The Impact of Agriculture on Body Condition in the California Ground Squirrel

Cassandra Olivas

B.S. Candidate, Department of Computer Science and Biological Science, California State University Stanislaus, 1 University Circle, Turlock, CA 95382
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Abstract

California's Central Valley is a drastically altered landscape, with almost every arable square mile converted to agriculture (Mitchell et. al. 2015). The impact of agriculture can be detrimental due to habitat loss and the subsequent loss of biodiversity, or beneficial if those crops serve as a supplemental food resource for local species. In California ground squirrels (CGS), populations adjacent to agriculture experience benefits, such as larger-bodied young-of-the-year with a higher body condition (Ulm 2019). However, there are no existing studies that have addressed the impact of agriculture on individual fitness within these populations. Using a geospatial analysis software (ArcGIS v10.6), the foraging range was estimated for each individual squirrel based on capture points, and the percentage of overlap with agriculture was quantified. Analyses using general linear models have found no significant relationship between the percentage of overlap with agriculture and body condition in CGS, but did find sex, site, and year to be significant contributors to variation in body condition.

Introduction

The California ground squirrel (*Otospermophilus beecheyi*) is a native California species ranging from Baja California to north-central California (Smith et al. 2016). As the name implies, it is a facultatively social mammal that creates complex, underground burrow systems used for shelter and food storage. However, these burrow systems undermine infrastructure such as irrigation canals, levees, or building foundations (Ordenaña et al. 2012). This, in addition to seasonal crop-raiding, is why *O. beecheyi* continues to remain one of the most destructive agricultural pests in California (Marsh 1998; Baldwin et al. 2014). Despite the documented economic impact that CGS impose on California agriculture, little is known on how crop food resources influence CGS in terms of individual fitness and population persistence. For small mammal species in general, the relative costs and benefits of relying on agricultural food resources is a topic which has not received much attention.

It is well documented that the large-scale production of agriculture can have a significant impact on many native species (Lindenmayer and Fischer 2006; Didham 2010). Standard agricultural practices such as tillage, drainage, and pesticide use can result in soil degradation, water pollution, and habitat fragmentation or loss. Furthermore, seeds from domesticated crops can spread into areas of natural vegetation and outcompete native species which threatens the ecosystem (Driscoll et al. 2014). For these reasons, agriculture is one of the largest contributors to the loss of biodiversity worldwide (McLaughlin et al. 1995).

The impact of agriculture on each species varies, and certain species may benefit directly or indirectly from living in proximity to human food crops. For example, in Argentina during the 20th century, 90% of the Pampas grassland was converted to agriculture and pastures. While certain species suffered a complete regional extinction, other herbivorous birds, rodents, and pollinating/crop-associated insect species seemed to increase in abundance (Medan et al. 2011). In southwestern Idaho, Moulton et al. (2006) observed a higher biomass of common prey species (genera *Peromyscus*, *Mus, Perognathus*, *Reithrodontomys*, *Dipodomys*, and *Spermophilus*) adjacent to agricultural fields (alfalfa, sugar beets, and mint) as opposed to natural vegetation.

Generally, animals exhibit a flexible activity budget, where time spent foraging and time devoted to other behaviors such as vigilance, bonding, courting, or mating can be traded-off in response to environmental cues, such as food availability. For example, Gwendolyn Bachman (1993) observed that when juvenile Belding's ground squirrels (*Spermophilus beldingi*) were limited to energy-poor foods for six consecutive days, they increased their foraging duration and decreased their vigilance despite only a moderate reduction in energy stores. Alternatively, Royaute (2017) found an increase in behavioral plasticity in populations of house crickets (*Acheta domesticus*) fed consistently on a high-energy diet. If multiple generations have access to a stable, high-energy food supply, this can even improve the relative fitness of offspring (*Urocitellus parryii plesius*, Werner et al. 2015).

Although other factors may contribute to these changes, diet has been shown to be a significant population parameter in small mammals (Eva et al. 2016). When studying two rodent species (*Apodemus sylvaticus* and *Microtus arvalis*) near various types of agricultural crop, Eva et. al. found the quantity and quality of their diet to be significantly influenced by the type of crop food available, but not age, month of trapping, sex, or body size. This is supported by Benedek and Sîrbu (2017), who found that among rural mosaic landscapes including farmed and semi-natural habitats in Central Romania, vegetation traits were the most important factors influencing small mammal communities. This suggests that when assessing population dynamics, diet should be a primary area of focus.

