**History of energetic compensation at the site**

For the first two decades of the experiment, from 1977-1996, small granivores were more abundant and used more energy on exclosure plots than on control plots, but came far short of compensating for the shortfall in energy use caused by removing kangaroo rats from exclosure plots. The compensatory gains in energy use by small granivores on exclosures accounted for only 16% of the energy used by kangaroo rats on controls, and total energy use on exclosure plots averaged 25% of total energy use on controls. While there was some degree of functional overlap between kangaroo rats and small granivores, evinced by the increase in abundance and energy use of small granivores on exclosures relative to controls, it was highly restricted. Most - ~80% - of the energy being used by kangaroo rats appears to have been inaccessible to small granivores, even in the absence of competition from kangaroo rats.

This arrangement changed in the late 1990s, following the arrival of a new species of small granivore, *Chaetodipus baileyii*, at the site. *C. baileyii* preferentially established on exclosure plots. As *C. baileyii* became more abundant, the compensatory gains from the whole small granivore guild increased from 16% to 52% of kangaroo rat energy use, and the total energy use on exclosure plots increased from 25% to 67% of controls. *C. baileyii* is intermediate in size between kangaroo rats and the small granivores that were already present at the site, and may have been better equipped to access a subset of the resources used by kangaroo rats that were inaccessible to smaller granivores.

Over the 1980s and 1990s, the rodent community at the site shifted from being strongly dominated by kangaroo rats (a mean of 90% of energy use on controls from 1988-1996) to a more even mixture of kangaroo rats and smaller granivores (~72% kangaroo rats on control plots). This shift began in the early 1980s as *Dipodomys spectabilis* declined at the site, and continued over the 1990s and 2000s. Over the same time period, the vegetation at the site transitioned from grassland to patchy shrubland. This habitat transition may partially explain the shift in the rodent community favoring small granivores. While kangaroo rats are well-equipped to forage for seeds in open landscapes, smaller granivores often avoid foraging in the open as an antipredator strategy. The transition to shrubland may have increased the availability of resources – seeds – in sheltered microhabitats, thereby increasing the proportion of resources accessible to small granivores.

Following a drought and community-wide population crash in 2009-2010, the composition of the rodent community on control plots underwent another transition, driven primarily by the decline of *C. baileyii*. From 1996-2009, *C. baileyii* accounted for ~15% of energy use on controls; from 2010 onwards, this declined to ~5%.

We investigated the extent of *C. baileyii*’s decline on exclosure plots and its impacts on energetic compensation, within the broader context of the long-term shift in habitat and community composition at the site. Since its arrival at the site, *C. baileyii* has been scarce on control plots and dominant on exclosure plots; its decline on control plots does not necessarily signal a catastrophic decline on exclosure plots. If *C. baileyii* no longer persists in large numbers even on exclosure plots, then the small granivore community on those plots is now functionally missing the species that drove the compensatory effect observed in the 2000s. This could mean that the system will revert to its pre-1990s state, in terms of energetic compensation, with very little compensation from small granivores and a large discrepancy in total energy use between exclosures and controls. However, the shifts in habitat and community composition over the decades introduce additional possibilities. If the increased shrubbiness of the landscape means that small granivores – even those other than *C. bailyeii* – can now access a greater proportion of the resources used by kangaroo rats, the remaining small granivore community may achieve a greater degree of energetic compensation now than in the early days of the experiment. Or, if there has been an increase in partitioning between kangaroo rats and smaller granivores – for example, with kangaroo rats using resources in the open and small granivores using resources in sheltered microhabitats – the suppressive competitive effect of kangaroo rats on small granivores may be weakened, and the compensatory increase in small granivore energy use on exclosures may be minimal to nonexistent. Finally, the sitewide increase in small granivore abundance may shrink the discrepancy in total energy use between exclosures and controls, regardless of whether the *compensatory* response has changed.

**Results**

From 1996-2010, *C. baileyi* accounted for an average of 65% of energy use on exclosure plots, but from 2010-2020, this declined to an average of ~25%. Energetic compensation from small granivores on exclosure plots averaged 16% prior to *C. baileyi*’s arrival at the site and 52% when *C. baileyi* was dominant on exclosure plots. Following the decline in *C. baileyi* beginning in 2010, compensation declined to an average of ~20%, and not significantly different from the level observed from 1988-1996. Total energy use on exclosure plots averaged 25% of control plots prior to 1996, 67% from 1996-2010, and ~47% from 2010-2020.

**Discussion**

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