Population parameters of the Phillips kangaroo rat (*Dipodomys phillipsii*)

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Populations respond dynamically to biotic and abiotic changes in their habitat. The identification and description of such demographic oscillation can inform conservation plans that support threatened species. Human activities have reduced and fragmented the already restricted habitat of the Phillips's kangaroo rat (*Dipodomys phillipsii*), threatening its existence. The objective of this study was to describe and analyze *D. phillipsii*'s annual population cycle and structure in the context of its increasing vulnerability to extinction. The capture-recapture technique was performed monthly from 2012 to 2016. Total individual counts, age, reproductive condition, weight, and sex of *D. phillipsii* were determined and recorded. Daily temperature and precipitation data of the study area were analyzed with population parameters and frequency data. *D. phillipsii* populations responded to changes in temperature and precipitation. The highest population densities were recorded in the spring and summer and were correlated with the highest values of the environmental variables studied. Sex ratio was nearly equal during samplings, with non-pregnant females and males with abdominal testes as the most frequently presented secondary sexual characteristics. Most captured individuals were adults. Individual body weights were highly variable, which can be attributed to reproduction and fluctuations in resource availability. *D. phillipsii* populations severely decreased in the last year of the study, with low juvenile and pregnant or lactating female frequency counts. Anthropogenic pressures on *D. phillipsii* habitat persist, indicating that the proliferation of this species is at risk. Information from this study could be used to address the pressing need for the management and conservation of *D. phillipsii*.

Las poblaciones responden de manera dinámica a los cambios bióticos y abióticos de su hábitat. El conocimiento de estas oscilaciones es prioritario en especies con problemas de conservación o con interés en su manejo. La rata canguro de Phillips (*Dipodomys phillipsii*) se considera amenazada debido a la reducción y fragmentación de su restringido hábitat. Dada su vulnerabilidad, se tuvo como objetivo analizar su ciclo anual y estructura poblacional. Con la finalidad de obtener los parámetros poblacionales (edad, condición reproductiva y proporción de sexos) de la especie, se utilizó la técnica de captura-recaptura durante los años 2012 al 2016. Además, los datos de temperatura y precipitación de la zona y de los años de estudio fueron analizados junto con las frecuencias de las ratas canguro. *D. phillipsii* respondió a los cambios en la temperatura y precipitación. Sus densidades más altas se registraron en la primavera y verano. Además, coincidieron con los mayores valores de las variables ambientales estudiadas. La proporción de sexos fue casi equitativa durante los muestreos. Las hembras no preñadas y los machos con testículos abdominales fueron registrados con mayor frecuencia. Los adultos fueron los más abundantes. El peso de los organismos fue variable, probablemente causado por la reproducción y por su respuesta a los cambios de los recursos ambientales. Los resultados indican que, en los últimos años de estudio, las densidades poblacionales de la especie han disminuido severamente. Además los registros de juveniles, así como de hembras con condiciones de preñez o lactancia fueron bajos. Aunado a esto, las presiones antrópicas son persistentes, por lo que, la existencia de la especie está en riesgo. La información de este estudio podría ser utilizada para su lograr su inminente manejo y conservación.

Keywords: Density; desert rodents; Heteromyidae; México; reproductive characteristics; temperature.

Introduction

In habitats with high climatic variability, organisms temporally select for seasonally favorable conditions to complete certain aspects of developmental stages and reproduction. When conditions are unfavorable, organisms evade such conditions through various strategies (Walsberg 2000; Visser and Both 2005; Ward 2016). For example, in heteromyids rodents such as kangaroo rats (*Dipodomys spp.*), adaptive body temperature and metabolic changes occur as a response to unfavorable feeding and environmental temperature conditions (French 1993; Gummer 2005). Kangaroo rats also rely on a system of underground burrows, which with their regulated temperature and humid-ity, serve as a respite from intense solar radiation and food storage (Walsberg 2000).

Climatic variables can influence the growth of populations and modify the structure of heteromyid communities (Brown and Ernest 2002; Lima *et al.* 2008; Hernández et al 2005, 2011); temperature changes can stimulate the beginning or end of reproduction and hibernation (Lane *et al.* 2012), while precipitation is often correlated to food resource availability (Hoditschek and Best 1983; Ernest *et al.* 2000; Thibault *et al.* 2010). This is particularly relevant in desert systems (Lane *et al.* 2012) since precipitation is responsible for plant shoot emergence and seed production, the primary food sources of heteromyids (Reichman and Van

De Graaff 1975; Beatley 1976; Zeng and Brown 1987; Walsberg 2000; Hernández et al 2005, 2011; Thibault *et al.* 2010). As such, these environmental variables generally demark rodent reproductive periods (Beatley 1976; Walsberg 2000; Brown and Ernest 2002; Lane *et al.* 2012). Interruptions to precipitation cycles and prolonged periods of extreme heat can result in reproduction and survival rate decreases, causing population instability (Visser and Both 2005; Miller-Rushing *et al.* 2010; Lane *et al.* 2012). Demographic and reproductive data based on annual frequency records (Caughley 2000; Miller-Rushing *et al.* 2010) can identify vulnerable conditions and times of year for a threatened species (Daskalova *et al.* 2020; Price and Kelly 1994; Morrison *et al.* 1996; Purvis *et al.* 2000), making such records a valuable tool for effective conservation and management.

