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Doctor of Science
in Life Sciences
with orientation in Environmental Biology

Spatio-temporal population dynamics of the San Quintín Kangaroo Rat (*Dipodomys gravipes*)

A dissertation
submitted in partial satisfaction of the requirements for the degree
Doctor in Science

By:

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Diámica poblaciona espacio-temporal de la rata canguro de San Quintín (*Dipodomys gravipes*)

Resumen aprobado por:

PhD. Eric Mellink Bijtel
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La rata canguro de San Quintín (*Dipodomys gravipes* Huey, 1925) es un roedor microendémico de la región de San Quintín-El Rosario, Baja California. Las poblaciones de la especie disminuyeron a finales los 1970s y principios de los 1980s. Después de diversos esfuerzos de búsqueda infructuosos a principios de la década de 1990, se consideró extinta y así fue declarada en 1994. Después de aproximadamente 32 años sin registros, fue redescubierta en un pequeño terraplén rodeado de campos de cultivo abandonados. Sin embargo, este redescubrimiento subyace una necesidad urgente de confirmar el hallazgo. Además, el tiempo transcurrido entre el último registro de la especie y su redescubrimiento, dejó importantes vacíos de conocimiento sobre la biología y ecología de *D. gravipes*. Se sabe poco sobre la distribución actual de la especie y las preferencias de ocupación del sitio, y la variación estacional en la abundancia de la especie, los ciclos reproductivos y la influencia de las variables ambientales en estos parámetros. Por lo tanto, este trabajo de investigación doctoral tiene como objetivo general elucidar la identidad taxonómica, distribución actual, características de hábitat y la dinámica espacio–temporal poblacional de colonias de *D. gravipes.* En este trabajo se compararon medidas externas y morfométricas craneales y datos mitocondriales de individuos de la especie supuestamente redescubierta con las de individuos confirmados como *D. gravipes* y con las de especies simpátricas de Baja California. Con base en lo anterior se logró la confirmación morfométrica y molecular de la presencia de la especie después de más de 32 años sin registros. Posterior a esto, con base en un extenso estudio de campo, se documentaron 19 localidades de la especie, de las cuales 6 están fuera de su rango de distribución histórico, expandiendo este último en ~60 km. La mayoría de los sitios ocupados por la especie se encuentran en tierras agrícolas abandonadas en etapas tempranas de sucesión ecológica. Los datos respaldan que en el paisaje agrícola altamente transformado, la especie pudo sobrevivir sin ser detectada y colonizar/recolonizar sitios una vez que el hábitat se volvió adecuado después del abandono agrícola. Esto demuestra que la especie es altamente resiliente y persistió como una metapoblación. Además, se examinó la variación espacio-temporal en la abundancia de *D. gravipes* y el estado reproductivo. Este trabajo revela que la abundancia de *D. gravipes* está influenciada por el aumento de la cobertura vegetal; cuando esta última disminuye, la abundancia de la especie aumenta y viceversa, revelando un patrón de abundancia estacional que es aproximadamente sincrónico entre localidades. El estado reproductivo no está fuertemente influenciado por el cambio de la cobertura vegetal en ninguna localidad, pero el aumento de la vegetación herbácea podría conducir a una mayor proporción de juveniles, lo que en última instancia conduce a un aumento de la población. Por último, los resultados de este trabajo proporcionan una comprensión más profunda de la ecología de la especie después de 32 años de vacíos de conocimiento. Al mismo tiempo, proporcionan pautas para futuras investigaciones y planificación de la conservación de la especie.

Palabras clave: *Dipodomys gravipes*, mtDNA, expansión agrícola, tierras de cultivo, Baja California, abundancia, estatus reproductivo

Abstract of the thesis presented **by Jorge Alberto Andrade Sánchez** as a partial requirement to obtain the Doctor of Science degree in Life Science with orientation in Environmental Biology.

Spatio-temporal dynamics of the San Quintin Kangaroo Rat (*Dipodomys gravipes*)

Abstract approved by:

PhD. Eric Mellink Bijtel
Thesis Co-Supervisor

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The San Quintin kangaroo rat (*Dipodomys gravipes* Huey, 1925) is a microendemic rodent to San Quintin-El Rosario, Baja California. The populations of the species severely decline in the late 1970s and early 1980s. After several unsuccessful survey efforts in the early 1990s, it was considered extinct and was declared so in 1994. After approximately 32 years with no records, it was rediscovered in a small embankment surrounded by abandoned cropland. Yet, this rediscovery underscores an urgent need to confirm this finding. Furthermore, the elapsed time between the species' last record and its rediscovery left important knowledge gaps in the biology and ecology of *D. gravipes*. Little is known about the species' current distribution, site occupation preferences, and the seasonal variation on the species abundance, reproductive cycles, and the influence of environmental variables on these parameters. Therefore, this doctoral research work has the general objective of elucidating the taxonomic identity, current distribution, habitat characteristics and the spatiotemporal population dynamics of *D. gravipes* colonies. In this work, external body measurements, cranial morphometric measurements and mitochondrial data of individuals of the purposely rediscovered were compared to those of confirmed individual of *D. gravipes* and of those of sympatric species of Baja California. This study comprises a morphometric and molecular confirmation of the presence of the species after 32 years with no records. Based on an extensive field survey, 19 localities of the species were documented, of which 6 are beyond its historically known distribution range, expanding the latter by ~60 km. Most of the sites occupied by the species occur in abandoned farmland in early ecological successional stages. The results support that in the highly transformed agricultural, the species could survive undetected and colonize/recolonize sites once the habitat became adequate after agricultural abandonment. This exhibits that the species is highly resilient and persists as a metapopulation. Moreover, this work covers the spatio-temporal variation in *D. gravipes* abundance and reproductive status. This study reveals that *D. gravipes* abundance is influenced by increasing vegetation cover when the latter decreases and vice versa, showing a seasonal abundance pattern roughly synchronous across localities. Reproductive status is not strongly influenced by vegetation cover change in any locality. Still, an increase in herbaceous vegetation might lead to a more significant proportion of juveniles, ultimately leading to a population increase. Lastly, the results provide a deeper understanding of the species' ecology after 32 years of knowledge gaps. At the same provides guidelines for future research and conservation planning for the species.

Keywords: *Dipodomys gravipes*, mDNA, agriculture expansion, farmland, Baja California abundance, reproductive status

Dedication

To my son Diego Andrade Chavira.

To my grandfather Marco Rosario Peralta Duarte (†).

To my grandfather Miguel Andrade Murillo (El Jefe) (†).

To my grandmother Socorro Durán (La Jefa) (†).

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Chapter 1. Introduction

1.1 *Dipodomys gravipes* and its conservation status

The San Quintin kangaroo rat (*Dipodomys gravipes* Huey, 1925; *D. gravipes* hereinafter) is a microendemic Mexican kangaroo rat, part of the family Heteromyidae, a family endemic to North America represented by four genera (*Chaetodipus*, *Dipodomys*, *Microdipodops* and *Perognathus*). *Dipodomys gravipes* is, together with the Dulzura kangaroo rat (*Dipodomys simulans*), the Sonoran kangaroo rat (Dipodomys desertii), and the Merriam's kangaroo rat (*Dipodomys merriami*), one of the four species of the genus *Dipodomys* distributed in the Baja California Peninsula.

Dipodomys gravipes, is as microendemic species restricted to narrow coastal plain between San Telmo and El Rosario (31 y 30° respectively), on the Pacific coast in the northern section of the peninsula of Baja California in an area of about 1,000 km^2 (Best & Lackey, 1985). To the north of Arroyo El Rosario, the species occupies sites with flat surfaces and little topographic relief with friable soils on coastal plains adjacent to rolling hills and mesas that are covered sparsely by coastal sage scrub (sensu Kirkpatrick & Hutchinson, 1977). At Arroyo El Rosario, the species occupies the alluvial fan of the arroyo on relatively flat surfaces adjacent to mesas and low hills (Best, 1983). The historical distribution of *D. gravipes* ranges from San Telmo in the north to Arroyo El Rosario in the south (Best & Lackey, 1985). Currently, distribution range has expanded ~10 km north from Colonet to Malvar, ~50 km in the south (Andrade et al., 2024).

Dipdomys gravipes is "a heavy-bodied kangaroo rat, small-eared with a thick tail of medium length; the tip of tail dark; five toes on extremely large-boned hindfoot; pelage medium-coarse dorsally (Huey, 1925). The lower surface of the body, entire forelegs and feet, upper surface of hindfeet, and hip stripes are withe; upper parts, including hip spot, are pinkish buff and have interspersed black hairs or hairs with black tips; the purest pinkish buff is on the cheeks and sides, and the darkest area is on the rump; a small white spot is over the eye; area around the ear is white, with the white extending downward rather than posteriorly or between the ears; white lateral tail stripes are narrow, extending almost to the tip, where they disappear in the long dark hairs of the tuft; hairs in the dorsal stripe of the tail are more uniformly dark than the ventral stripe; soles of the hindfeet, from base of toes to ankle, are nearly black" (Huey, 1925; Fig. 1).

Regarding mean external measurements, *D. gravipe's* total length ranges from 208 to 320 mm, tail length from 161-187 mm, and hindfeet from 51-45 mm (Tremor et al., 2019); ear length varies between 11 and 16 mm (Best, 1983). However, ear measurements were taken differently over time and thus are not comparable. The tail is 1.36 times (range of means 1.30 to 1.39) the length of the head and body (Best, 1983). Compared with its congeneric counterpart (*D. simulans*), *D. gravipes* is bigger in most dimensions: Total, tail, and hindfoot lengths (Best, 1978, 1983; Tremor et al., 2019), while ear length is smaller.

The cranium has a prominent, sharp postero-external angle in the maxillary root of the zygomatic arch. The width across the maxillary root of the zygomatic arches is more than 54.8% of the greatest length of the skull (Hall, 1981). Considering 14 diagnostic morphological measurements: Basal length, greatest length, maxillary arch spread, nasal length, intermaxillary width, alveolar length, lacrimal length, maxillary arch width, basioccipital length greatest depth, greatest width, zygomatic width, nasal width, and interorbital width, the cranium of *D. gravipes* is larger than *D. simulans* and *D. merriami* in all dimensions (Best, 1978, 1983).

Figure 1. The San Quintin kangaroo rat (*Dipodomys gravipes*). The image shows a female individual at El Campito, Baja California, Mexico.

Karyotypic data and mitochondrial DNA (Cytb and COx) as well morphometric measurements, suggest that

D. gravipes is within the hermanni group with other congeneric species, including the Stephens kangaroo rat (*Dipodomys stephensi*), the giant kangaroo rat (*D. ingens*), the chisel-toothet kangaroo kat (*D. microps*), the Heermans kangaroo rat (*D. heermanni*) and the panamint kangaroo rat (*D. panamintinus*) (Lidicker, 1960; Lackey, 1967; Best & Lackey, 1985; Stock 1974; Alexander & Riddle, 2005). Thus, from a phylogenetic perspective, *D. gravipes* is distinguishable from *D. simulans* and *D. merriami*, as well as from other kangaroo rats.

Little has been reported regarding ontogeny and reproduction of the species. Nonetheless, previous research suggests that juveniles are born throughout the year, with birth peaks in winter, particularly in November and December and spring and summer, particularly March, April, June, July and August (Best & Lackey, 1985). There is considerable work to be done regarding the reproduction and breeding behavior of *D. gravipes*. Moreover, investigating the environmental drivers of the reproductive status of *D. gravipes* is important. This information is crucial as it directly influences birth rates, population size and growth and ultimately leads to a better understanding of population trends and fluctuations. Moreover, studying the environmental drivers influencing reproduction and breeding behavior is possible to understand key conditions that hinder reproduction.

Regards *D. gravipes* burrow system characteristics, has been reported based six burrows systems from San Quintin an greatest depth of 39.8 cm, greatest length of 584 and width 318.5 cm; each system consist of an average of 4.7 openings of which main entrance have an average height and width of 8.4 and 7.6 cm, respectively; have 3.3 nests and 10.1 food caches with and average depth of 31.6 and 29.2 cm respectively (Best & Lackey, 1985). Also has been noted that there are no burrow systems nor entrances under vegetation (Best & Lackey, 1985).

Besides the detailed species description, Lawerence Huey's work on *D. gravipes* from 1925 to 1945 revealed 8 localities across the species historical range (Fig. 2) and reported total counts per survey. Huey noted that a population of the species on a specific area called "Mesa Agua Chiquita" consisted of 1,000 individuals per 10 acres (~250 per hectare), labeling it as the "mother-lode" because of it (Huey, 1925) but provided no more data on its abundance. Further research by the decades of 1970 and 1980 augmented the knowledge of the species distribution. Two new localities were documented, and the southern distributional limit expanded (Fig. 2; Best & Lackey, 1985). With the latter, the species distribution ranges were established.

During the decades of 1970 and 1980, one of the most concerning pieces of information was the decline of the species' populations. Total counts of individuals on several sites declined over these decades (Best & Lackey, 1985). A locality near the "mother lode" yielded only two individuals out of 1,000-night traps in 1986 (Alvarez-Castañeda & Lacher, 2018). Habitat change from native vegetation to agricultural land during this period in the *D. gravipes* localities was claimed to be the main cause of *D. gravipes* population decline reported; changing soil cover (Best & Lackey, 1985).