While approximately 40% of the land in the United States is dedicated to farmland (NASS 2013), the Central Valley of California has been particularly impacted. According to Mitchell et al. (2015), nearly every square mile of arable land within the Central Valley has been transformed by agriculture. In the Central Valley, it has been documented that CGS engage in crop-raiding and use agriculture to supplement their diet (Smith 2016). McGrann et al. (2014) - found a positive correlation between CGS burrow density and the percent cover of perennial fruit/nut crops in the Central Valley, and reported that CGS were 8.40 times more likely to occur adjacent to perennial nut crops than to grasslands. This suggests that agricultural food resources are being used to maintain abnormally high population densities of CGS.

To date, there have been no studies quantifying the contribution of crop foods to the natural diet of this species, although a clear preference for nut crops over corn has been experimentally determined (Ulm 2019). Additionally, there have been no studies which explore the impact that agriculture - has on population demographics, life history, or survival in CGS. However, while studying three populations of CSG within the Central Valley in proximity to almond orchards (high-energy supplemental food source), corn fields (low-energy supplemental food source), or completely reliant on natural grassland (experimental control), Ulm observed that males have a larger average body condition than females, but only in populations adjacent to agriculture. This species is slightly sexually dimorphic, with males being larger and more muscular than females. Ulm's study did not discriminate between muscle and fat tissue when measuring body condition, but it is possible that higher soft tissue reserves allow males to spend less time foraging and instead allocate more effort toward actively seeking mates or increasing their home range. Ulm also found that young-of-the-year adjacent to agriculture (corn and almonds) emerged at a larger average skeleton size and higher body condition than young-of-the-year adjacent to shrubland or other natural vegetation. In addition, young-of-the-year in populations adjacent to corn fields emerged from their natal burrows two weeks before the pups in other populations. This raises some questions: what is the impact of agriculture on CGS within a population and do individuals adhere to these population-level patterns?

We hypothesize that access to agriculture influences individual body condition in CGS. - Individual squirrels within the same population that are in close proximity to agriculture will exhibit a higher body condition than squirrels without. If this is true, then we predict that the overlap between the estimated foraging range for individual CGS and agriculture will be positively associated with a high body condition.

Methods

Mark-Recapture and Morphometric Data Collection

Since 2015, CGS have been studied by California State University, Stanislaus students at three separate locations within the Central Valley: Merced, San Luis and San Joaquin River National Wildlife Refuges (Fig. 1). Trapping seasons generally ranged from February to November with each site visited once every three weeks. During trapping seasons, CGS were live-trapped using Tomahawk traps that were baited with a combination of in-hull sunflower seeds and peanut butter. At San Joaquin River NWR in 2019, the traps were baited with raw walnuts for one month before returning to the sunflower seed and peanut butter mixture. Traps were baited at dawn and checked within four hours to avoid excessive heat exposure. Within each site, 50-75 traps were placed at least 25 feet apart in areas where a high active burrow density was observed. This typically was along roads adjacent to pastures or other grassland. The GPS coordinates for each trap were obtained using a Garmin GPSMAP 64s unit (± 5 meters) (2015-2017) and Google Maps (± 10 meters) (2018) and updated as trap locations changed. However, from 2015-2017, traps often remained in the same location unless removed due to damage. In 2018, additional traps were placed at the San Luis NWR in order to obtain a higher density of trapping locations. During that trapping year, traps were placed at approximately 10-15 feet apart in select locations regardless of whether the burrow appeared active or not. If a squirrel was caught, the trap was shifted to an adjacent burrow entrance and left until another squirrel was caught.

On initial capture, individuals were placed in a canvas cone-shaped handing bag (Koprowski 2002) and categorized based on sex, age/reproductive status (juvenile, sexually mature, pregnant/lactating) (Glover

2018). Weight was measured using a digital hanging scale (lbs) based on two readings with the average weight recorded. Digital calipers (mm) were used to measure left and right hindfoot length, and anogenital distance was measured to confirm sex. A tissue sample (approximately 1 mm) was collected from the tip of the ear for genetic analysis and unique, self-piercing ear tags were placed at the base of each ear (Ulm 2019). Beginning in 2019 at San Luis NWR, squirrels were also given a unique combination of colored pipe cleaners twisted around each ear tag, which helped identify individuals from a distance. When recaptured, body measurements and weight were updated and any ear tags/pipe cleaners that were missing were replaced. On the rare occasion (N < 25) a recaptured squirrel was missing both ear tags and could not be identified, it was treated as a new capture. Individuals were released within 1 meter of the capture site.