Kangaroo rats (*Dipodomys spp.*) provide multiple benefits to North American arid ecosystems (Daskalova *et al.* 2020). Known as ecosystem engineers, kangaroo rats modify vegetative species composition and soil micro topology with the construction of underground burrows. They also consume and store forb and grass seeds, increasing plant dispersal (Longland and Dimitri 2021). Since their feeding habits favor the establishment and permanence of native species, kangaroo rats are keystone species for arid and semi-arid deserts (Hafner 2016; Longland and Dimitri 2021). As keystone species, kangaroo rat populations can serve as indicators of overall ecosystem health (Fernández *et al.* 2014). Additionally, they represent an important protein source for reptiles, birds, and other desert mammals (Hafner 2016; Longland and Dimitri 2021). The Phillips kangaroo rat (*Dipodomys phillipsii*) is endemic to arid or semi-arid regions of the Northern Valley of México, Southern Puebla, and Northern Oaxaca, dominated by sandy soils and xerophytic and grassland vegetation (Jones and Genoways 1975; Hafner 2016). Despite its ecological relevance, little is known about the natural history, ecology, distribution, and demography of this rodent (Hafner 2016; Flores-Zamarripa and Fernández 2018; Montero-Bagatella y Cervantes 2022). Only 40 % of the Phillips kangaroo rat's original habitat remains due to the expansion of human land use (Sánchez-Cordero *et al.* 2005) for agricultural practices and livestock (Montero-Bagatella *et al.* 2017; Durán-Antonio and González-Romero 2018). Despite its classification as "Threatened" by the Official Mexican Standard (SEMARNAT 2019), the International Union for Conservation of Nature classifies *D. phillipsii* as a species "of least concern" (Álvarez-Castañeda *et al.* 2016). Anthropic pressures continue to affect arid and semi-arid habitats (Sánchez-Cordero *et al.* 2005; Fernández *et al.* 2014; Jiménez-García *et al.* 2014; Durán-Antonio and González-Romero 2018; Flores-Zamarripa and Fernández 2018), which, coupled with an already restricted range, makes this species especially vulnerable to extinction (Purvis *et al.* 2000; Sykes et al. 202019; Longland and Dimitri 2021). In the face of such anthropic pressures, long-term demographic characteristics (*i. e.*, body mass, population size structure, reproductive viability) and environmental habitat (*i. e.*, biotic and abiotic) monitoring should be prioritized in order to effectively conserve a species (Price and Kelly 1994; Durán-Antonio and González-Romero 2018; Daskalova *et al.* 2020; Braun *et al.* 2021). This research describes and analyzes the annual demographic cycle of *D. phillipsii* and examines its relationship between climatic conditions and *D. phillipsii* population dynamics. This much-needed information can and should be used to support their conservation.

Material and methods

The presented study was conducted in the Perote Valley in the municipality of Perote, Veracruz, México. This valley, located between the Sierra Norte de Puebla and the Cofre de Perote mountain ranges (Sánchez-Cordero *et al.* 2005; Fernández *et al.* 2014) has high rates of endemism for flora and fauna. Altitude ranges between 2,300 and 2,700 masl. The climate is the most humid of the semiarid climates with a mean annual temperature of 14 ºC and a mean annual rainfall of 500 mm, making for a semi-arid ecosystem (Gerez-Fernández 1985). Vegetation includes pine-oak forest, tascate forest, scrubland, natural and induced grassland, and halophytic vegetation (Montero-Bagatella *et al.* 2017). The area is facing severe conservation problems due to intensive agricultural practices and livestock, that have fragmented and decreased the limited available habitat in the region (Gerez-Fernández 1985; Montero-Bagatella *et al.* 2017).