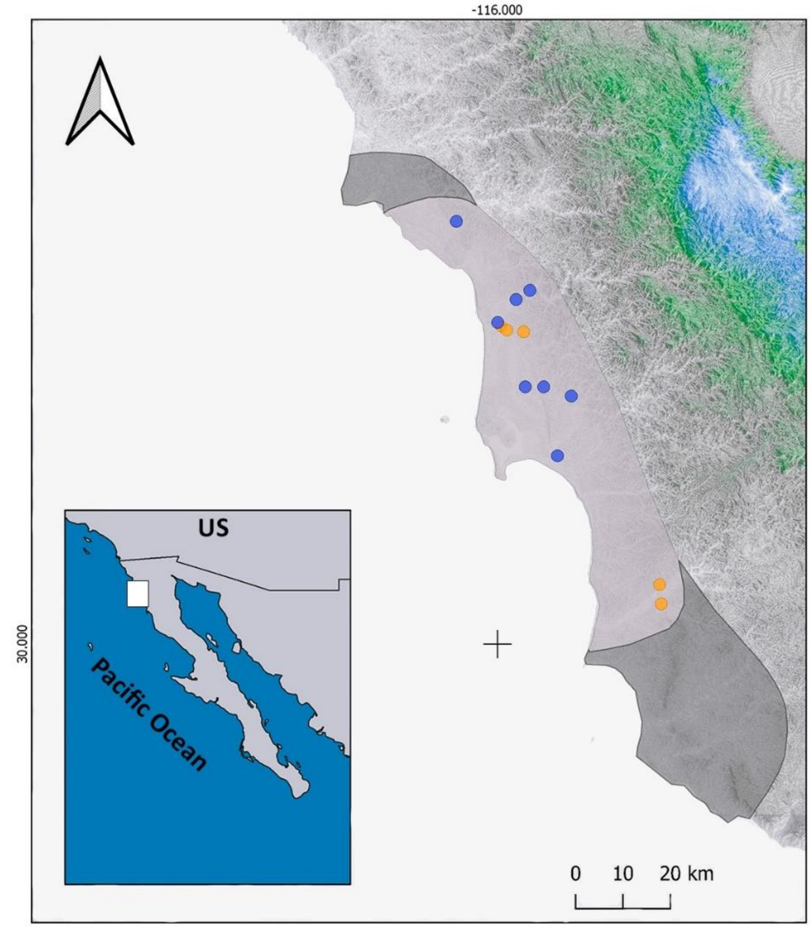

Figure 2. Historical range distribution in light gray, current extended range in dark grey and localities of *D. gravipes*. Blue circles correspond to captures prior agricultural development (Huey, 1945). Orange circles correspond to captures during agriculture intensification (Best & Lackey, 1985). Hillshade is used to present topographic and geography differences between northern and southern populations. Data was downloaded from vernet database (vernet.org) and hillshade was constructed in QGIS based on ASTER GDEM data.

Early work on the species's habitat described it as flat areas within the coastal plains and adjacent rolling hills and mesas covered with low open Californian coastal sage scrub (*sensu* Kirkpatrick and Hutchinson 1977). South of the El Rosario mountain range, it was found at sites within the Arroyo El Rosario floodplain with low open vegetation cover and bordered by mesas and hills (Best, 1983). The qualitative assessment of *D. gravipes* and *D. simulans* habitat highlights that the latter species occupied sites with higher elevation and denser vegetation. However, it was sometimes found in lower areas (Best & Lackey, 1985). Considering the abiotic component of the habitat, no quantitative information about temperature, humidity, light exposure, or soil texture was reported in early habitat descriptions.

Interspecific interaction includes the parasitism of a protozoan parasite, *Eimeria scholtysecki* (Best & Lackey, 1985). No other interspecific interaction has been reported so far. However, based on similarities with other kangaroo rats, its main predators could be coyotes (*Canis latrans*), the Barn Owl (*Tyto alba*), and rattlesnakes (*Crotalus spp*).

After the species population decline reported in the 1980, researchers, in early 1990s search for the species with no success (Mellink, 1992, 1996). After a period of about 25 years without documenting the species, it was declared potentially extinct in the wild by the Mexican environmental regulation (SEMARNAT, 2010 and as critically endangered by the International Union of Conservation of Nature (IUCN); Álvarez-Castañeda & Lacher, 2018). Later, the San Quintín kangaroo rat was rediscovered in 2017 (Tremor et al., 2019). At that time, four individuals were captured on a ~ 3,000 m2 embankment surrounded by cropland, 5.6 km east of San Quintín, near Huey´s “mother-lode” site. However, *D. gravipes’* current populations and distributions remain to be investigated.

1.2 Ecology of the genus *Dipodomys*

Heteromyd rodents are distributed across different habitats that span a wide range of water and energy availability (French, 1991). These environments range in aridity from seasonally dry tropical forests inhabited by species of *Liomys* to the driest and hottest deserts of North America where *Dipodomys, Chaetodipus* and *Perognathus* genus are abundant (French, 1991). The kangaroo rats (*Dipodomys* spp.) are restricted to North American arid and semi-arid regions, including warm and cold deserts, covered by grasslands, chaparral, and different types of xerophytic shrubblands (Alexander & Riddle, 2015).

The North American arid and semi-arid environments are characterized by high summer temperatures that ranges from and 30-45 °C, and unpredictable and scarce precipitation of <25 and < 50 cm pp., respectively. As consequence, these environments have low primary productivity and, thus, impose a set of environmental pressures in order to cope with low and fluctuating food and water availability (French, 1991). Family Heteromyidae is considered one of the most adapted organism to arid and semi-arid environments. This set of adaptations includes physiological strategies such as low rates of evapotranspiration to reduce both respiratory and cutaneous water loss (French, 1991). Another physiological trait for water conservation is urine concentration, which employs highly efficient kidneys and allows individuals to excrete with minimum water loss. Presumably, the genus *Dipodomys* and other Heteromyd rodents produce more metabolic water from their food intake. However, research suggests that the amount of metabolic water is slightly lower than other mammals of similar size (Brower, 1970; Hinds & McMillen, 1985). Then, water balance in the kangaroo rats relies on water produced during oxidative metabolism from its diet. Still, its conservation depends on the low rates of water loss.

Temperature regulation in both cold and warm temperatures in kangaroo rats influences the activity patterns both under and above ground. Research suggests that the energetic cost of this thermal regulation in cold environments is lower than in other small mammals. At near-freezing temperatures, the kangaroo rat's hypothalamic regulator of body temperature is reset downward during slow-wave sleeping compared to wakefulness (Glotzbach & Heller, 1976). The latter means that the primary function of this state of slow-wave sleeping is energy conservation (Berger, 1975). Torpor is a well-developed physiological trait in <40 g Heteromyd rodents but weakly developed in kangaroo rats (MacMillen, 1983). Then, it appears that Kangaroo rats use slow-wave sleeping during near-freezing conditions without achieving a state of torpor as a means of energy conservation (MacMillan, 1982). On the other extreme of the environmental temperature spectrum, heat dissipation is rarely a problem due to low heat production when resting. Kangaroo rats, like the rest of the Heteromyd rodents, remain relatively inactive underground during the day (French, 1991). Kangaroo rats seldom remain motionless per half-hour periods during the warmest parts of the year and move vertically in their burrows to reach the lowest point of terminal neutrality according to seasonal and daily variations (Kenagy, 1973).

Once an individual leaves its burrow, time is invested in foraging, mating search, exploration, territory maintenance, or return to the burrow (Riechman & Price, 1991). The latter sequence of decisions is influenced by environmental temperatures, reproductive conditions, presence of competitors and predators, and seasonal and year-to-year patterns in food availability (Reichman & Price, 1991).

Species of genus *Dipodomys* are primarily granivorous, although their diets can reflect the seasonal availability of insects and green vegetation (Alcoze & Zimmerman, 1973; Flake, 1973; Best & Hoditschek, 1982; Reichman & Van De Graaff, 1975). Foraging behavior appears to be similar across the species of this genus i.e., bipedal and ricochetal locomotion, due to elongated hindfeet, enable alternation periods of locomotion with stops during which the individual collects seeds, either directly from the plants or on the ground with the fore-feet while balancing on their hind-feet (Reichman & Price, 1991). Despite the kangaroo rats spend most of their time collecting seeds from the ground, there are reports of individuals climbing to forage green parts of plants (Kenagy, 1973).

Heteromyd rodents and, of course, the kangaroo rats have external, fur lined external cheek pouches that evolved from oral cavities and function as temporal food storage to carry seeds (Kawashima et al., 2020) (Fig. 3), and are considered a synapomorphy of the superfamily Geomyoidea, including the Geomyidae and Heteromydae (Ryan, 1986). They enable the individuals to separate seed harvest and consumption in time and transfer harvest back to their burrows (Reichman & Price, 1991). If a rich seed patch is found, the individual will repeatedly return until depletion (Janzen, 1982; Lockard & Lockard, 1971). Cheek pouches also allow the individual to harvest dormant seeds that can be stored for extended periods by caching them in excess of immediate requirements in large hoards in their burrows (Smith & Reichman, 1984).

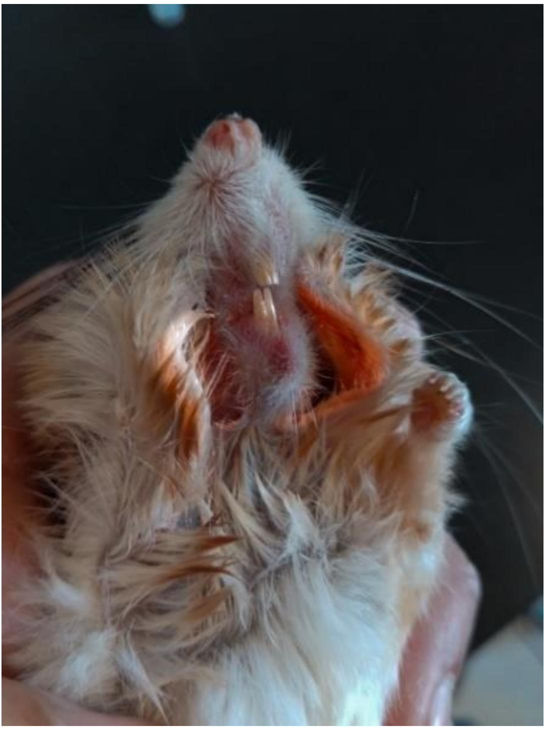

Figure 3. External cheek pouches of a male individual of *Dipodomys gravipes*.

The kangaroo rats have different morphological strategies to avoid predation. For example, evasive bipedal leaps enable kangaroo rats to dodge rattlesnake strikes (Whitford et al., 2019). Auditory bulla is more inflated than other Heteromyids (Price et al., 1991), which is known to affect the sensitivity of low-frequency sounds in heteronyms (Webster & Webster, 1975). The latter enables the Kangaroo Rats to detect the strike of its predators, most commonly rattlesnakes and owls, thus enhancing predation avoidance abilities. These adaptations may allow the kangaroo rats to gather seeds in the open, contrary to other quadruped rodents that appear better adapted to collect seeds from the plants or disperse on the ground beneath the plants (Shroeder, 1979).

Mating behavior has been rarely documented in the wild, and most of this trait came from studies in captivity (Kelt, 1988; Garrison & Best, 1990). These studies reveal that mating is preceded by the male following the female and vice versa, nosing its genitalia (Kelt, 1988; Garrison & Best, 1990). Presumably, females are receptive during one day at each cycle (Hayssen, 1991), and copulation (in captive animals) requires only a few seconds (Kelt, 1988). Evaluating the kangaroo rat's time spent above the ground is difficult. Therefore, the time the kangaroo rats have been devoid of matting, foraging, exploration, and territory maintenance during time over ground is not well documented. Radio-tracking technologies enable researchers to study this by analyzing stop durations (Shroder, 1979).

Kangaroo rats forage seeds in the open ground and they prefer open habitats with low vegetation cover and few to no shrubs. Habitat description for some species of kangaroo rats' highlights that they can be found in sites with low vegetation cover, mainly by grasses and herbs and few scattered shrubs (Jones & Genoways, 1975; Bleich, 1977; Price & Heinz, 1984; Carter et al., 1985; Kelt, 1988; Intress & Best, 1990; Best, 1992). However, some species have been documented in habitats with denser vegetation cover (Best & Lackey, 1985; Hayssen, 1991). Habitat preferences appear to vary across species, ranging from a clear preference for open habitats to no clear preference for any habitat feature (Shroder, 1987).

Kangaroo rats play a key role in shaping vegetation cover and structure affecting other animal species (Brown & Heske, 1990). The absence of kangaroo rats produces changes in the relative abundance of annual plants and, later, causes major changes in vegetation cover, particularly that of certain grasses, which increase and can also negatively affect mesquite seedlings (Valone & Thornbill, 2001). The latter indirectly affects other rodent species, through aggressive interactions and resource depletion (Heske et al., 1994).

Some kangaroo rat species overlap in their distributions and habitat at a broad scale (e.g., *D. gravipes*, *D. simulans*, and *D. merriami*). However, at finer scales, species of similar body mass rarely are found in the same sites and, thus, at this scale their distributions do not overlap (Price, 1978; Bowers & Brown, 1982; Price et al., 1991; Schmidly et al., 1993). Literature suggests that the species of similar body size rarely overlap. This lack of overlap might be the result of ongoing interspecific competition that causes species to maintain distinct ranges or might reflect different niche requirements that evolved as a result of past competition or independent of it (Connell, 1980). When two species of similar body mass meet in the wild, these engage in fights, highlighting that the genus *Dipodomys* is considered a behaviorally dominant competitor towards small seed-eater rodents of comparable mass (Riechman & Price 1993; Christensen et al. 2019). However, in some cases, species of similar body mass co-occur in the same sites. Still, preference for distinct microhabitat features, understood as areas so small that many are traversed during the ordinary course of foraging (Pulliam, 1976), allows this co-existence. An example of the latter is the case of the ord's kangaroo rat (*Dipodomys ordi*) and the Merriam's kangaroo rat (*Dipodomys merriami*), which are sympatric over a portion of distribution ranges and have striking physical similarities but don't compete over the same microhabitat features (Shroder, 1987).

