* 78:764–773
- Rodgers L (1998) Mechanical defense in seeds adapted for ant dispersal. *Ecology* 79:1669–1677
- Ronel M, Lev-Yadun S (2012) The spiny, thorny and prickly plants in the flora of Israel. *Bot J Linn Soc* 168:344–352
- Samuni-Blank M, Izhaki I, Dearing MD, Gerchman Y, Trabelcy B, Lotan A, Karasov WH, Arad Z (2012) Intraspecific directed deterrence by the mustard oil bomb in a desert plant. *Curr Biol* 22:1218–1220
- Seifert AW, Kiama SG, Seifert MG, Goheen JR, Palmer TM, Maden M (2012) Skin shedding and tissue regeneration in African spiny mice (*Acomys*). *Nature* 489:561–565
- Shkolnik A (1966) Studies in the comparative biology of Israel's two species of spiny mice (genus *Acomys*). Department of Zoology, Hebrew University, Jerusalem, Israel, PhD dissertation
- Shkolnik A, Borut A (1969) Temperature and water relations in two species of spiny mice (*Acomys*). *Am Soc Mamm* 50:245–255

- Sork VL (1983) Mammalian seed dispersal of pignut hickory during three fruiting seasons. *Ecology* 64:1049–1056
- Taraborelli P, Borruel N, Mangeaud A (2009) Ability of murid rodents to find buried seeds in the Monte Desert. *Ethology* 115:201–209
- Tewksbury JJ, Nebhan GP (2001) Seed dispersal. Directed deterrence by capsaicin in chilies. *Nature* 41:403–404
- Torregrossa AM, Dearing MD (2009) Nutritional toxicology of mammals: regulated intake of plant secondary compounds. *Funct Ecol* 23:48–56
- Vander Wall SB (1990) Food hoarding in animals. University of Chicago Press, Chicago
- Vander Wall SB (1993) Salivary water loss to seeds in yellow pine chipmunks and Merriam's kangaroo rats. *Ecology* 74:1307–1312
- Vander Wall SB (2010) How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Phil Tran Roy Soc B* 365:989–997
- Vander Wall SB, Kuhn KM, Gworek JR (2005) Two-phase seed dispersal: linking the effects of frugivorous birds and seed-caching rodents. *Oecologia* 145:281–286
- Velho N, Isvaran K, Datta A (2012) Rodent seed predation: effects on seed survival, recruitment, abundance, and dispersion of bird-dispersed tropical trees. *Oecologia* 169:995–1004
- Volobouev V, Auffray JC, Debat V, Denys C, Gautun JC, Tranier M (2007) Species delimitation in the *Acomys cahirinus-dimidiatus* complex (Rodentia, Muridae) inferred from chromosomal and morphological analyses. *Biol J Linnean Soc* 91:203–214
- Vonshak M, Dayan T, Kronfeld-Schor N (2009) Arthropods as a prey resource: patterns of diel, seasonal, and spatial availability. *J Arid Environ* 73:458–462
- Wang B, Chen J (2009) Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. *Ecology* 90:3023–3032
- Wittstock U, Haliker BA (2002) Glucosinolate research in the *Arabidopsis* era. *Trends Plant Sci* 7:263–270
- Wolfe LM, Burns JL (2001) A rare continual flowering strategy and its influence on offspring quality in a gynodioecious plant. *Am J Bot* 88:1419–1423