Population structure and annual cycle. To capture the kangaroo rats, three sites with the succession of native pastures (*Jarava. ichu* and *Bouteloua scorpioides)*, some succulents and shrub were sampled. Sites 1 and 2 were enclosed with barbed wire and electric fencing to prevent grazing and intrusion by domestic fauna (Montero-Bagatella *et al.* 2017; Figure1). Each worksite consisted of two plots (1 ha) separated from each other by 100 m. In each plot, 36 Sherman traps (30 x 10 x 8 cm) were placed in a grid (6 x 6 traps) and separated from each other by 20 m. Traps were baited with peanut butter and oat flakes and activated from 17:00 to 8:00 hrs. From 2012 - 2016, rodents were surveyed monthly using the capture, mark, and recapture technique for two consecutive nights (Durán-Antonio and González-Romero 2018; Caughley 2000). Captured individuals were marked in the ventral region with a permanent marker. Sex, age, and secondary sexual characteristics (*i. e.*, scroted testicles in adult males and signs of pregnancy / lactation in adult females; Price and Kelly 1994; Kaufman and Kaufman 2015; Durán-Antonio and González-Romero 2018) were recorded for each specimen captured. Size, weight, coat coloration, and reproductive condition were used to estimate age (*i. e.*, juvenile or adult; Price and Kelly 1994). After data recording, organisms were released *in situ* (Sikes and Gannon 2011; Durán-Antonio and González-Romero 2018). In 2015, heavy rains interrupted sampling continuity, resulting in an incomplete data set for this year. In addition, as the sampling was carried out at the same time as the research of the Perote ground squirrels' activity
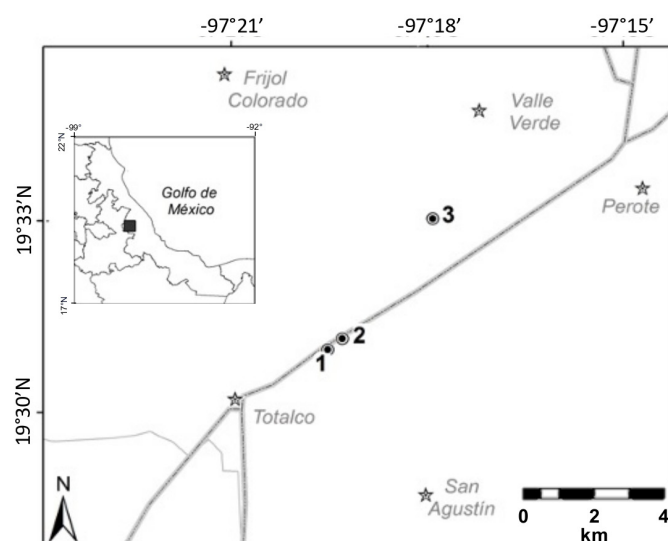
Figure 1. Map of study sites. Areas 1 and 2 had fencing and surveillance. Stars = villages. Black points = study sites. Grey and black lines = roads.

Table 1. Total captures of the Phillips´ kangaroo rat (*Dipodomys phillipsii*) recorded by year, sex, and age category, from Perote, Veracruz.

	Females		Males	
Years	Juveniles	Adults	Juveniles	Adults
2012	12	191	15	211
2013	5	40	0	31
2014	3	178	6	185
2015	3	61	4	47
2016	2	10	0	19

cycle ([Montero-Bagatella *et al.* 2017](#)), February and November were not sampled.

Temperature and precipitation data for the study area were provided by the Comisión Nacional del Agua (CONAGUA; [https://smn.conagua.gob.mx/](#)). For each study site, live individual totals, sex ratio, age, and reproductive condition of individuals were recorded ([Caughley 2000](#)). In order to examine annual reproductive cycles, the years of study and demographic variables were grouped by annual seasons (*i. e.*, spring, summer, winter, and fall). Temperature, precipitation, and reproductive status were analyzed by one-way analysis of variance (ANOVA) and a *t* - test. Body weights were compared using one-way ANOVAs. In order to detect differences between ages and sexes, Tukey's *post hoc* tests were performed. Spearman correlations were made between the precipitation of the same year and previous year and the number of *D. phillipsii* individuals, as well as the number of *D. phillipsii* individuals and temperature ([Ernest *et al.* 2000](#)). Analyses were performed using Minitab 21.1.1.0 software.

Results

The total sampling effort was 4, 536 trap / nights (Table 1). Figure 2 shows total live individual counts, monthly precipitation, and average monthly temperature from 2011 to 2016. The highest abundance values mostly coincide with the peaks in temperature and precipitation. The highest temperatures were registered in April and May (spring). In October (fall), temperatures began to drop. The warmest year was 2011, and the coldest 2013. The average temperature of the study area was 24.9 °C. Temperature values for annual seasons differed significantly (F = 3.11, *d. f.* = 3, P = 0.05), with the post hoc test showing differences between fall and spring (P = 0.033). Significant differences existed between average temperatures and study years (F = 5.95, *d. f.* = 5, P = < 0.001); Tukey's test indicated differences

between 2011 and 2013 (P = < 0.001), as well as between 2013 and 2014 (P = 0.001). Precipitation was statistically different between seasons (F = 11.16, *d. f.* = 3, P = < 0.001), with the *post hoc* test indicating differences between winter and summer, and winter and spring (P = 0.001 for both). Statistical differences were found between fall and spring (P = 0.012), as well as between fall and summer (P = 0.011). 65 % of all annual precipitations occurred during spring and summer months, with little precipitation in winter months. The rainiest year studied, exceeding 170 mm. was 2013. There was no correlation between temperature and the number of captures of *D. phillipsii* (r = 0.12, P = 0.58), the previous year's precipitation and the number of captures (r = 0.20, P = 0.38) and same-year precipitation and the number of captures (r = 0.12, P = 0.58).

The highest number of live captures for *D. phillipsii* occurred in August 2012 with 130 individuals, contrasting with the lowest number of capture individuals (2 individual) in July 2015. There was a continuous decrease in captures from 2013 to 2016. Most captured individuals were adults, with juvenile capture numbers peaking in the month of May (Figure 3). Sex ratios for both adults and juveniles were maintained steadily at 1:1 with no significant differences for neither adults (F = 0.01, *d. f.* = 1, P=0.93) nor juveniles (F = 0.32, *d. f.* = 1, P = 0.58). Overall numbers of adults and juveniles were just at the margin of statistical differences (F = 3.93, *d. f.* = 1, P = 0.063). There were however, significant differences between numbers of adult vs. juvenile for both males (F = 9.0, *d. f.* = 1, P = 0.010) and females (F = 8.8, *d. f.* = 1, P = 0.010).