The knowledge of the adaptations described above are of crucial importance to understand how the species of the genus *Dipodomys* interact with their biotic and abiotic environment and how this dynamics change over space and time. When it comes to design management and conservation strategies, this basic knowledge acquires other level of significance. Moreover, if we consider that the Capitaloscene epoch (*sensu* Crutzen, 2002), imposes treats to wildlife in general, such as agriculture expansion, is crucial to fulfill knowledge gaps of the species that might face treats to its conservation.

1.3 Agriculture and its relationship with rodents

Agricultural expansion and intensification are considered one of the most critical threats to wildlife worldwide and, beyond dispute, a crucial driver of biodiversity loss and habitat degradation (Norris, 2008). Historically, agriculture has expanded exponentially. By 2023, the cropland, understood as land used to grow crops excluding pasture used for livestock, occupied around 1.58 and 1.63 billion ha globally (HYDE, 2023; FAO, 2024). Moreover, this cropland area is projected to expand by 7% by 2030 (Alexandratos & Bruinsma, 2012) and up to 50 % by 2050 (FAO, 2018). Actually, the agricultural landscape is, to date, one of the most extended biomass in the world (Ellis et al., 2010).

Agricultural practices range from highly technified agriculture to low-input agriculture. The first, the dominant type of production worldwide (HYDE, 2023), is highly mechanized and consists primarily of monocultures, which heavily rely on agrochemicals to manage pest damage and mechanization (Richardson, 1998; Abhilash & Nandita, 2009). Conversely, low-input agricultural production is typified by little external input of energy and nutrients and little mechanization (Riojas-Lopez et al., 2018).

The effects of agricultural practices on the biological diversity also vary according to the type of agriculture. The highly mechanized agriculture or high-input agriculture is widely recognized to have adverse effects on biodiversity. In Europe and North America, the numbers and ranges of numerous bird species have decline as result of the expansion of this type of agriculture practices (Tucker & Heat, 1994). For example, the numbers of grassland bird species are higher at natural patches comparing to monoculture cropland patches (Wolff et al., 2002). However, in some cases birds are benefited by intensification of agriculture since higher nitrogen inputs increases soil invertebrate's populations (Atkinson et al., 2005). Similarly, arable cropland provides important source of seeds and recruits insects which ultimately, benefits foraging opportunities for birds (Marshal et al., 2003). At a larger scale, heterogeneous agricultural landscapes which also includes high-input agriculture, can benefit bird's abundances (Wolf et al., 2002; Johnson et al., 2011).

Low-input agriculture has been the center of attention of recent research as there is growing evidence that these practices support high species richness of different taxa in comparison with high-input agriculture and serve as a corridor between patches (Riojas-Lopez et al., 2018). Regarding to birds it has been suggested that low-input agriculture sustained and increase populations of bird species when compared to regional trends (Henderson et al., 2009). Similar patterns have been described for insect community on which the diversity insects decreases when management of crops increases (Sanderson et al., 2018).

The effects of the various agricultural practices on rodent populations need to be studied more. Search on databases such as Google Scholar and Web of Science resulted on most rodent pest control and management papers. There is growing evidence that high-input agriculture negatively influences rodent diversity (Horvát, et al., 2001; Balestrieri et al., 2019). In the other hand, it has been suggested that small-scale agrosystems can sustain more diversity of rodents compared to natural ecosystems (Mellink, 1985). The value of these low-input agrosystems for rodents has been traditionally neglected from research. Yet, in the last decade, research on this topic has increased (Riojas-López et al., 2018). This increase in research regarding low-input agrosystems is biased toward temperate and tropical environments, and relatively few studies address arid and semi-arid systems (Riojas-López et al., 2018).

Agriculture and rodents represent a complex relationship between human activity and biodiversity conservation. Rodents could become pests in agriculture and damage crops and stocks, leading to substantial economic losses worldwide (Brown et al., 2007; Stenseth et al., 2003; Diagne et al., 2023). Therefore, they are often classified as among the most critical global pests (Singleton et al., 1999).

However, few species are considered to behave as pests (Lidicker, 1989; Wood & Singleton, 2015). Considering the 5 suborders of rodents, the species considered pests are among 3 suborders: Myomorpha, Hystricomorpha, and Sciuromorpha, and globally, relatively few species of these have become pests (Wood & Singleton, 2015). Rodent infesting agrosystems is also context-dependent, but the small portions of species behaving as pests appear to be similar in a global context (For details, see Wood & Singleton, 2015).

In addition, with the farmland expansion of about 217 Mha between 2003 and 2009, 79 Mha of gross agricultural land abandonment took place (FAO et al., 2022), and it is predicted to continue in Europe, Russia, Central and East Asia, and the Americas (Crawford et al., 2022). Similarly to low-input agrosystems, the value for rodent conservation of these abandoned farmlad areas has been neglected in research. Early rodent descriptions, particularly those of the *Dipodomys* genus, highlighted that abandoned cropland often serves as a habitat for species of this genus. For example, *D. ingens* can establish colonies in fallow, dry-land grain fields when there are extant colonies on uncultivated ground nearby (Best et al., 1989), and *D. venustus'* burrows can be located in open, abandoned agricultural land (Best, 1992).

Rodents are sensitive to changes in the structure and composition of the vegetation (Brown & Heske, 1990; Riojas-López et al., 2011) and, at the same time are considered indicators of ecological changes and ecosystem integrity (Riojas-Lopez et al., 2018). Research regarding effects of agriculture practices on rodent species should be addressed into more detail.

1.4 Agriculture in the Colonet-El Rosario region in Baja California

Baja California is one of many examples of the complexity of agriculture and its conflict with biological conservation. This state has three central agricultural regions: Mexicali Valley; the intermountain region, which includes the valleys of Guadalupe, Trinidad, Ojos Negros, Santo Tomás, and Llano Colorado; the west coast plains including San Carlos-Maneadero, and the region from San Vicente to El Rosario, which also harbors Camalú, Colonet, and San Quintin (Fig. 4).

Agriculture in the Colonet-El Rosario region started with an unsuccessful attempt at cultivation, mainly wheatgrass, and colonization during the second half of the XIX and the beginning of the XX centuries (Velasco et al., 2014). The Mexican government promoted this incipient development, which granted land in Baja California to producers of western Mexico whose lands were expropriated during the Agrarian

Reform (Reding, 2008). Lack of water for cultivation and unsuitable soil were presumably the main factors for the failure of this attempt (Reding, 2008; Rangel & Riemann, 2014).

In 1960, the region's agriculture faced steady growth as a consequence of governmental stipends to grow fruits and vegetables, meaning an important change in agricultural products (Reding, 2008; Rangel & Riemann, 2014). By 1970, the production was intensive, pesticides were heavily used, and producers were medium-scale farmers with low-technified farms (Pombo, 2014). At that time, agriculture grew around a governmental subsidy system, mainly through the "Ley de Energía para el Campo" (DOF, 2002, 2012) and by water concessions granted by the National Commission of Water (CONAGUA by its acronym in Spanish). However, during the same decade, the government's economic support ceased and, in conjunction with water scarcity, decreased agricultural production.

Technological and infrastructure advances enable producers to cope with these challenges, and agricultural production has changed from rain-fed to irrigated agriculture. In this context, agriculture gradually became an essential economic activity with a total increase of 40% (~10 000 ha) in rain-fed and 62% (~25 000 ha) in irrigated farmland between 1980 and 2010 (Fig. 5; Riemann, 2015). Today's agriculture is typified by high productivity which is prompted by technological advancements in water consumption. This agriculture type led to accelerated human demographic growth: from 8559 persons in 1970 to 92 177 in 2010, a density of 38 inhabitants/ha (Velasco et al., 2014; Pombo, 2014; Riemann, 2015).

Agricultural production in this region is still limited by available water for irrigation. Even in the early years of agriculture, water in this region was scarce, and the Mexican government classified the aquifers as overexploited (Pombo, 2014). Limitation in water availability has been counteracted to some degree with water sequestration from local streams, drip irrigation, and greenhouse farming. This represented a change in agricultural orientation and resulted in farmland abandonment (Vanderplank et al., 2014).

The demand for agricultural products for international commerce from the Colonet-El Rosario region has increased over time, putting ever higher pressure on limited water resources but providing high economic returns that stimulated the development of private desalinization plants to provide water for agricultural production. Desalinization of water from the nearby Pacific Ocean and salinized aquifers has been used at a low scale since the 1990s (Pombo, 2015). Since then, there has been a shift towards big agricultural companies with significant financial resources investing in large desalinization plants, and 52 desalinization plants provide water for agriculture in addition to the traditional sources (Alducy et al., 2017). The extra water now available allows the re-cultivation of abandoned farmland. Ultimately, this can lead to an intensification on agricultural production that might need to be socially and environmentally sustainable (Smith et al., 2020).

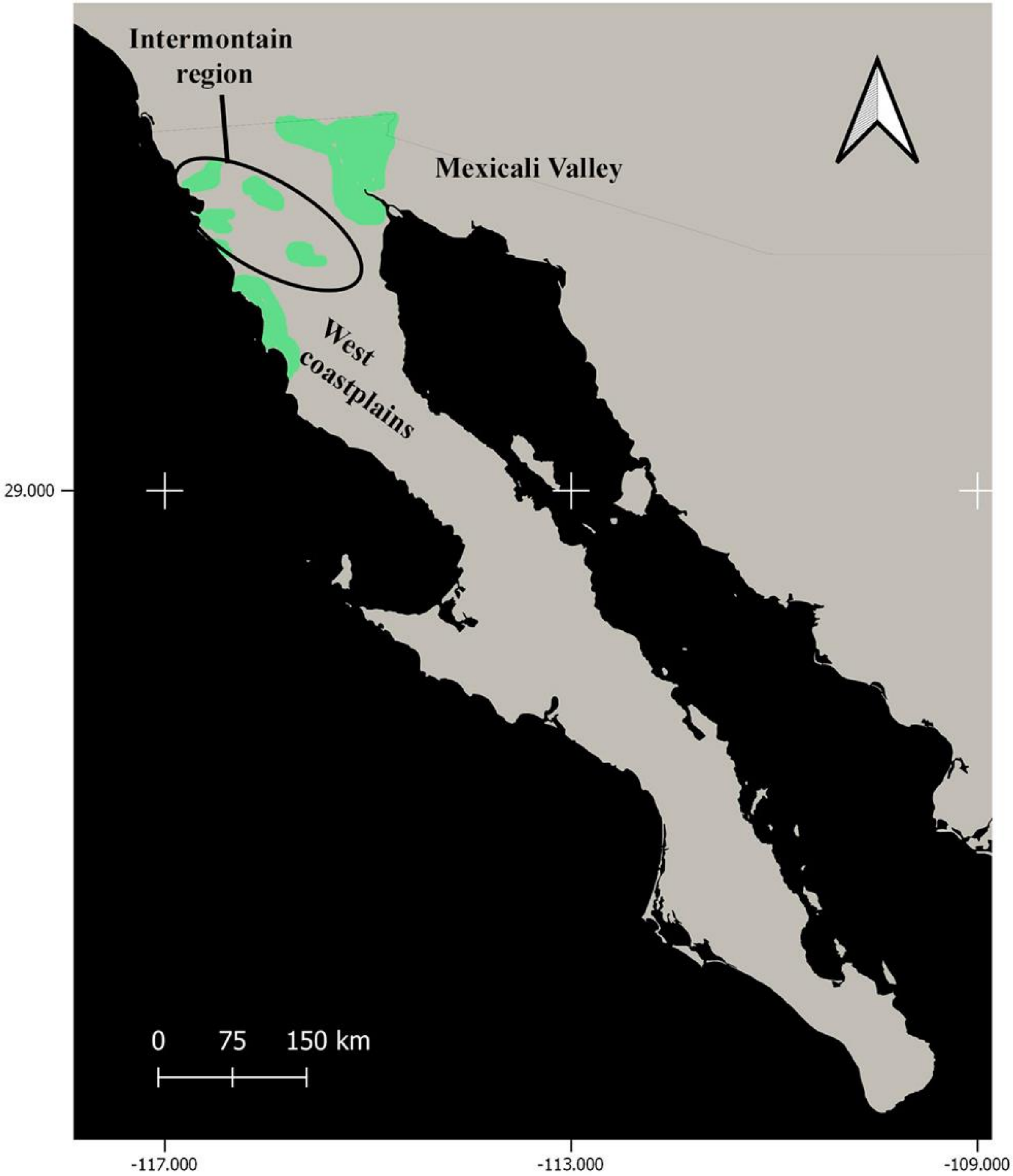

Figure 4. Localization of the three most important agricultural regions in Baja Califorina, Mexico.