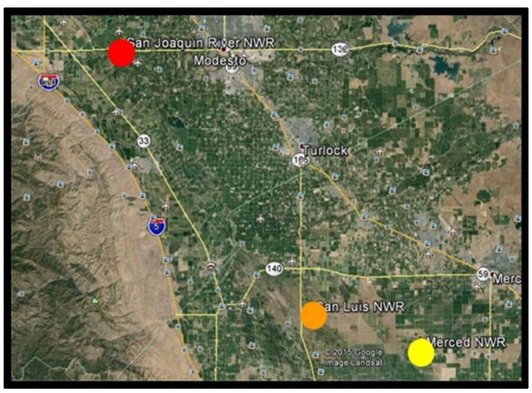

Figure 1: Trapping sites within the Central Valley: San Joaquin River NWR (red), San Luis NWR (orange), and Merced NWR (yellow). Imaging obtained using Google Earth. GPS data were collected using a mobile device with the Google Maps app.

Agricultural Crop Data Collection

Within each National Wildlife Refuge, I delineated plots by eye and assigned into categories: hardscape, natural vegetation, shrubland, pastures/alfalfa, corn, almonds, or seasonal vegetable crops. While each NWR is surrounded by a patchy mosaic of natural grassland, shrubland, and grazed pastures or alfalfa crops (all with the same relative caloric output), Merced NWR and San Joaquin NWR are also adjacent to agricultural lands, in close proximity to the CGS under study. Because the CGS is a foraging granivore, several of these crops (i.e. corn and almonds) may constitute a significant portion of the squirrel's diet while other crops (i.e. cotton or alfalfa) may not. It should be noted that while San Luis NWR has adjacent agriculture, the closest agricultural plot is approximately 985 meters away from the nearest trapping location, and therefore is not considered to be a significant source of food for the population.

I further subdivided Merced NWR into two separate sites where CGS trapping efforts were concentrated (Fig. 2). These sites are separated by a rural highway. Each is largely surrounded by natural grassland, shrubland, and pastures reserved for cattle grazing (all with same relative caloric output), but the southern site has an area where seasonal vegetable crops are grown (Fig. 2a) as well as another area where corn is grown seasonally to feed migratory fowl (Fig. 2d). A cattle barn is located in the center of the northern site (Fig. 2c) where grain is stored. The northern and southern trapping sites are within 550 meters, and it is possible that squirrels transfer between locations during their lifetime, or even during foraging bouts.

Similarly, I further subdivided San Joaquin River NWR into northern and southern trapping locations, which are also separated by a rural highway (Fig. 3). These two sites are at a greater distance from one another (8,000 meters), thus the probability of individual squirrels transferring from one site to another is very low. The northern site (Fig. 3c) is immediately adjacent to a NWR-managed corn field, as well as privately owned plots where a variety of seasonal vegetables are grown. A portion of the southern site (Fig. 3a) is adjacent to an almond orchard.

Data Analysis

Morphometric Data Analysis

I measured body condition using a commonly employed approach, where average hind foot length for an individual is regressed against body mass, for all adult individuals sampled within a population. I excluded juveniles in order to obtain a more accurate population distribution of body condition, not affected by developmental variation. For recaptured squirrels, body condition values were averaged across all capture events.

Agriculture Crop Data Analysis

I used ArcGIS(v10.6) to analyze satellite imagery of National Wildlife Refuge lands, to delineate the landscape plots into agriculture or non-agriculture, with pastures/alfalfa categorized as the latter. I used GPS capture location data as a centroid for estimating foraging range for individual CGS. The diameter of the centroid was dependent on the number of distinct GPS locations for an individual. For individuals captured at a location designated by a single GPS point, I created a 50-meter buffer around that point (Fig. 4) as a proxy for the estimated foraging range (Ulm 2019). This resulted in a total square area of 8,804 meters^2. For squirrels caught 2+ times and with a recapture distance less than or equal to 25 meters, I connected the GPS points with a line and created a 50-meter buffer around the centroid.