Non-pregnant females and males with abdominal testicles were the most abundant (Figure 4), and pregnant or lactating females were the least abundant. Statistical differences existed between frequencies of pregnant or lactating vs. non-pregnant females (F = 3.93, *d. f.* = 2, P = 0.010). Males with abdominal testicles were present throughout all the samplings, their abundance increasing in May. Scroted males were present during all samplings, reaching maximum numbers in the spring. The number of males with abdominal vs. scrotal testicles was close to being statistically significant (*t* = 1.98, *d. f.* = 13, P = 0.069). Adults body weights varied evenly throughout the seasons (Figure 5); female body weights were highest in the summer, exceeding the weights of the males. The weights of the juveniles did not vary by season, and there were no differences between male and female juvenile weights (F = 0.01, *d. f.* = 1, P = 0.93).
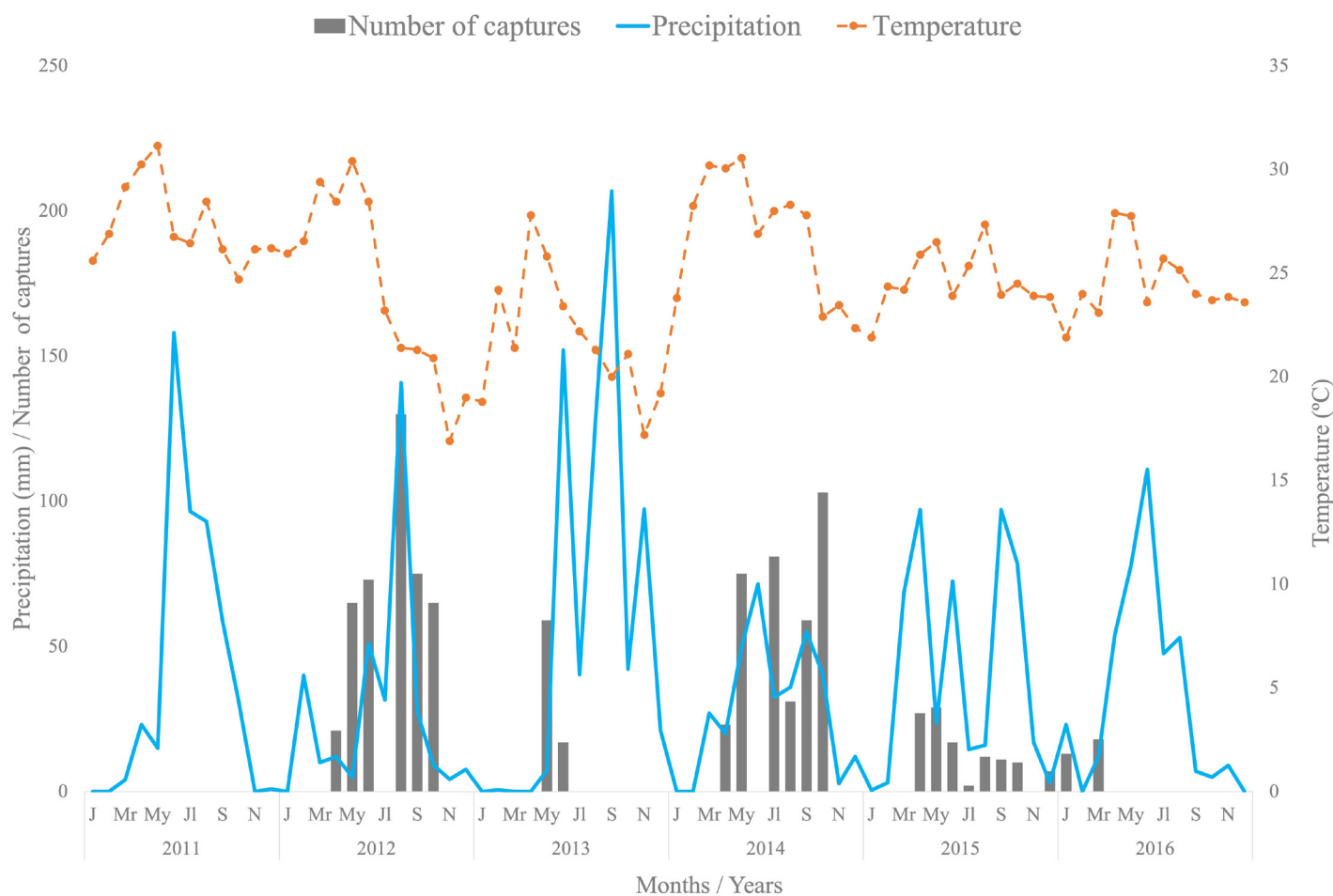
Figure 2. Average rainfall and temperatures of Perote, Veracruz and Phillips' kangaroo rats (*Dipodomys phillipsi*) monthly frequencies.