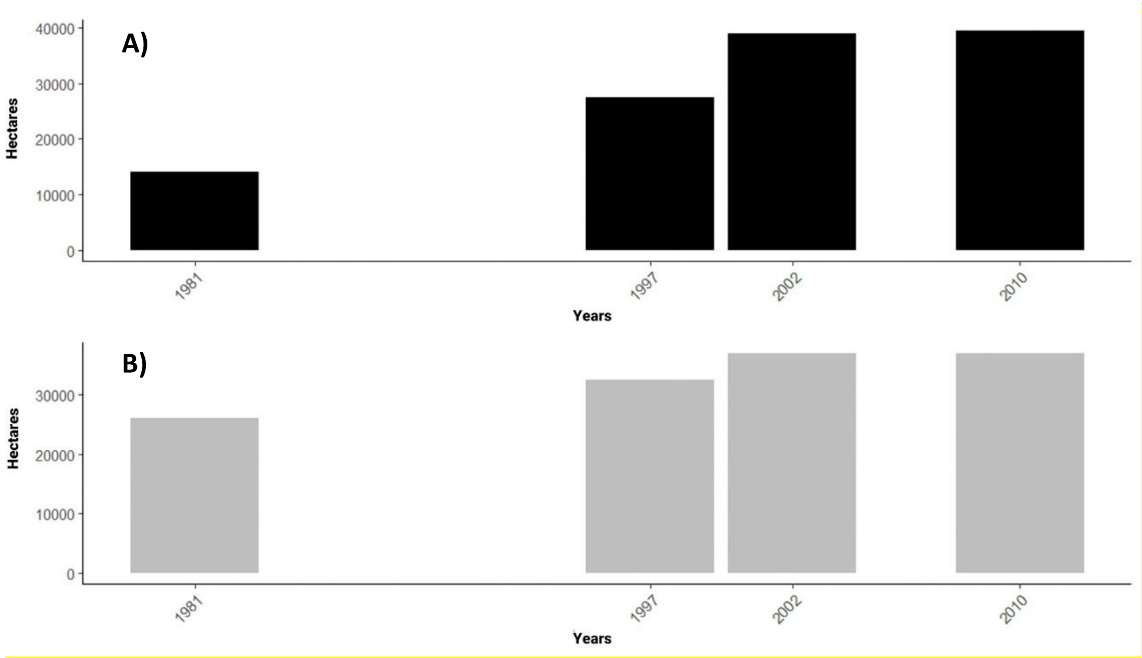

Figure 5. Agriculture expansion in hectares from 1980 to 2010 in the San Quintin-El Rosario region. A) Irrigated agriculture; B) rain-fed agriculture. Source: www.inegi.org.

1.5 Reseach problem statment

Agricultural crops have replaced diverse wild habitats such as coastal sage scrub, chaparral, and riparian vegetation. It is estimated that 30% of the natural vegetation of the San Quintin region has been transformed to agriculture, induced grasslands, and urban settlements, mainly in the 1990s (Vergés et al., 2014). Interestingly, the abandonment of irrigated land due to salt accumulation in the soil (Cardona et al., 2014) in the 1980s and 1990s resulted in anthropogenic to natural vegetation cover change (Vergés et al., 2014). However, in general terms, the loss of natural cover to agricultural expansion is labeled as a primary driver of the decline of biodiversity in the region (Cardona et al., 2014). This has led to the extirpation of 22 native taxa of plants, including 80% of vernal pool taxa (Vanderplank et al., 2014). Regarding small mammals, the threats imposed by agriculture intensification are less known. However, the decline of some rodent's species populations are most likely due to agriculture intensification. For example, *D.gravipes* population's decline in the 1970s and 1980s, is attributed to agriculture intensification (Best & Lackey, 1985).

The rediscovery of *D. gravipes* on a small embankment surrounded by agriculture landscape after 32 years suggest that the species is resilient. Yet, this rediscovery underscores an urgent need to confirm this finding. Moreover, considering the elapsed time between the species last record and its rediscovery, there are a considerable knowledge gaps on the biology and ecology of *D. gravipes*. It is poorly known about the specie's current distribution and site occupation preferences, and population dynamics, e.g. seasonal variation on the species abundance, reproductive cycles, and the influence of environmental variables on these parameters.

1.6 Justification

Without precise identification drawing conclusions regarding the ecology and conservation of any species becomes unattainable, posing a fundamental pre-requisite for research and conservation efforts (Kürzel et al., 2022; Galan et al. 2012). Considering *D. gravipes* is classified as potentially extinct in the wild by Mexican regulation and critically endangered by the IUCN, is crucial to provide support to the identity of the purportedly rediscovered species.

Dipodomys gravipes was rediscovered in 2017 following about 32 years without any records. Considering the latter, becomes imperative to document current localities and to delimit the current species distribution as well to describe the habitat characteristics of the occupied sites. This knowledge is a foundational step and pre-requisite to further investigate the spatial patterns of occurrence which at the same time can lead to research of structural and functional connectivity and lastly, inform spatially-explicit conservation plans. Therefore, the examination of current localities, its distribution and physical characteristics is of uttermost importance.

When it comes of an endangered species like *D. gravipes*, basic knowledge regarding abundance and other demographic parameters such as breeding cycles are critical. Identifying the variation of the latter and the environmental factors influencing these, are fundamental to begin to understand the species population dynamics. At the same time, this knowledge is a foundational step for examining population trends, effective population size and extinction risk. Ultimately, this lead to the design of conservation strategies of *D. gravipes*.

1.7 Hypothesis

This research aims to document the species-habitat dynamics, seasonal abundance patterns, providing a base line for conservation strategies for the endangered rodent. Is expected that, in the highly transformed agricultural landscape, into which the region was converted in the 20th century, the species was able to survive undetected and colonize/recolonize sites once habitat became adequate after agricultural abandonment. A greater abundance is expected to be found in flatter sites, with vegetation cover of no more than 10% and with low and scarce shrubs, and after the emergence of herbaceous plants, a greater proportion of juveniles.

1.8 Objectives

1.8.1 General objective

To elucidate the taxonomic identity, current distribution, habitat characteristics and the spatio-temporal population dynamics of *Dipodomys gravipes*.

1.8.2 Specific objectives

1) Confirm the identity of specimens recently identified as *D. gravipes*.

2) Delimit the current distribution range of the species.

3) Describe the habitat characteristics where the species has been captured.

4) Describe the temporal and spatial variation of the abundance and reproductive status and the influence of environmental variables on these parameters.

Chapter 2. Was the San Quintin kangaroo rat really rediscovered?

2.1 Abstract

The San Quintín kangaroo rat (*Dipodomys gravipes* Huey, 1925) is one of the three Kangaroo Rats in northwestern Baja California and the largest of them in most body dimensions. After a dramatic population decline in the 1980s, it was declared as potentially extinct in the wild by Mexican law. In 2017, the species was claimed to be rediscovered, but critical data supporting the species recognition were not provided. The question remained: Was the San Quintín kangaroo rat really rediscovered? We analyzed individuals identified by us as *D. gravipes* to validate our identification. We compared cranial morphometric and mitochondrial data of on-purpose collected specimens with those of historic specimens and with those of sympatric kangaroo rats in Baja California, particularly the dulzura kangaroo rat (*Dipodomys simulans* (Merriam, 1904). Cranial morphometry and body dimensions of current specimens are indistinguishable from those of historic *D. gravipes*, while being different from *D. simulans* in most dimensions. External measurements such as cranial traits adequately distinguish both species. The mitochondrial analysis revealed strong support for the species grouping of sequences of our specimens and DNA sequences of *D. gravipes* from the GenBank repository. This study comprises a morphometric and molecular confirmation of the presence of the species after >25 years of failures to find it.

2.2 Graphical abstract

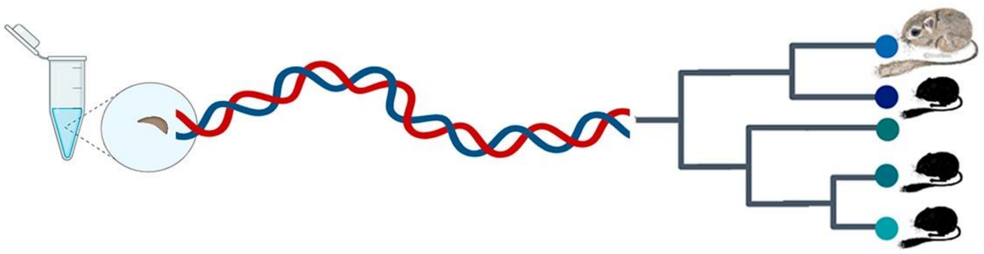

Figure 6. Graphical abstract of chapter 2

2.3 Introduction

The family Heteromyidae is a group of arid-adapted rodents consisting of six genera: *Chaetodipus, Dipodomys, Heteromys, Liomys, Microdipodops, and Perognathus* (Alexander and Riddle, 2005). This family occurs as far north as British Columbia and as far south as Colombia and Ecuador (Patton, 1993; Schmidly et al., 1993; Williams et al., 1993; Alexander & Riddle, 2005).The *Dipodomys* genus is restricted to North America's arid and semi-arid regions, including warm and cold deserts, grass- lands, and chaparral (Alexander & Riddle, 2005). The kangaroo rats (*Dipodomys* spp.) play essential roles in the composition and structure of the ecosystems they inhabit; thus, their preservation must be considered a priority among conservationists (Goldingay et al. 1997). The San Quintín kangaroo rat (*Dipodomys gravipes* Huey, 1925) is one of the 22 species of kangaroo rats found from Canada to southern Mexico and one of four kangaroo rats in the Peninsula of Baja California, Mexico. It was originally described by Lawrence M. Huey based on morphological traits in 1925 (Huey, 1925) and studied in some detail in the 1970s and early 1980s (Best, 1976, 1978, 1981, 1983; Best & Lackey, 1985).

The distribution range of *D. gravipes* was given as within a small coastal region from San Telmo to El Rosario in Baja California, Mexico, on relatively flat terrain having open spaces, with low and scarce vegetation (Best & Lackey, 1985). The part of the Pacific Ocean adjacent to this region, where our study was conducted, is under the influence of the California Current, where dominant northwesterly winds generate seawater up- welling year-round (Bakun & Nelson, 1977). These conditions cause a Mediterranean climate. The area is at the southern limit of the California Mediterranean region, according to its vertebrates (Mellink, 2002), but eco-climatically it is transitional between the true Mediterranean and the Vizcaino desert (Delgadillo, 1992; González-Abraham et al., 2010). It is also part of the California Floristic Providence, one of the 35 biodiversity hot spots in the world Myers et al., 2000 (). Additionally, it comprises of one of the most endangered ecosystems worldwide: the Mediterranean coastal sage scrub (Bullock, 1999; Cox & Allen, 2008).

Dipodomys gravipes' distribution range overlaps with those of two other kangaroo rats, *Dipodomys simulans* (Merriam, 1904) and *Dipodomys merriami* Mearns, 1890, which have much larger distribution ranges. *Dipodomys gravipes* has been included in the heermanni group, to which sympatric *D. simulans also* belongs (Stock, 1974; Best, 1978), a grouping later supported by mitochondrial analysis (Alexander & Riddle, 2005). *Dipodomys gravipes* is readily separable from *D. simulans* and *D. merriami*, based on cranium and baculum morphology (Best, 1978; Best & Lackey, 1985; Best et al., 1986), while body measurements have been used to separate them in the field.

Dipodomys gravipes has been severely impacted by agricultural development since the mid-20th century. In the 1980s, two of the significant populations of *D. gravipes* declined dramatically due to agricultural conversion (Best, 1983; Best & Lackey, 1985). Subsequent surveys in the early 1990s failed to find the species (Mellink 1992, 1996). Since then, and given the lack of further captures, biologists and conservationists have feared that the species could have become extinct (Ceballos & Navarro, 1991; Mellink 1992, 1996; Mellink & Luévano, 2005), and in 2010 the Mexican government declared the species as potentially extinct in the wild (SEMARNAT, 2010). The International Union of Conservation of Nature considers it critically endangered, and its small mammal's specialist group considered it one of the 20 small mammals for which the determination of its status and conservation needs were urgently needed.

After a >25-year hiatus in survey efforts, the species was claimed to have been rediscovered in 2017 in a small embankment surrounded by agricultural land Tremor et al., 2019 (). External measurement and their comparison with those of the other kangaroo rat species in the region supported its identification. However, neither cranial strict morphometric nor molecular information has been provided to support the identity of the purportedly rediscovered species. Given the relevance of the species' rediscovery for biodiversity conservation, verification beyond any doubt is crucial. The objective of the analysis we report here is to report the formal verification of the identity of specimens recently identified as *D. gravipes*.

2.4 Material and methods

Our study area was centered around the historic species' distribution range, 180 km south of the Mexico–United States border, with localities explored south and north of it. The area covers less than 1000 km2, from Mesa de Colonet to Arroyo El Rosario, on Baja California´s coastal plain west of the peninsular northern mountain ridge (Maderey, 1975).

After the presumed rediscovery of the species, we conducted 12 surveys from 2017 to 2021, covering the months of February, March, April, May, July, August, September, October, November, and December, to locate as many colonies as possible within our study area, including all historic localities listed in the San Diego Natural and History Museum database and records from the Vertnet (www.vernet.org) and GBIF (www.gbif.org) databases, as well as seemingly suitable localities beyond our study area to the north and south.

Once potential habitat was identified, we looked for burrow systems with height and width of burrow opening around or above 8.0 and 7.0 cm, respectively, as these dimensions are considered large enough to be of *D. gravipes* (Best & Lackey, 1985). In each potential location, we opportunistically set three large Sherman traps (30.5 cm long) per bur- row entrance baited with rolled oats and left from sundown to dawn. The total number of traps depended on burrow density at the locality, but the average trapping effort was 200 trap nights per field trip for 2400 trap nights overall. Typically, we surveyed an average of two localities per field trip. We recorded every site's geographic coordinates and created a Geo-Database with all surveyed sites. We took external measurements of all kangaroo rats captured, including mass, total length, vertebral tail length, hindfoot length, and ear height.

We collected eight individuals of *D. gravipes* and obtained skins, skulls, and tissue samples from internal organs, as well as small clippings of earlobes of four individuals that were not collected. To obtain the latter, we numbed the earlobe with xylocaine anesthetic spray (5%) and cut a small piece with sterilized surgery scissors and forceps. The collected individuals were euthanized by thoracic compression as it is accepted as a human method to kill small mammals and does not distort important body measurements nor destroys skeletal elements (Sikes & Animal Care and Use Committee of the American Society of Mammalogists, 2016). We deposited the tissue samples in 2 mL vials with 96% ethanol for trans- port to the laboratory.