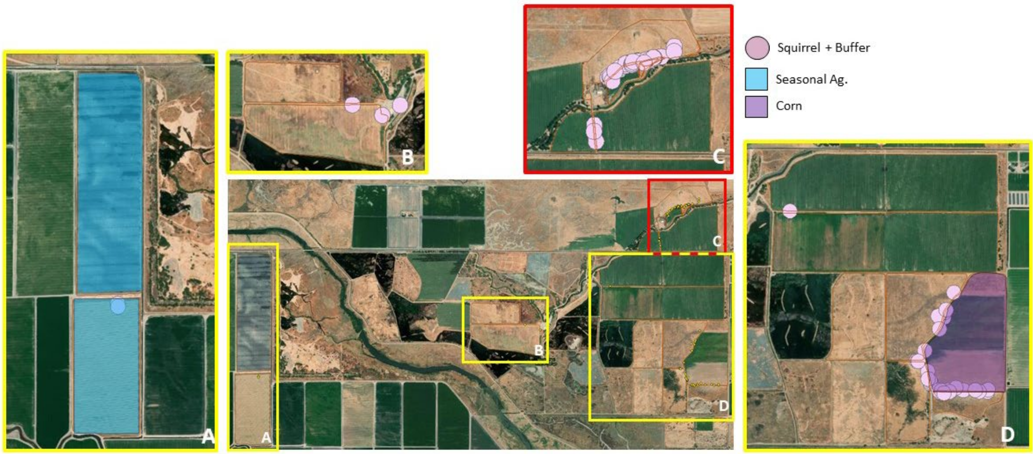

Figure 2: Trapping locations at the Merced NWR. The northern site (highlighted in red) and southern site (highlighted in yellow) are separated by Sandy Mush Road. Each site is surrounded by pastures/alfalfa, natural vegetation and shrubland with accessible food crops highlighted. Imaging shows each capture point including a 50-meter buffer which was used as an estimate for foraging range. For further details, see Agricultural Crop Data Analysis. Imaging obtained using ArcGIS(v10.6).

For squirrels caught 2+ times and whose recapture distance exceeded 25 meters, I connected the GPS points with a line and created a 25-meter buffer around the centroid (Fig. 5). I then calculated the percentage by which the estimated foraging range overlapped agricultural crops and non-crop vegetation (excluding hardscape).

Statistical Analysis

To address the question of whether individual CGS body condition is influenced by the degree to which estimated foraging range overlaps with agricultural crops, I used a general linear modeling approach. General linear models assume normality for dependent variables, so I performed a Kolmogorov-Smirnov test for normality on the variable body condition, using the pooled data from all three populations sampled. The preliminary test for normality was significant, therefore I performed a log10 transformation of the body condition data. I subsequently conducted a univariate GLM analysis with the full model described as *body condition = % agriculture + sex + site + year.* Body condition and % agriculture are continuous variables, and sex, site and year are categorical variables. I treated % agriculture, site and year as random variables, and sex as a fixed variable. Preliminary model building tested only for main effects from the four explanatory variables, using a Type III sums of squares approach. I conducted all statistical analyses in SPSS (IBM, v. 26).

Results

We captured a total of 652 individual California ground squirrels between the three National Wildlife Refuge locations from 2015-2019. Excluding juveniles and individuals with incomplete information, I used 424 adults in this analysis (Table 1). Approximately 55% of the individuals were trapped at

Figure 3: Trapping locations at the San Joaquin River NWR. The northern site (highlighted in red) and southern site (highlighted in yellow) are separated by Hwy 132. Each site is surrounded by pastures/alfalfa, natural vegetation and shrubland with accessible food crops highlighted. Imaging shows each capture point including a 50-meter buffer which was used as an estimate for foraging range. For further details, see Agricultural Crop Data Analysis. Imaging obtained using ArcGIS(v10.6).

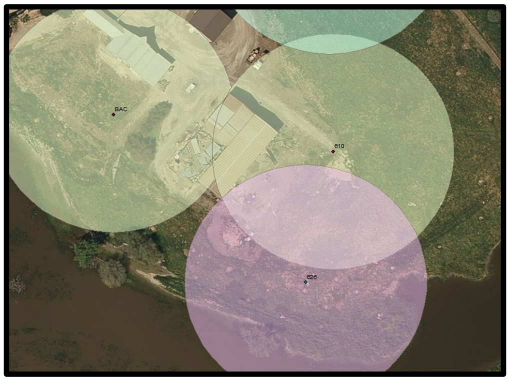

Figure 4: The 50-meter buffer zone of squirrels 626, 610, and BAC (San Joaquin River NWR) based on a single recapture point. Hardscape has not yet been excluded from the total area. Imaging obtained using ArcGIS(v10.6).