Discussion

This study captures the population oscillations of *D. phillipsii* in response to temperature and precipitation changes, as has been described for other species of its genus (Bradley and Mauer 1971; Hoditschek and Best 1983; Morrison *et al.* 1996; Brock and Kelt 2004; Kelt 2011; Kaufman and Kaufman 2015). The maximum captures coincided with peaks in precipitation and temperature as reported for *D. merriami* and *D. stephensi* (Price and Kelly 1994; Koontz *et al.* 2001). Heavy rains interrupted sampling continuity, resulting in a lack of information that could have influenced the correlations values. Studies such as Ernest *et al.* (2000) and Hernández *et al.* (2005, 2011) have demonstrated a positive correlation between the number of rodent captures and precipitation; nonetheless, their study sites were in arid ecosystems with marked seasonality of droughts. In contrast with the Chihuahuan desert, where 60 % of annual precipitation occurs in the summer (Brown and Ernest 2002), the Perote Valley´s precipitation maximums occurred equally in both spring and summer. Hence the distinct rainy seasons and the amount of precipitation received may make it more difficult to discern statistical patterns of response (Hernández et al 2005). Authors such as Reichman and Van De Graaff (1975), Ernest *et al.* (2000), as well as Kaufman and Kaufman (2015) report a synched

phenology for vegetative growth and the reproductive seasons *Dipodomys* genus species after rainfall, thus complementary studies as cover vegetation could be used as indicator of the species' response to rainfall (Hernández et al 2005).

In this study, reproductive activity lasted from January to October. Neither pregnancy nor lactation was common among captured individuals, as females with such conditions typically remain in their burrows caring for their young (Eisenberg 1993). Studies by Bradley and Mauer (1971), as well as Hoditschek and Best (1983) indicate that male *D. merriami*, *D. ordii*, and *D. stephensi* have longer reproductive periods than females, thus the species can have more than one litter per year (Bradley and Mauer 1971; Hoditschek and Best 1983; Price and Kelly 1994).

Gestation periods can influence extinction risk (Purvis *et al.* 2000); in animals with long gestation stages that produce few offspring this risk increases. While juvenile counts in this study were low, as reported by Durán-Antonio and González-Romero (2018), gestation periods for *D. phillipsii* are short and populations can grow relatively fast (Eisenberg 1993; Hafner 2016). Predation and burrowing life can result in low trapping success (Hafner 2016) which in this case could have accounted for the low capture numbers (Zeng and Brown 1987). Males, which tend towards disper-

sal are more likely to be captured than females, which tend toward philopatry (Hafner 2016). Additionally, males' home ranges may overlap with multiple females (Zeng and Brown 1987; Kaufman and Kaufman 2015; Hafner 2016). While overall numbers for males were slightly higher, a 1:1 sex ratio was maintained, as indicated by Durán-Antonio and González-Romero (2018). Continuous capture data, even the regular catches of juveniles, indicated that this species is active throughout the entire year, a behavior that has also been reported for *D. nitratoides*, *D. merriami, D. ordii*, *D. stephensi*, and *D. simulans* (Bradley and Mauer 1971; Jones and Genoways 1975; Hoditschek and Best 1983; Morrison *et al.* 1996; Brock and Kelt 2004; Kelt 2011; Kaufman and Kaufman 2015). *D. ordii* and *D. merriami* can go into torpor during extreme climatic and dietary conditions (French 1993; Gummer 2005), but torpor in *D. phillipsii* is yet to be confirmed; Jones and Genoways (1975) reported activity in this species during low-temperature conditions, yet no observations of feeding activity during heavy rains.

In this study *D. phillipsii* population densities varied by both month and year; in 2016, the population drastically declined, an occurrence also observed by Durán-Antonio and González-Romero (2018). Such population declines are present in other *Dipodomys* genus species; *D. spectabilis* populations fluctuated in response to human activities and alterations to plant species compositions (Valone *et al.* 1995); *D. nitratoides*, *D. elator* and *D. gravites* are at risk of extinction due to the continual degradation of their rare and restricted habitat (Hafner 2016; Patton *et al.* 2019; Braun *et al.* 2021). Indirect effects of human disturbances to these vulnerable populations include increased predation (Wilkening *et al.* 2019) and zoonotic diseases (Valone *et al.* 1995; Brown and Ernest 2002), with endemic species being the most vulnerable to such threats (Sykes et al. 202019; Purvis *et al.* 2000). It is likely that the restricted distribution of Phillips´s kangaroo rat populations are already responding to both direct and indirect effects of human activities (Sykes et al. 202019).