Skulls were cleaned using hide beetle (*Dermestes maculatus* DeGeer, 1774) larvae (Timm et al., 2020). Soft tissues from internal organs and earlobes were stored in vials at 20 ◦C. We performed genetic analysis on seven samples from both earlobes and internal organs from five localities spread throughout the study area: Monte Ceniza, Mesa El Rosario, San Carlos, Las Pintas, and Punta Azufre (Fig. 7).

We conducted this study in conformance with the Mexican environmental law (handling and collecting authorizations: SGPA/DGVX/3150/19; SGPA/DGVX/3150/22) and in agreement with the guidelines of the American Society of Mammologistsfor the use of wild mammals in research (Sikes & Animal Care and Use Committee of the American Society of Mammal ogists, 2016). Fieldwork within the private natural reserves owned by Jardin Botánico San Quintín and Terra Peninsular was carried out with the owners' permission.

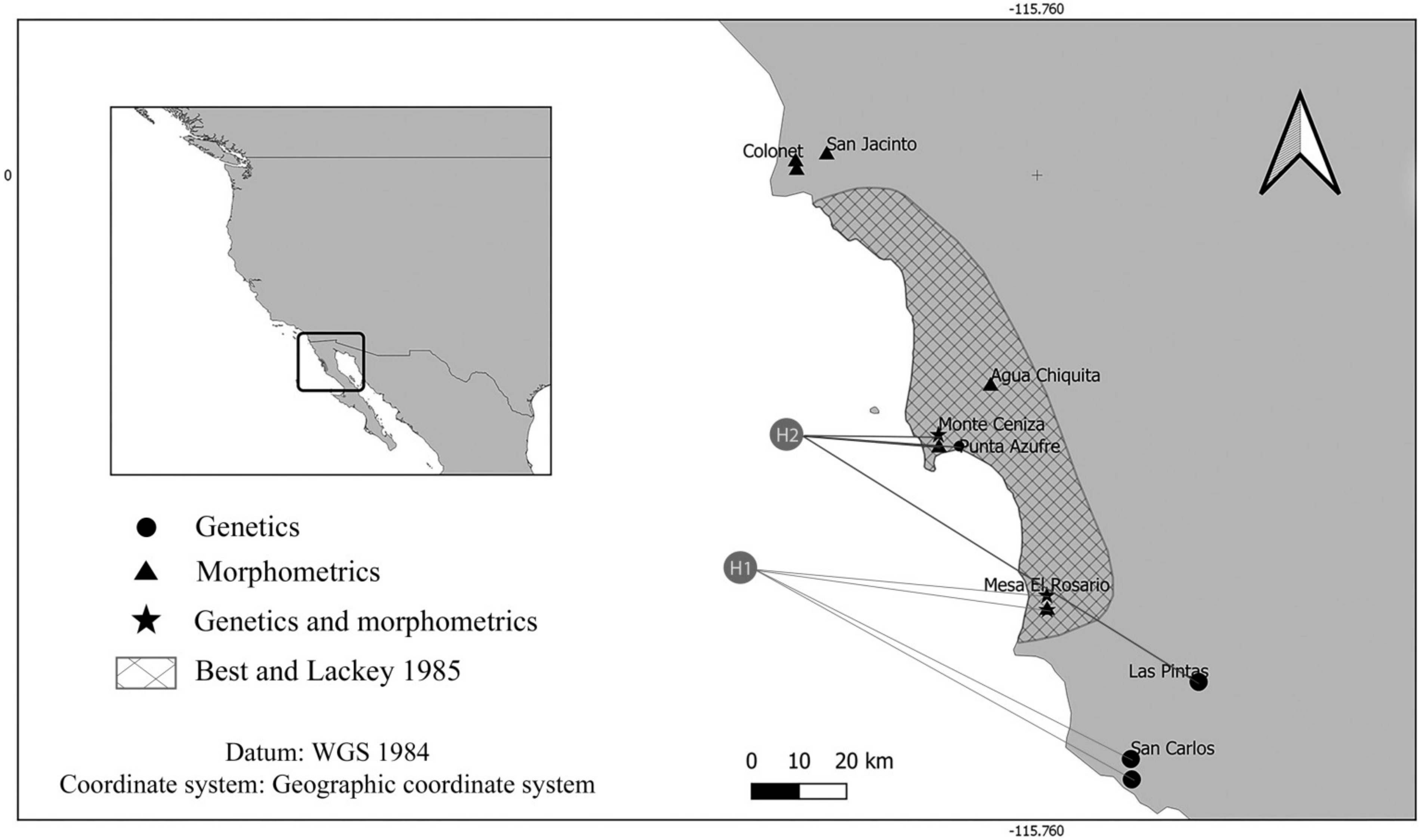

Figure 7. Study area, historical distribution range (Best & Lackey 1985), location of individuals for analysis, and haplotype distribution. H1 corresponds to the haplotype sequence in the GenBank repository (AY926442), while H2 corresponds to the new haplotype (OP038562). Basemap made with Natural Earth.

2.4.1 Linear morphometric analysis

Rodent species descriptions and identification historically have been based on morphometric descriptors. Such descrip tors continue to be the standard method of their identification. We used both gross body measurements (mass, total length, vertebral tail length, hindfoot length, and ear height) as well as standard cranial measurements (basal length, greatest length, maxillary arch spread, alveolar length, lacrimal length, maxillary arch width, basioccipital length, greatest depth, greatest width, zygomatic width, and nasal width; Fig. 8) to compare our specimens with those of *D. gravipes* collected by Best (1983), and to regional specimens of sympatric *D. simulans* (Best, 1976, 1978).

Dipodomys simulans exhibits remarkable variability of morphometric characteristics within its entire range. Therefore, we used only data from the localities in the San Quintín–El Rosario region (Best, 1976, 1978), which coincide with the distribution of *D. gravipes*. For consistency, all cranial measurements were made by J. Andrade-Sánchez using a conventional caliper with a resolution of 0.1 mm. Young and sub-adult individuals were excluded, and our final sample consisted of eight recently collected specimens. These were compared with the average values of 56 males and 54 females of *D. gravipes* (Best, 1983) and the average values of 33 males of *D. simulans* from La Escoba, El Socorro, Rosario, Catarina landing, and San Agustin localities and 22 females of *D. simulans* from Socorro, Rosario, Catarina landing, and San Agustin provided by Best (1976). For gross body measurements, we compared with contemporary *D. simulans* measurements we took in the field.

We performed two separate one-way ANOVAs, one for gross body measurements and the other for cranial measurements, to identify variation among species using the corresponding function (“AOV”) in R environment. We performed a metric multidimensional scaling (MDS) to explore the level of dissimilarity between all cranial measurements using the corresponding function (“MDS”) in R enviroment. The outcomes were analyzed by k-means and clustered to identify groups using the function “k-means” in R environment.

2.4.2 Genetic analysis

We extracted the total genomic DNA of seven individuals from five localities using a DNeasy Kit

(Qiagen) (Supplementary information 1, Fig. 34). Three of these were from internal organs and four from earlobes of the non-collected individuals. We used internal organs from collected individuals devoted to cranium analysis as these tis-sues were available. Nonetheless, we prioritized DNA extrac tion of earlobes as this technique avoids unnecessary euthanizing. We sequenced a Cox3 (mtDNA) fragment of 680 bp with the primers L8618 and H9323 (Riddle, 1995). We added 1 U of Taq polymerase per 25 µL of reaction volume. The final 1× buffer had a 0.4 µmol/L concentration of each primer, 10 mmol/L dNTP, and 3 nmol/L MgCl2. For the amplification, the thermal profile consisted of an initial denaturation cycle at 95 ◦C for 3 min, followed by 30 cycles at 95 ◦C for 45 s, 55.7 ◦C for 1 min, and 72 ◦C for 2 min, and a final extension at 72 ◦C for 5 min. Amplifications were performed in a Perkin- Elmer GeneAmp PCR system 9600 (Applied Biosystems, Foster City, CA).

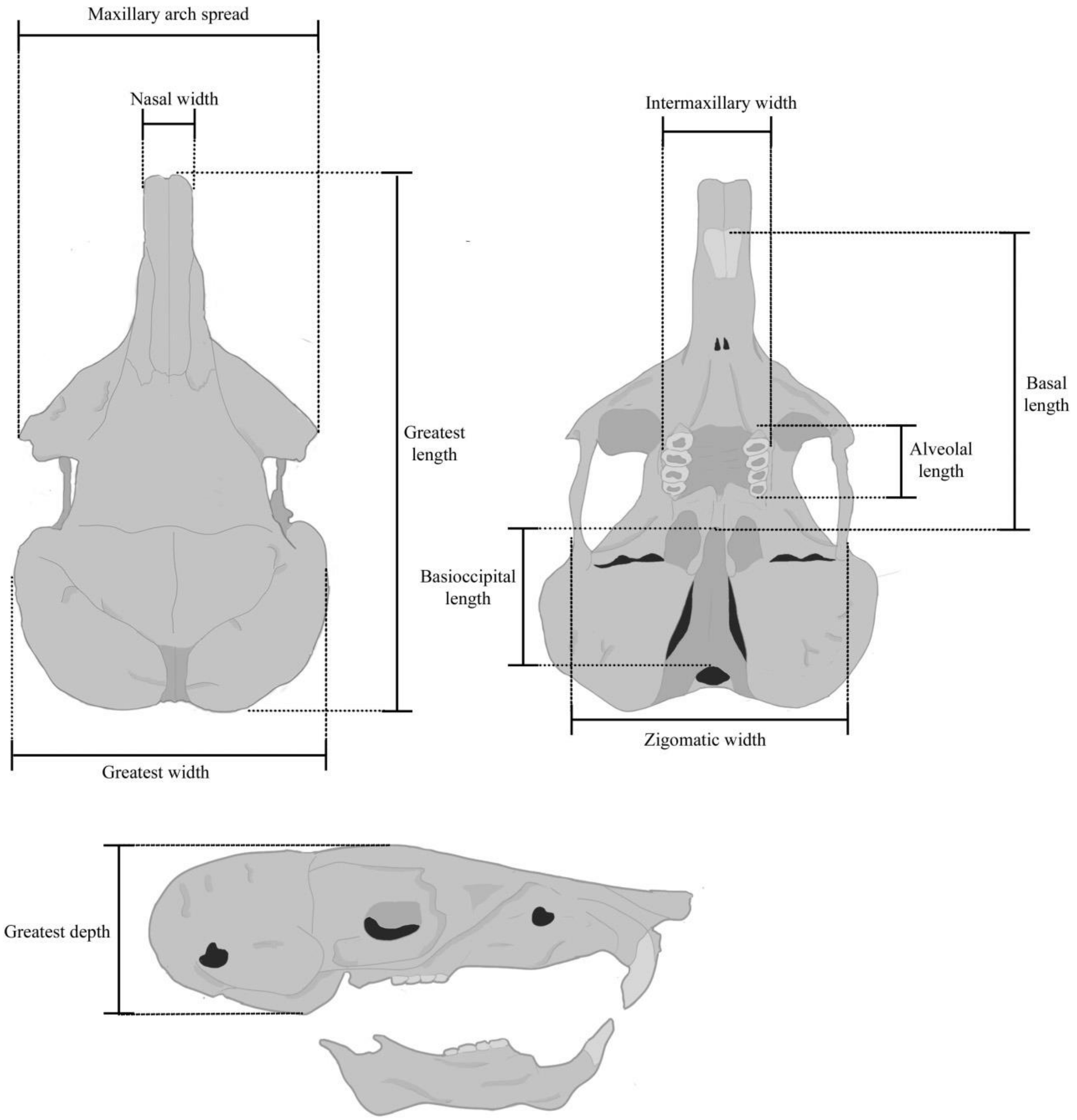

Figure 8. Cranial measurements used for linear morphometric analysis.

We aligned the seven Cox3 sequences from *D. gravipes* with 11 sequences downloaded from GenBank (*D. gravipes*: AY926442; *D. simulans*: AY926434; *D. nelson*i Merriam, 1907: AY926431; *D. spectabilis* Merriam, 1890: AY924649; *D. deserti* Stephens, 1887: AY926448; *D. agilis* Gambell, 1848: AY926433; *D. venustus* (Merriam, 1904): AY926440; *D. venustus elephantinus* (Grinnell, 1919) = *D. elephantinus* (Grinnel, 1919): AY926441; *D. californicus* Merriam, 1890: AY926435; and two sequences from *D. merriami*: AY926430, AY926450 (Alexander & Riddle, 2005) using ClustalW (Thompson et al. 1997) in Bioedit 7.0.5 (Hall, 1999).

We used the Akaike information criteria in jModelTest (Posada, 2008) to determine that GTR G was the best-fit evolution model for the phylogenetic analysis. We inferred a phylogenetic tree using maximum-likelihood analysis implemented in Mega 6 (Tamura et al., 2013). Five thousand boot- strap replicates evaluated the nodal support of the branches. Finally, using our seven sequences, we estimated the polymorphic sites and the nucleotide diversity using DnaSP 5.0 (Librado & Rozas, 2009).

2.5 Results

All external and cranial measurements of individuals identified by us as *D. gravipes* are non-distinguishable from those reported by Best & Lackey (1985) of the same species (Tables 1 and 2) and different from those of *D. simulans* specimens (Tables 1 and 2). ANOVAs exhibited that both the body and the 13 cranial measurements differed significantly between species (Tables 1 and 2). MDS resulted in two groups, one including our 2017–2021 individuals and the averaged measurements provided by Best (1983) of *D. gravipes*, and the othergroup with only *D. simulans* (Fig. 9).