Figure 5: The 25-meter buffer zone of squirrel AAL (San Joaquin River NWR) based on two different recapture points. The buffer zone excludes hardscape from the total area. Imaging obtained using ArcGIS(v10.6).

San Luis NWR: while we spent a disproportionate number of trapping days at San Luis NWR to collect data for other purposes, we also experienced the highest rate of trapping success at location (3.33 squirrels per hour of trapping effort, compared to 3.29 squirrels/hour at Merced NWR and 1.43 squirrels/hour at San Joaquin River NWR).

A preliminary Kolmogorov-Smirnov test indicated that pooled body condition did not follow a normal distribution, D (424) = 0.049, p = 0.018; however, the log10 transformation of pooled body condition data yielded a non-significant test result D (424) = 0.027, p = 0.200, suggesting that the transformation imposed a normal distribution on the data. In the univariate GLM analysis, tests of between-subjects effects revealed three of the four terms in the model were significant contributors to variation in body condition. The power to detect small effect sizes was substantial for all terms, ranging from 1.000 (sex) to 0.718 (year). Sex was the strongest contributor to variation in body condition (F = 60.43, df = 1, p ≤ 0.000), with males exhibiting higher mean body condition (1.237, N = 189) than females (1.183, N = 235). Site was the next most important contributor to the model (F = 13.07, df = 2, p ≤ 0.000), with mean body condition highest in San Joaquin River NWR (1.24, N = 102), followed by Merced NWR (1.21, N = 92) and San Luis NWR (1.19, N = 130). The least important, yet still significant contributor to the model was year (F = 3.08, df = 3, p = 0.028), with mean body condition values following a sequential decline by

year: 2016 (1.26, N = 27); 2017 (1.22, N = 180); 2018 (1.20, N = 103); 2019 (1.19, N = 114). The model term % agriculture was not a significant contributor to variation in individual body condition.

Discussion

A previous study on California ground squirrels (Ulm 2019) found agriculture to be a significant factor influencing variation in juvenile skeletal size and body condition among Central Valley populations. Within these same populations, I was unable to detect a significant relationship between individual body condition and the percentage of overlap of estimated foraging range with agriculture. However, I did find that sex, site, and year were significant factors contributing to variation in body condition.

It is not surprising that sex was the most significant factor given that CGS are a sexually dimorphic species; adult males are consistently larger than adult females in body and cranial morphometrics (Smith et al. 2016) and exhibit higher average muscle mass. In our own populations, the average weight for adult males was 615.4 g, and 522.1 g for adult females. Differences can be attributed to how each sex allocates energy reserves; for example, in Richardson’s ground squirrels (*Spermophilus richardsonii*), juvenile males have been shown to allocate more energy to skeletal growth than to fat reserves, in comparison to juvenile females (Michener and Locklear 1990). Notably, however, rodents including CGS are known to deviate from “Rensch’s rule” (Matějů & Kratochvil 2013), which states male-biased sexual size dimorphism (SSD) increases with increasing body size. According to Matějů & Kratochvil, in CGS specifically, body size and social system could not explain this deviation, which suggests the existence of ecological or other selection factors preventing the evolution of extensive SSD.

Site was the next most important contributor to variation in body condition. This supports Ulm’s interpopulation analysis, where she found that the

	Males	Recaptured Males	Recapture Rate (%)	Females	Recaptured Females	Recapture Rate (%)	Total Sample
SJR NWR	36	4	11.1%	66	3	4.5%	102
MC NWR	39	10	25.6%	53	14	26.4%	92
SL NWR	114	46	40.4%	116	35	30.2%	230

Table 1: Captures of adult California ground squirrels from 2015 to 2019 at National Wildlife Refuges within the Central Valley of California: San Joaquin River (SJR), Merced (MC) and San Luis (SL).

average adult body condition for males and females was higher at Merced and San Joaquin River NWR than it was for San Luis NWR. However, she did not find a significant difference between Merced and San Joaquin NWR themselves. In this analysis, site was a significant factor influencing body condition, but percent of home range overlap with agriculture was not a significant factor, which suggests that my current approach for estimating foraging range may be flawed.