The preferred habitat of species of *Dipodomys* genus is a landscape with short, sparse vegetation, which allows them to see and hide from potential predators (Hafner 2016; Longland and Dimitri 2021). The presented study areas were composed of dense, tall grassland vegetation with shrubs (Montero-Bagatella *et al.* 2017; Durán-Antonio and González-Romero 2018), potentially restricting food availability (Thibault *et al.* 2010). These vegetative conditions often cause individuals to search for new habitat areas (Goldingay *et al.* 1997; Bliss *et al.* 2019), despite the associated mortality risks (Zeng and Brown 1987; Thibault *et al.* 2010). *Dipodomys* species are often classified as granivorous, yet many are known to also consume vegetative plant material (Bradley and Mauer 1971; Reichman and Van De Graaff 1975; Soholt 1977; Longland and Dimitri 2021). Controlled grazing has the potential to maintain short and sparse grassland ecosystems free of woody plants (Goldingay *et al.* 1997; Montero-Bagatella *et al.* 2017; Durán-
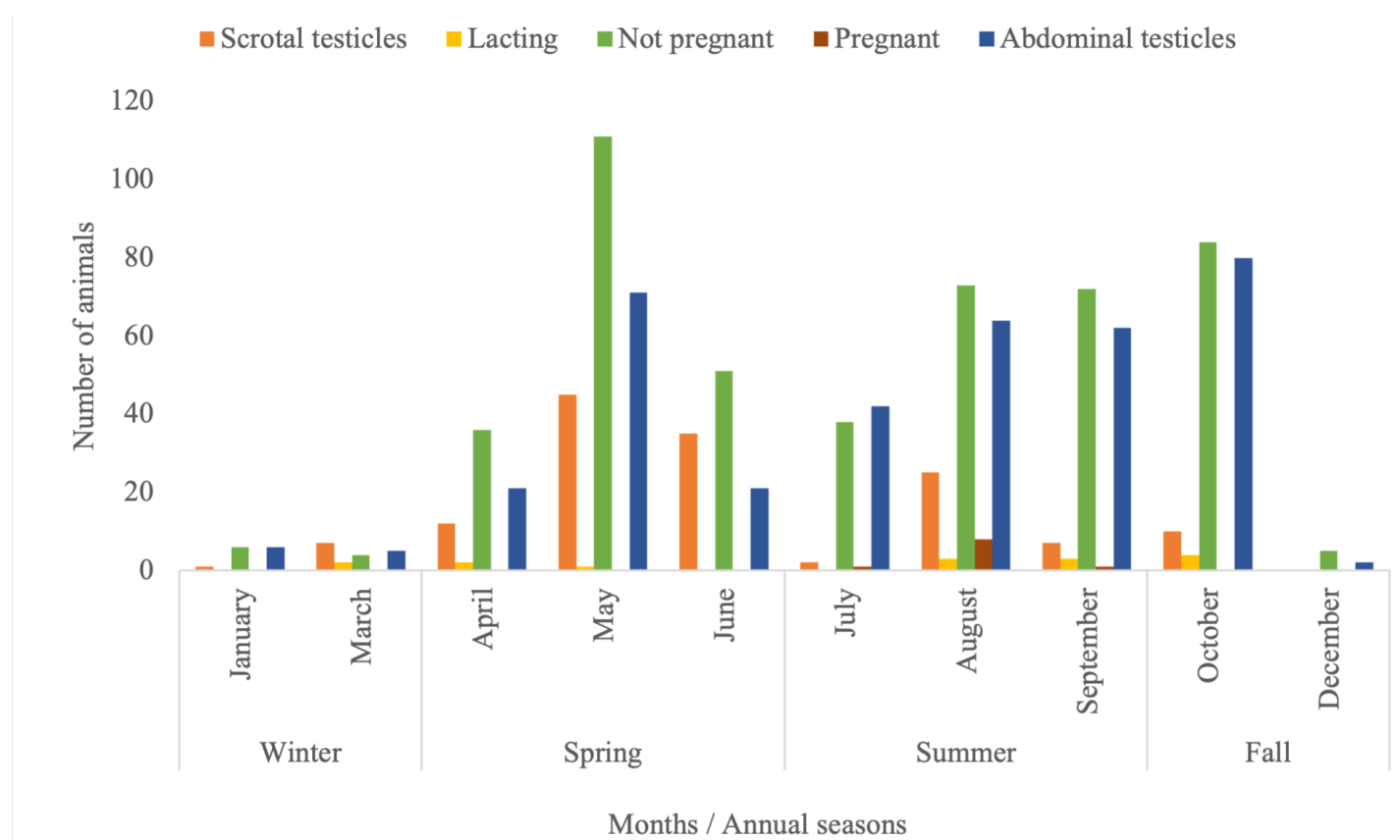