Our genetic data provided a strong support (bootstrap = 100) for a species group including our seven samples and the *D. gravipes* sequence available at the GenBank repository, clearly separated from other kangaroo rats, including its two sympatric species (Fig. 10). We identified one polymorphic site in the seven sequences of sampled individuals, resulting in two haplotypes and a nucleotide diversity of 0.0008. Four of our sequences are the same haplotype as the *D. gravipes* sequence in the GenBank repository (AY926442) and occurred in two localities: San Carlos and Mesa El Rosario(Fig. 1). The other three sequences with a different haplotype(OP038562) occurred in Las Pintas, Monte Ceniza, and Punta Azufre (Fig. 10).

Table 1. External measurements of 2020–2022 specimens of presumed *Dipodomys gravipes*, and their comparison with those ofconfirmed specimens of this species and of *Dipodomys simulans* from the study region.

	Dipodomys gravipes			*Dipodomys simulans*				
	2020-22 specimens	Best, 1983		Best, 1976		This study		ANOVA
Descriptor	♂ (*n* = 11)	♂ (*n* = 56)	♀ (*n* = 54)	♂ (*n* = 22)	♀ (*n* = 17)	♂ (*n* = 48)	♀ (*n* = 54)	F-values
Mass (g)	92.3	-	-	-	-	-	-	-
Total length (mm)	297.5	306.8	300.0	283.9	282.2	257.7	252.2	$F_{[1,5]} = 10.576$, $p < 0.05$
Vertebral tail (mm)	178.8	176.1	173.2	169.7	165.5	160.3	156.1	$F_{[1,5]} = 12.149$, $p < 0.05$
Hindfoot length (mm)	44	44.8	44.1	43.0	42.3	39.9	39.4	$F_{[1,5]} = 8.7231$, $p < 0.05$

Note: One specimen was excluded as it had a docked tail. Seven 2020–2022 specimens were later confirmed to be this species by genetic analysis.

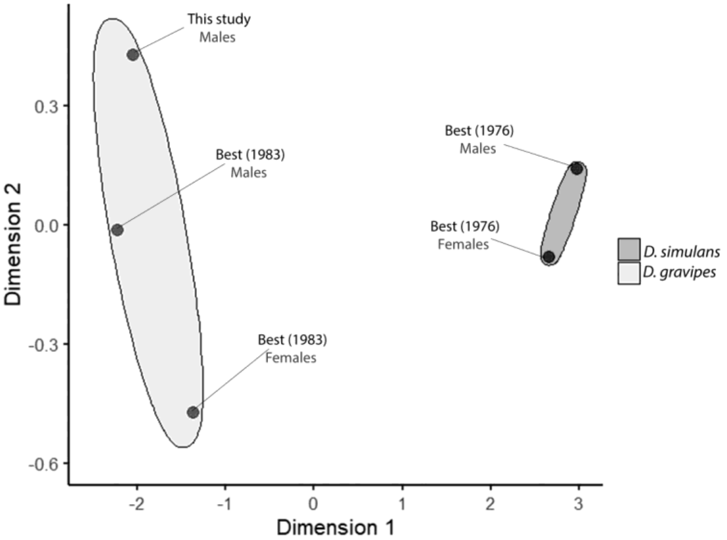

Figure 9. MDS grouping according to cranial measurements. *Dipodomys gravipes* measurements correspond to the measurements provided by Best (1983) and this study, and *Dipodomys simulans* measurements correspond to the measurements provided by Best (1976).

Table 2. Cranial measurements (in mm) of 2020-22 specimens of presumed *D. gravipes*, and their comparison with those of confirmed specimens of this species and of *D. simulans* from the study region. Three 2020-22 specimens were later confirmed as to this species by genetic analysis.

Descriptor	*D. gravipes*			*D. simulans*		
	2020-2022 specimens	Best, 1983		Best, 1976		ANOVA
	♂♂ (*n*=8)	♂♂ (*n*=56)	♀♀ (*n*=54)	♂♂ (*n*=33)	♀♀ (*n*=22)	*F*-values
Basal length	23.2	23	22.9	21.5	21.6	$F_{[1,3]} = 281.66, p < 0.001$
Greatest length	41.3	41.6	40.6	39.1	39.0	$F_{[1,3]} = 29.559, p < 0.05$
Maxillary arch spread	23.2	23.6	23.4	21.0	21.3	$F_{[1,3]} = 312.91, p < 0.001$
Nasal length	14.5	14.8	14.6	13.9	13.9	$F_{[1,3]} = 97.797, p < 0.01$
Intermaxillary width	7.7	7.9	8	7.3	7.5	$F_{[1,3]} = 36.905, p < 0.01$
Alveolar length	5.2	5.3	5.3	5.0	5.1	$F_{[1,3]} = 31.947\ p < 0.05$
Lacrimal length	4.4	4.5	4.5	3.6	3.7	$F_{[1,3]} = 242.35, p < 0.001$
Maxillary arch width	6.4	6.1	6.1	4.9	5.0	$F_{[1,3]} = 56.925\ p < 0.01$
Basioccipital lenght	6.2	6.2	6.1	5.4	5.4	$F_{[1,3]} = 60.242, p < 0.01$
Greatest depth	13.9	13.7	13.6	13.2	13.3	$F_{[1,3]} = 11.749\ p < 0.05$
Greatest width	25.9	26	25.7	24.5	24.6	$F_{[1,3]} = 58.862, p < 0.01$
Zigomatic width	20.6	21.2	20.9	18.6	18.9	$F_{[1,3]} = 88.605, p < 0.01$
Nasal width	3.8	4	3.9	3.6	3.5	$F_{[1,3]} = 63.214, p < 0.01$

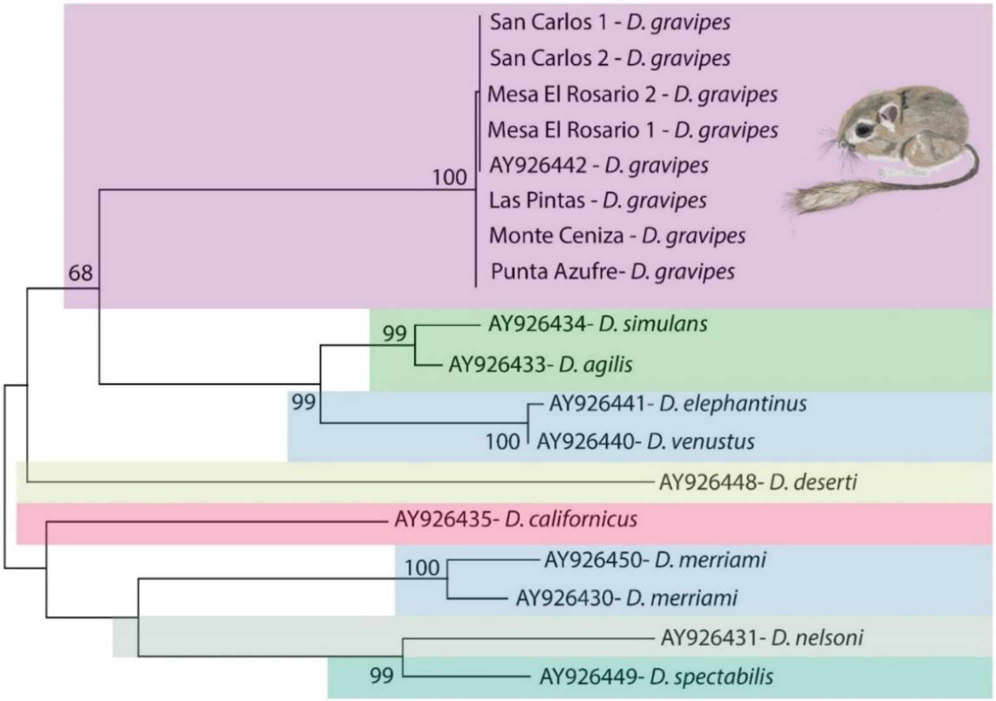

Figure 10. Maximum-likelihood phylogenetic tree of *D. gravipes* based on 680 bp of Cox3. Sequences per species are as follows: *Dipodomys gravipes*: AY926442; *Dipodomys simulans*: AY926434; *Dipodomys nelsoni*: AY926431; *Dipodomys spectabilis*: AY924649; *Dipodomys deserti*: AY926448; *Dipodomys agilis*: AY926433; *Dipodomys venustus*: AY926440; *Dipodomys venustus elephantinus*: AY926441; *Dipodomys californicus*: AY926435; and two sequences from *Dipodomys merriami*: AY926430, AY926450 (Alexander and Riddle 2005).

2.6 Discussion

The traditional external body measurements, the cranial measurements, and the genetic information presented in this study verify that specimens recently identified as *D. gravipes* by ourselves do indeed belong to that species. Our three sets of data all converge on proving beyond doubt that such identification has been correct. Recent *D. gravipes* specimens differ from *D. simulans* as was defined in the species' description in most gross body measurements (Huey, 1925; Hall, 1981).

Our results suggest that the specimens documented by Tremor et al., (2019) correctly belonged to *D. gravipes*. Even though Tremor et al., (2019) provided means of only three individuals, these correspond to key external measurements, the same as we reported in this study: total length, vertebral tail length, and hindfoot length, used as a standard way to identify the species by Best (1983). The genetic confirmation of all individuals tested in this study validates that field identification of kangaroo rats in the San Quintín region by means of gross body measurements is unequivocal if done correctly. In addition to the measurements we tested, *D. gravipes* also has smaller ears than *D. simulans* (Huey, 1925; Best, 1978), but although this feature is visible in the field, differences in measurement technique throughout time made it unadvisable to compare between our specimens and historical ones of both *D. gravipes* and D. *simulans*. Nevertheless, it is a useful and valid criterion for field identification if accompanied by the length of the hindfoot, especially for the experienced field mammalogist, as has been supported by Hall (1981), Huey (1925, 1964), Best & Lackey (1985).

Recent studies have evidenced a tendency to increase gross body measurement due to climate change among various taxa, including rodents (Ryding et al., 2021). This could be a potential source of bias when identifying rodent species in the field, as the sympatric species could be bigger in most dimensions. Nonetheless, we have included historical and con- temporary data for both congeneric species and our statistical analysis revealed significant differences between species in the means on all its gross body measurements.

The phylogenetic analysis performed by us endorses the classical taxonomic arrangement of the kangaroo rats of the Mediterranean region of Baja California by allocating *D. gravipes* and *D. simulans* to the same species group (heermanni) (Alexander & Riddle, 2005). The two haplotypes with low nucleotidic diversity found in the wide area sampled by us suggest low genetic diversity in the *D. gravipes* population.

The confirmation of the presence of the species after 30 years made in this study and the underlying endorsement of its rediscovery in 2017 (Tremor et al., 2019) is a cornerstone for its conservation. Further ecological and genetic studies must be done in the near future to ensure the long- term conservation of the species.

From the results presented here, we conclude that (i) individuals identified as *D. gravipes* during the last 3 years are un- ambiguously so; (ii) field identification of this species based on external measurements by competent mammalogists is highly reliable, and distinguishes it adequately from sympatric *D. simulans*; and (iii) further studies are required to assess the level and geographical distribution of genetic variation of *D. gravipes*.

Chapter 3. Site occupation and range expansion by the highly endangered, Mexican microendemic San Quintin kangaroo rat (*Dipodomys gravipes*, Huey, 1925).

3.1 Abstract

The San Quintin kangaroo rat, a rodent species microendemic to the San Quintin–El Rosario region in Baja California that was considered potentially extinct in the wild, was recently rediscovered. This stimulated subsequent searches by us throughout its known distribution range and on sites that seemed suitable beyond its limits. We captured the species at 19 out of 42 localities surveyed, of which 6 are beyond its historically known distribution range, expanding the latter by ~60 km. Most sites occupied by the species occur on abandoned farmland in early ecological successional stages. Our data support that in the highly transformed agricultural landscape into which the region was converted in the 20th century, the species was able to survive undetected and colonize/recolonize sites once habitat became adequate after agricultural abandonment. This exhibits that the species is highly resilient and persisted as a metapopulation. Further research and conservation actions must be framed within context of the region's agricultural development.

3.1 Graphical abstract

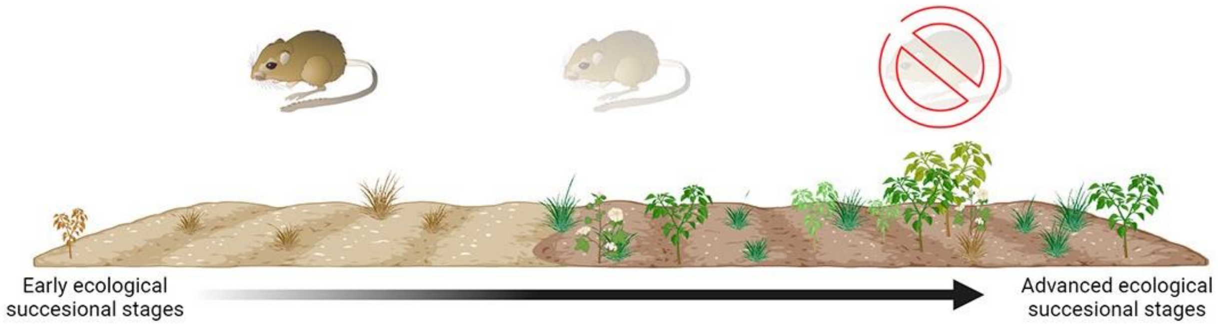

Figure 11. Graphical abstract of the chapter 3

3.2 Introduction

The San Quintin kangaroo rat (*Dipodomys gravipes*) is a "…largesized, heavy-bodied, small-eared kangaroo rat, with a thick tailof medium length, the tip of tail dark, 5 toes on the extremely large-boned hindfoot" (Huey 1925). It is microendemic to the San Quintin coastal plain in Baja California—from San Telmo in the north to El Rosario in the south (Huey,1964; Best & Lackey, 1985; Fig. 12). The eastern extent of the range is limited by thicker vegetation, steep slopes, and rockier soils. The first specimens of this species were collected in 1925 at the mouth of the Santo Domingo River canyon, and the species was described from them (Huey, 1925). Validity of the species was later confirmed by karyotypic (Stock, 1974), morphological (Schnell et al., 1978; Best, 1981), and molecular analysis (Andrade-Sanchez et al., 2023).