Home range size in this species is a highly plastic trait, exhibiting variation with and among populations across a variety of habitats. Estimates range from 626-902 m² for adult females and 313-376 m² for adult males (Owings et al. 1977), to 4,217 m² for adult females to 5,466 m² for adult males (Boellstorff and Owings 1995). Our own preliminary, unpublished data fall within these values (575 m² to 3436 m² for adults of both sexes, Russell 2020). When estimating foraging range, I used buffer sizes of 25 m or 50 m, which produced estimated ranges from 2,426 to 11,859 m². These values may not be an accurate estimate, but because we could only place traps adjacent to private agricultural lands (and not within them), reducing the diameter of the buffer of a trapping location would mean that the individual would exhibit 0% overlap with agricultural crops in the area. This would have under-estimated the degree to which individuals exploit crop food resources, based on our own observations of squirrel crop raiding behavior. It is likely that squirrels living near agriculture modify their own ranging behavior to take advantage of these calorie-dense food resources, in ways which have yet to be documented in the literature.

Finally, year was the third most significant contributor to individual body condition within my model. Given the variation in select agricultural plots and annual precipitation, exacerbated by California being in an "exceptional drought" (D4) from 2015-2016 (NIDIS 2020), this statistical result is convincing. Notably, however, the average body condition across all the populations *declined* each year despite the Central Valley's improvement to only a "moderate drought" (D1) by 2018 and "abnormally dry" (D0) by 2020. This may be due to a variety of factors, including a transition to a more nutritional but less calorie-rich diet as natural vegetation began to recover. Additionally, as San Luis constituted the largest portion of the sample and did not have any agricultural crops nearby to supplement diet, there may be a delayed effect on body condition seen most prominently in this population that affects the overall analysis.

It is possible that the multi-year drought influenced CGS body condition to such a degree that it influences the evolution of Central Valley populations. In unstable climatic environments, the relative strengths of size-dependent and size-independent mortality can lead to antagonistic selection pressures between early maturation and large body size through delayed maturation (Brown and Sibly 2006). Evidence of trade-offs in post-drought body size are seen in aquatic salamanders with different body sizes and maturation rates (*Siren lacertina* and *Siren intermedia*). Using field data and a discrete-time model, Luhring and Holdo (2015) found under mild conditions, the small-sized, fast-maturating species (*S. intermedia*) outcompeted the large-sized, late-maturing species (*S. lacertina*). However, as drought severity increased, *S. lacertina* experienced less of a decrease in its population and was able to encroach into areas normally dominated by *S. intermedia*. Aquatic and semi-aquatic species are especially adaptable to fluctuating environments given they are constrained by freshwater availability and therefore often unable to disperse into new territories. CGS, on the other hand, exhibit slight male-biased sex dispersal (Ulm 2019) and secondary dispersal has been observed in both sexes. This suggests that CGS may depend on dispersal into new territories to accommodate food shortages and may not prioritize growth rate over fecundity when food resources are scarce. As CGS are listed as a species of "least concern" (Smith et al. 2016), there is very little information on how this species copes with food shortages, and how variation in body condition directly influences life history strategies and lifetime reproductive success.

In the future, I may reconsider how the data for recaptured squirrels are analyzed. In this analysis, body condition for each adult recapture was averaged across all years, with the most recent year used as a reference. I did this to provide a more accurate estimate of foraging range, as each GPS location per capture event was used to determine the foraging range. However, given my results, this may be an inaccurate representation of accessible food. Limiting recaptures by year or even season would provide better insight and should be considered for future revisions.

Conclusion

Unlike many other native mammals, CGS have shown themselves to be a resilient species thriving in the modified landscape that makes up California's Central Valley. While CGS are a historically well-documented species, little is known about how this species responds to fluctuations in climate or food availability. While population-level analysis is important for observing general trends, intrapopulation analysis will provide the greatest insight in the long-term impact a high-calorie diet has on individuals, especially in conjunction with individual behavior or genotypic profile. The results presented here provide a more accurate representation of how small mammal populations may be impacted by variation in human agricultural crop availability. Given that agricultural production is expected to rise by 70% in 2050 (FAO 2009), this information is crucial in maintaining local biodiversity.

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