Figure 3. Average sex and age breakdowns of captured Phillips´ kangaroo rat (*Dipodomys phillipsii*) by season for 2012-2016, from Perote, Veracruz.
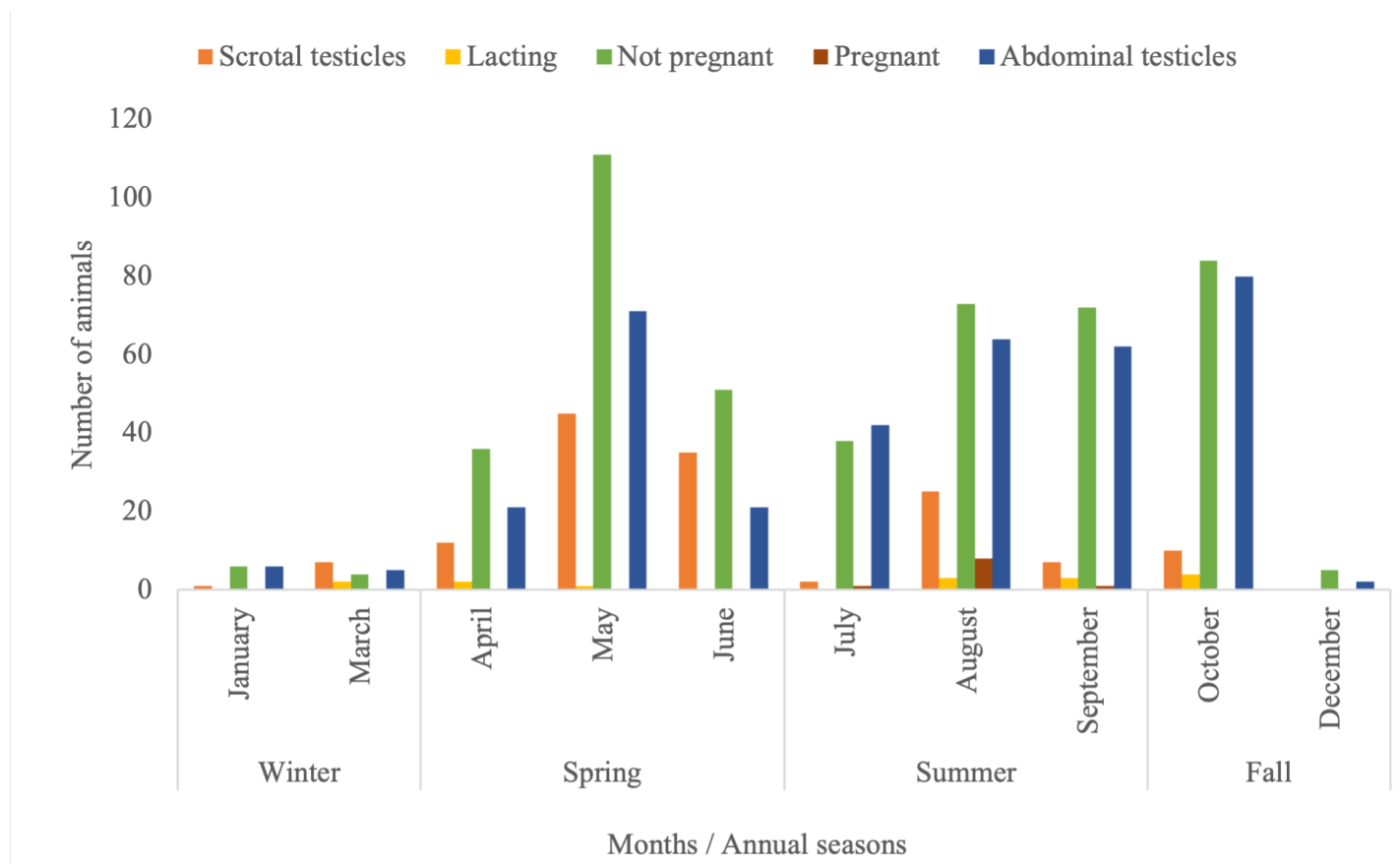
Figure 4. Frequency counts of secondary sexual characteristics for Phillips´ kangaroo rat (*Dipodomys phillipsii*) individuals by month and season, from Perote, Veracruz.

Antonio and González-Romero 2018), providing rodent species with tender shoots, stems and leaves as food resources. *Dipodomys* rats also consume insects (Bradley and Mauer 1971; Longland and Dimitri 2021); it is likely the summer abundance of Orthoptera, as well as mealworm beetles (Coleoptera) which were found daily inside the traps, are part of *D. phillipsii*'s diet. Since such inputs are ephemeral, a diverse diet throughout the year is required to meet the demanding energy requirements for growth and reproduction (Soholt 1977; Zeng and Brown 1987). These energetic demands can be reflected in the weight of the organisms (Bradley and Mauer 1971; Zeng and Brown 1987), which in our study, were like those of Durán-Antonio and González-Romero (2018). The overall weights of individuals decreased significantly in late summer and winter. Such patterns have been observed in *D. merriami* and were attributed to meteorological and food availability changes (Bradley and Mauer 1971; Zeng and Brown 1987) as well as the energetically costly maintenance of homeostasis during temperature lows (Gummer 2005). In winter, these energetic needs are met by the consumption of seasonal vegetation, which is tightly linked to summer rainfall. Consequently, droughts can have serious repercussions on the proliferation and reproduction of these rodents (Beatley 1976; Ernest *et al.* 2000).

Summer food availability is also related to summer reproduction (Lima *et al.* 2008; Thibault *et al.* 2010), where grasses and succulents can provide the necessary requirements