The historic range of the San Quintin kangaroo rat covered approximately 1,000 km2. North of the El Rosario mountain range, the species occupied flat areas with friable soils that are found within coastal plains and adjacent rolling hills and mesas and are covered with low open Californian coastal sage scrub (sensu Kirkpatrick & Hutchinson, 1977)—and to the south was found in the Arroyo El Rosario floodplain (Best, 1983). The area occupied by the San Quintin kangaroo rat was prime agricultural land that after 1970 was almost entirely transformed to intensive farmland (Riemann, 2015). Consequently, the species declined dramatically in abundance (Best, 1983), and after 1,000 trap-nights north of San Quintin in July 1980 only 2 individuals (Best, 1983) were detected. The species was last recorded in 1986 (Alvarez-Castaneda & Lacher, 2018), although the locality was not indicated, and searches in the 1990s failed to find the species (Mellink, 1996). Based on lack of captures and scale of land change, specialists considered it possibly extinct (Ceballos & Navarro ,1991; Mellink, 1996; Mellink & Luevano, 2005), and the Mexican government listed it as "potentially extinct in the wild" in 2010 (SEMARNAT, 2010). The International Union of Conservation of Nature considers it critically endangered (Alvarez-Castaneda & Lacher, 2018).

After over 25 years since the last recorded observation, the San Quintin kangaroo rat was rediscovered in 2017 (Tremor et al., 2019). At that time, 4 individuals were captured on a ~3,000 m2 embankment surrounded by cropland, 5.6 km east of the town of San Quintin. This stimulated further searches by us throughout its known historic range, as well as on sites that seemed suitable to the north and south of its recorded range limits. Based on the results of these surveys, we present the current distribution of the species, gross habitat characteristics, and hypothesize on processes and drivers involved in its site occupation dynamics.

3.3 Material and methods

3.3.1 Study area

We searched for the San Quintin kangaroo rat through its known historic range, as well as ~60 km farther to the north and ~50 km farther to the south (Fig. 12). Most of the area on Sierra El Rosario and to the north is within the southern extreme of the California Floristic Province—1 of 35 world biodiversity hotspots (Mittermeier et al., 2011). Our study area south of Sierra El Rosario is part of the Vizcaino Desert Province, a transitional zone that has vegetation characterizing both California Mediterranean and Sonoran Desert ecoregions.

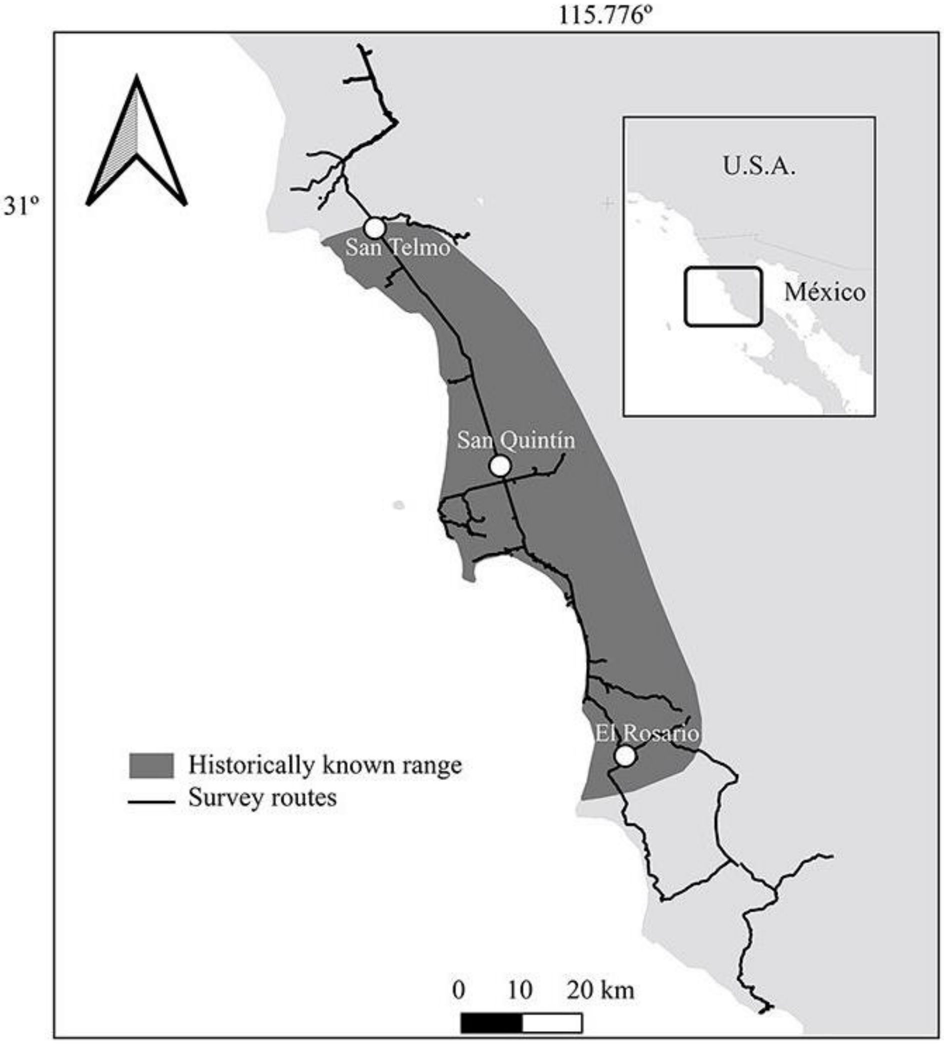

Figure 12. Known distribution of the San Quintín kangaroo rat (dark shade), and main routes of searches for its presence.

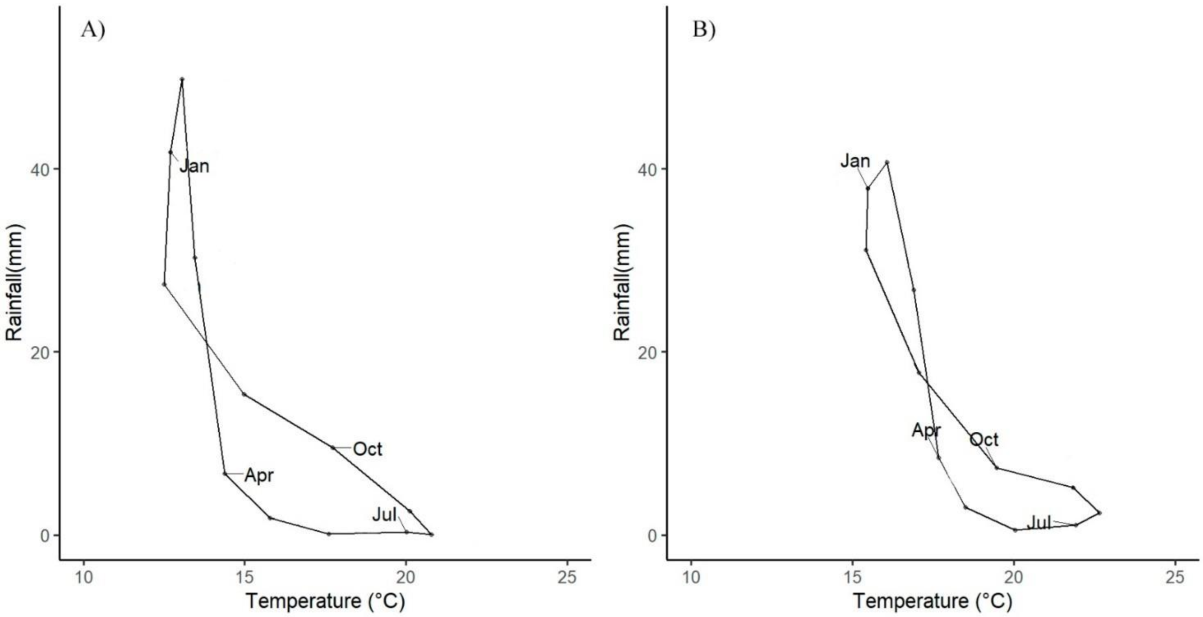

Figure 13. Climographs of the northern part of the San Quintín coastal plain (A) and El Rosario region (B), Baja California. Figures drawn by LA-S from data in http://clicom-mex-cicese.mx.

3.3.2 Fieldwork

From 2017 to 2021 we surveyed all historical localities that were not actively farmed or urbanized, based on the San Diego Natural History Museum database, Lawrence M. Huey's field notes, Vertnet (www.vernet.org), and the Global Biodiversity Information Facility (GBIF; www.gbif.org). We searched for potentially occupied sites within and beyond the historically documented distribution range of the species based on habitat that had been occupied (Best & Lackey, 1985). At each promising site—both historical and potential—we looked for their distinctive round burrow entrances ≥8.4 cm high and ≥7.6 cm wide (Best 1976) and long runways. If we found sign of apparent presence of the species, we placed 3 Sherman traps (30.5 cm long) baited with rolled oats at the entrance of every active burrow and left them open from dusk to dawn. Our purpose was to confirm presence of the species, and 1 night of trapping was sufficient to do so. Total number of traps deployed at each site depended on number of active burrows. Additionally, in 2023 we scouted habitat along the dirt road to Puerto Santa Catarina and surroundings but did not find evidence of potential presence of the species.

We identified all kangaroo rats captured to species level based on external characteristics. Although the species is similar to the dulzura kangaroo rat (*D. simulans*), body measurements are highly reliable to diagnose adults of both species (Andrade-Sanchez et al., 2023). We obtained body weight as well as total, tail, hindfoot, and ear length.

The area sampled at each survey site was determined by the surface occupied by active burrows. At each survey site, we recorded the most abundant plant species, identified according to our knowledge of regional flora and using the field guide of Rebman & Roberts (2012). We qualitatively estimated the proportion of soil covered by herbs and shrubs across each area sampled. Sites were assigned to land use categories of (i) no evidence of previous farming; (ii) abandoned farmland; (iii) urban; and (iv) garbage dump. We considered a site as "abandoned farmland" if original vegetation had been removed and old furrows were visible. We also noted land use in areas surrounding each colony.

We obtained elevation (m asl), slope (°), and terrain ruggedness values (Riley et al. 1999) from the 30 × 30 m ASTER Global Digital Elevation Model Ver. 3 at NASA's Land Processes (https://asterweb.jpl.nasa.gov/gdem.asp). For all calculations, we used the Raster Terrain Analysis tools and the raster calculator of Quantum GIS (QGIS; Version 3.8.0; Zanzibar). Additionally, soil classification of all sites was extracted from Mexico's national continuum soil spatial layer at a scale of 1:250,000 (INEGI 2016), using the Point Sampling tool of QGIS. The proportion of cases that did not show evidence of previous farming, and of those classified as abandoned farmland were compared between sites currently occupied by the species versus those not occupied by the species through a $\chi 2$ test. A $\chi 2$ test was also utilized to determine whether type of habitat adjacent to the sites surveyed influenced presence or not of the species. We used an alpha level of $P = 0.10$ for all statistical tests.

3.3.3 Ethical standards

We conducted this study in agreement with the Mexican environmental law (permits SGPA/DGVX/3150/19 and SGPA/DGVX/3150/22) and guidelines in Sikes et al. (2016).

3.4 Results

Our trapping effort totaled ~2,400 trap-nights on 42 sites—34 within and 8 beyond the known historical distribution. We captured a total of 83 San Quintin kangaroo rats at 13 sites within and 6 beyond the known distribution (Fig. 14). The species was not captured at 23 of the sites surveyed. Of the 13 localities on which the species was captured within its historical distribution, 5 were localities at which it had been captured before the 1970–1980s decline, and 8 were localities at which it was recorded for the first time in our study. No signs of activity nor individuals of the species were captured at 3 localities where it had been trapped before its population collapse. The species was captured beyond its known historical geographic distribution at 2 sites to the north and 4 to the south. During the scouting trip to Puerto Santa Catarina and its surroundings, we found no burrows of the species in the few open patches explored.

Locations at which the species was present either historically or currently (*n* = 22) had an elevation of 6–251 m asl, a slope of 0.7–8.5°, and a ruggedness value of 0.37–3.12. Soil type was fluvisol at 5, planosol at 3, regosol at 4, solonchak at 1, and xerosol at 10 locations. Sites that we considered potential and explored for the species presence but were we did not find signs of it (*n* = 19) had values of 7–128 m asl elevation, 0.5–9.7° slope, and 0.5–5.12 ruggedness—and soil types of fluvisol at 3, planosol at 1, regosol at 3, solonchak at 5, and xerosol at 7 locations. To detailed physical characteristics see supplementary information 2 (Table 8).