for the most demanding stages of gestation and lactation (Soholt 1977). Summer was the season with the highest individual weights, number of captures and was comparatively higher to previously reported numbers for other species of the genus (Zeng and Brown 1987; Goldingay *et al.* 1997). However, in May and June 2018, when the study area was resampled, no individuals were captured (González-Romero personal communication). Human alterations to the landscape surrounding the studied sites may have driven *D. phillipsii* from the area (Thibault *et al.* 2010). The Perote endemic squirrel (*Xerospermophilus perotensis*) also shows lower population densities in these sites than in areas that more closely resemble its original habitat (Montero-Bagatella *et al.* 2017). These two species share habitat preferences and may respond similarly to habitat modifications. Agricultural development and expansion are continuously shrinking their habitat which limits their potential to inhabit new areas (Sánchez-Cordero *et al.* 2005; Fernández *et al.* 2014; Jiménez-García *et al.* 2014; Flores-Zamarripa and Fernández 2018;). Traditional farming methods that promote native plant diversity and serve as a refuge for the Phillips kangaroo rat (Jiménez-García *et al.* 2014), are being phased out by conventional methods. The low dispersal capacity of the genus, habitat loss, and natural and anthropic barriers combine to limit the flow of individuals to other populations (Zeng and Brown 1987; Bliss *et al.* 2019; Patton *et al.* 2019; Wilkening *et al.* 2019), restricting genetic diversity and increasing the vulnerability to extinction of *D. phillipsii*´s (Patton *et al.* 2019).
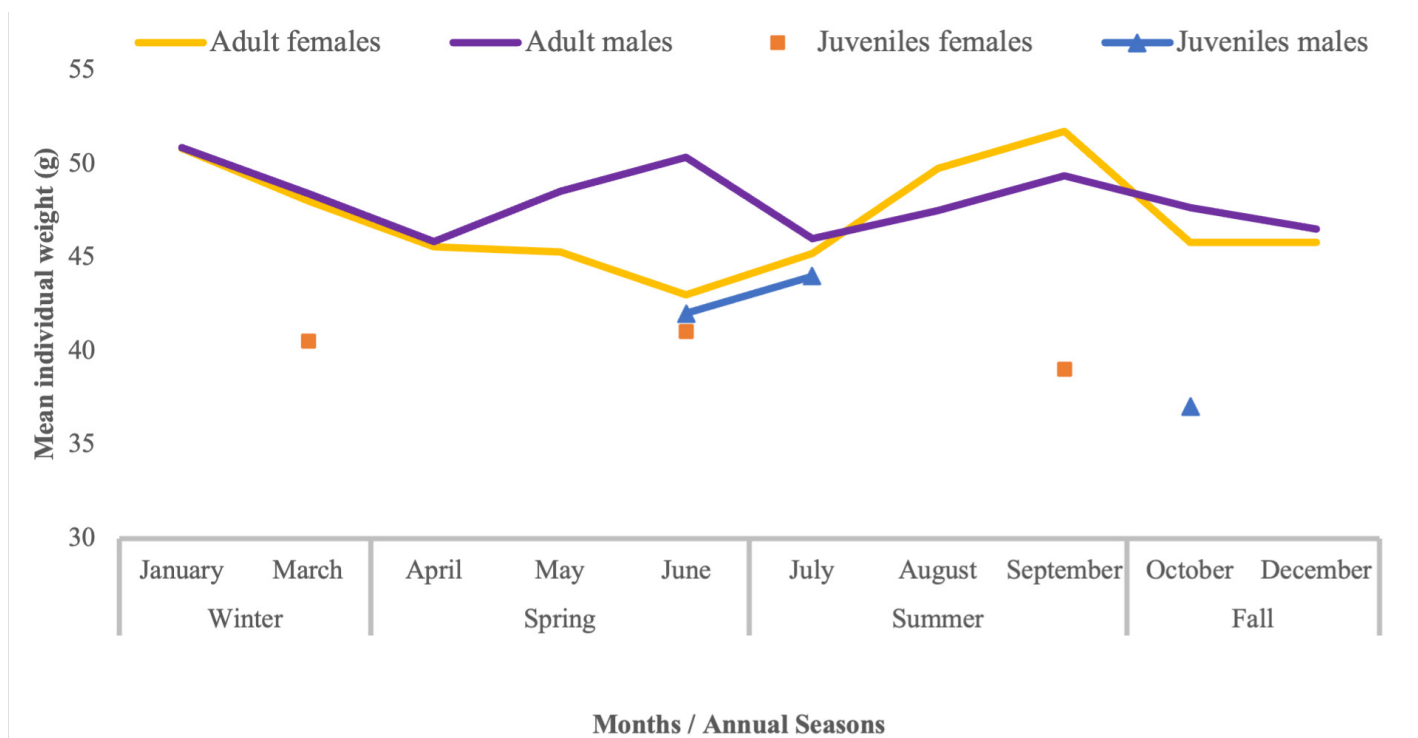
Figure 5. Average weights by age and sex of captured kangaroo rats (*Dipodomys phillipsii*), from Perote, Veracruz.

Further demographic and ecological studies about this species would complement the information presented in this study. The identification and study of additional populations could allow for *ex situ* conservation and reintroduction efforts to be considered (Patton *et al.* 2019; Wilkening *et al.* 2019). The implementation of certain agricultural practices (Jiménez-García *et al.* 2014; Montero-Bagatella *et al.* 2017; Durán-Antonio and González-Romero 2018) and enforced legal protection of the habitat of *D. phillipsii* has potential to greatly favor the preservation of this and other endemic species. However, the few legal protections that exist are disappearing; the "Natural Protection Area" status that once protected thousands of hectares, including a portion of the distribution range of *D. phillipsii* distribution range, was annulled (Gobierno del Estado deGovernment of the State of Veracruz 2019). The results of this study, together with the physiological and habitual characteristics of this species indicate that its long-term existence is threatened. Actions that support the protection of the Phillips´s kangaroo rat and its habitat are urgent, beginning with changing its national risk category, NOM 059 from "threatened" to "in danger of extinction".

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