The most common plant species found in survey sites— whether occupied or not by the species—were Vizcaino Saltbush (*Atriplex julacea*), Menzie's Goldenbush (*Isocoma menziesii*), Broom Baccharis (*Baccharis sarathoides*), and Crystalline Iceplant (*Mesembryanthemum crystallinum*). The last species an invasive exotic was present at all sites, whether they were or not occupied by the species (Table 3). The San Quintin kangaroo rat only used sites with <10% ground cover by plants, regardless of whether it was by herbaceous plants and an absence of shrubs (Table 4), except at 3 sites that had a few shrubs.

Eighty-four percent of the sites where we captured the species were abandoned farmland plots, including sites within the historic range as well as those in the expanded range, and 83% of historical locations where we captured the species were now abandoned farmland (Fig. 15, Table 4). The species tended to occupy abandoned farmland more commonly than sites without evidence of previous farming ($\chi2 = 3.11$, $P = 0.08$). There was no effect of adjacent habitat type on presence or absence of the species (Table 1; $\chi2 = 5.01$, $P = 0.41$).

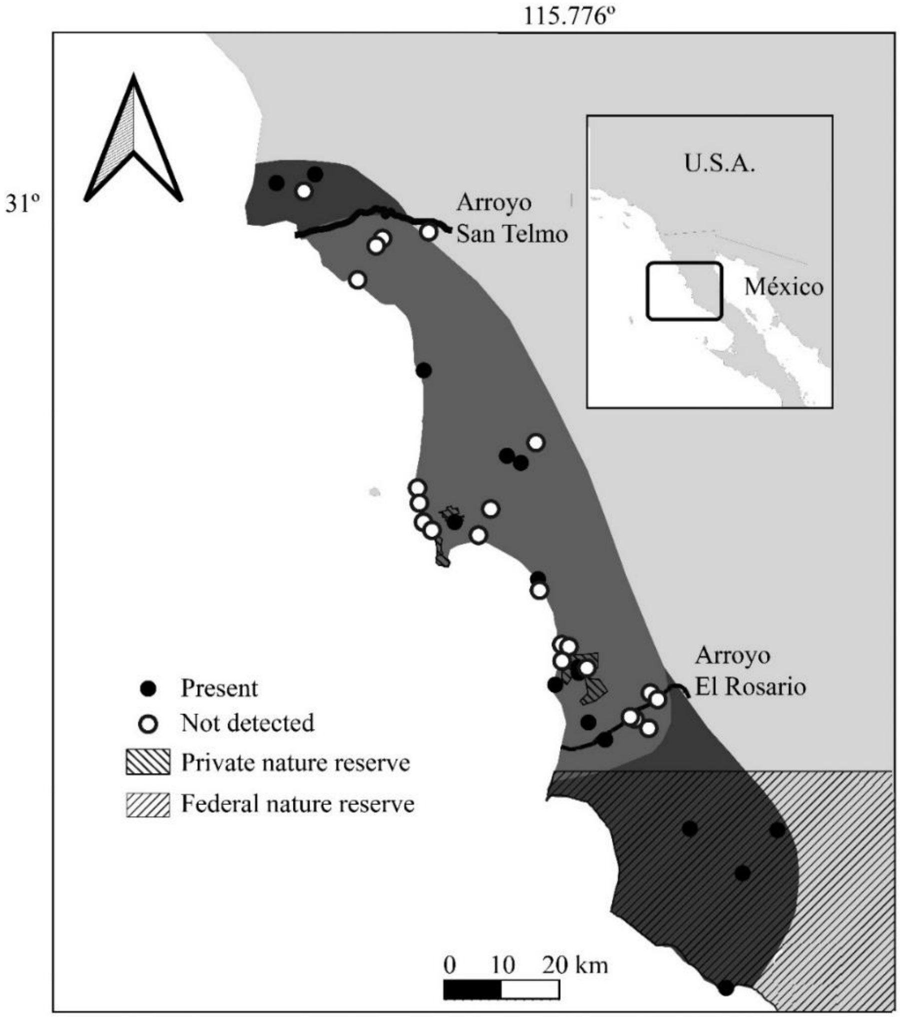

Figure 14. The San Quintín-Rosario area, Baja California, displaying the sites where the San Quintín kangaroo rat was captured, and sites with no captures of the species. 2017-2022. Closeness of some sites, where the species was captured resulted in overlapping circles.

Figure 15. The typical habitat of the San Quintin kangaroo rat, flat area with low cover by herbaceous vegetation at San Vicentito, an abandoned farmland.

Table 3. Current condition and adjacent habitat of sites on which San Quintín kangaroo rats were capture and of sites at which they were not. Numbers in columns are number of sites in each category. Baja California, Mexico. 2017-2022.

Case	Total	Current condition: % (Number)			Adjacent habitat: % (Number)					
		No farming evidence	Abandoned farmland	Garbage dump	Shrub patch	Coastal sage scrub	Dune vegetation	Marsh vegetation	Cropland	Crops & Urban
Absent in historic range	23	75 (9)	45 (13)	100 (1)	73 (8)	25 (2)	50 (2)	75 (3)	54 (7)	4 (1)
Historic site	4	8 (1)	7 (2)	100 (1)	27 (3)	0	0	0	0	100 (1)
Potential site	19	67 (8)	38 (11)	0	46 (5)	25 (2)	50 (2)	75 (3)	54 (7)	0
Present	19	25 (3)	55 (16)	0	27 (3)	75 (6)	50 (2)	25 (1)	46 (6)	5 (1)
In historic range	6	8 (1)	17 (5)	0	9 (1)	0	50 (2)	25 (1)	8 (1)	100 (1)
New in historic range	7	8 (1)	21 (6)	0	0	50 (4)	0	0	23 (3)	0
New in north expansion	2	0	7 (2)	0	0	0	0	0	15 (2)	0
New in south expansion	4	8 (1)	10 (3)	0	18 (2)	25 (2)	0	0	0	0

Table 4. Vegetation of sites on which San Quintín kangaroo rats were capture and of sites at which they were not. Numbers in columns are number of sites in each category. Baja California, Mexico. 2017-2022.

Case	Total	Soil cover by plants: % (Number)		Herbs: % (Number)		Shrubs >0.05m: % (Number)	
		<10%	>10%	No or few	Yes	No or few	Yes
Absent in historic range	23	44 (15)	100 (8)	100 (8)	44 (15)	49 (18)	100 (5)
Historic site	4	9 (3)	12 (1)	37 (3)	3 (1)	8 (3)	20 (1)
Potential site	19	35 (12)	88 (7)	63 (5)	41 (14)	40 (15)	80 (4)
Present	19	56 (19)	0	0	56 (19)	51 (19)	0
In historic range	6	18 (6)	0	0	18 (6)	16 (6)	0
New in historic range	7	20 (7)	0	0	20 (7)	19 (7)	0
New in north expansion	2	6 (2)	0	0	6 (2)	5 (2)	0
New in south expansion	4	12 (4)	0	0	12 (4)	11 (4)	0

3.5 Discussion

Our results not only document presence of the San Quintin kangaroo rat throughout its known historical distribution, but also extend it ~10 km to the north and ~50 km to the south, surpassing 2 historically active watercourses—Arroyo San Telmo and Arroyo El Rosario that had been considered as possible barriers to dispersal (Fig. 12, Table 3). Our research endorses the 2017 rediscovery of the species (Tremor et al., 2019) and allows for a general description of habitat characteristics of sites colonized or recolonized by the species.

The San Quintin kangaroo rat has been considered sensitive to habitat disturbance, and agricultural conversion was identified as a major driver of its population decline in the 1970s and 1980s (Best, 1983; Best & Lackey, 1985; Lidicker, 1989; Cab- Sulub & Alvarez-Castaneda, 2020). Our results complement the picture of the relationship of the species with agricultural conversion in that abandoned farmland can provide suitable habitat for the species, where we documented its occurrence on 55% of abandoned farmland plots that we surveyed, including 83% of all historical sites in our study where the species was present (5 out of 6), and in 86% of the new localities here reported (Table 4; Fig 12). Indeed, some places that were unsuitable when covered with their original habitat now provide suitable habitat for the species after being cleared for farming and later abandoned colonized after persisting in refugia during extensive farming of the San Quintin plain and El Rosario riverbed. This capability to colonize farmland after cultivation has been reported also for a congener the Stephens's kangaroo rat (*D. stephensi*; Thomas ,1975; Moore-Craig ,1984; Price & Endo, 1989; US Fish and Wildlife Service, 2020).

All locations at which we captured the species had <10% cover by herbs and few or no shrubs. This suggests that, in abandoned farmlands, the species uses sites in early successional stages. Those stages that had more than a few shrubs were not used by the species. In the region, sites in later stages include shrubs including Ragweed (*Ambrosia chenopodifolia*), Spiny Rush (*Juncus acutus*), Baja Desert-thorn (*Lycium brevipes*), and California Desertthorn (*Lycium californicum*).

Differences between abandoned farmland plots occupied and those that were not occupied is not clear. The fact that there were no differences in physical characteristics of the terrain (soil type, slope, elevation, and ruggedness) between plots occupied and not occupied indicates that factors other than those considered herein could explain habitat selection. Our results confirm that the San Quintin kangaroo rat occupies flatland with scarce vegetation, as also described by other researchers (Best, 1983; Best & Lackey, 1985). However, in addition to avoidance of sites with >10% plant cover and sites with shrubs taller than 0.5 m, additional habitat characteristics remain to be investigated.

The 6 sites beyond the traditionally accepted distribution range where we documented the species (Fig. 12) represent an important extension of its known range. The northern limit accepted in the literature was that defined by Huey (1964) and neither he nor other mammalogists appear to have carried out collecting immediately north of the San Telmo river according to GBIF, Vernet, and Huey's field notes.

Regarding the southern limit, Huey wrote in his field notes on 5 May 1925 "… I am satisfied that the large kangaroo rat - *D. gravipes* - found farther north does not occur this far south." Documentation of specimens in 1966 by T. Best in the El Rosario riverbed (Vertnet) after Arroyo El Rosario had ceased to be a perennial stream and water flows were greatly reduced could indicate colonization of this area between those 2 dates. As with the northern limit, there are no known small mammal surveys on the coastal plain between Arroyo El Rosario and Punta San Carlos (Fig. 14) prior to ours, or their results were not made public as publications or as specimens. Although the species could have occurred in this area but unnoticed, the fact that all colonies south of Arroyo El Rosario are on abandoned farmland indicate that a more recent colonization is more likely. As our reconnaissance of the road to Puerto Santa Catarina revealed, Punta San Carlos is currently the southernmost location of the species.

In 2018, the International Union for the Conservation of Nature (IUCN) published a distribution map of the San Quintin kangaroo rat (Alvarez-Castaneda & Lacher, 2018), without clarifying the procedure used to generate it. This map must be taken as a general approximation and not as a precise representation because: (i) range limits displayed were not supported by known records; and (ii) it includes a large area of mountainous terrain that is unsuitable for the species. The map was a good working approximation but must now be updated with information here presented.

This process of dispersal through a hostile agricultural matrix and colonization of abandoned farmland patches would have not been limited to the historical distribution range if previous barriers, if any, were removed. The species colonized patches outside the previous range after the lower sections of Arroyos San Telmo and El Rosario dried following ~4 decades of water extraction for human needs (Riemann, 2015).

Whether the species survived in one or multiple refugia after the San Quintin plain was extensively transformed for agricultural production is not known at this time, but subsequent colonization and, or recolonization of patches in an ecological time frame indicates that the species is currently subject to metapopulation dynamics (Hanski and Gilpin,1991). Analyzing spatial patterns of occurrence in more detail would all for an evaluation of structural and functional connectivity of populations and contribution of each patch for persistence, providing a foundation for informed spatially based conservation planning for the species. Based on our data, we hypothesize that abandoned farmland in early ecological succession enhances colonization by the species.

However, as shrubs encroach upon colonies the species ceases to use those patches. The current patchy spatial distribution of populations is largely due to anthropogenic activities–hence, further research and conservation actions must be framed within the context of agricultural development, as well as under a metapopulation approach.

Chapter 4. Spatio-temporal patterns of *Dipodomys gravipes* colonies

4.1 Introduction

The San Quintin kangaroo rat (*Dipodomys gravipes*) is a Mexican microendemic rodent whose populations severely decline in the late 1970s and early 1980s (Best & Lackey, 1985), leading to ~32 years without any records of the species until rediscovered in 2017 (Tremor et al., 2019). Before the specie's population decline and after its description in 1925, the species biology and ecology were described uncovering crucial knowledge. The species general and diagnostic characters are well described (Huey, 1925). As well, inter-locality variations on morphological cranial traits are well documented (Best, 1978; Best, 1983; Best & Lackey, 1985). However, regarding the specie's ecology little information has been provided to date. In this context, the species habitat characteristics described prior the species decline uncover general information of occupied sites such as inclination and vegetation characteristics on which highlights the fact that the species occupy flatland with short vegetation (Best & Lackey, 1985). Regarding the species reproduction has been noted that that juveniles are born throughout the year, with birth peaks in winter, particularly in November and December and spring and summer, particularly March, April, June, July and August (Best & Lackey, 1985). Yet, abundance was not documented at the occupied sites nor its seasonal and cyclic variation. Similarly, the environmental factor influencing the latter remains to be investigated.

An association between precipitation, plant production, and the stimulation of reproduction of rodents has been documented in kangaroo rats in California and Baja California (Kenagy & Bartholomew, 1985; Best & Hoditsheck, 1986; Bradley & Mauer, 1971). *Dipodomys simulans* and *D. merriami*, sympatric species to *D. gravipes,* show a positive relationship between rainfall-plant productivity-reproduction-population growths (Price & Endo, 1988). However, in other kangaroo rats the relationship seems to be time-lagged. For example, the population growth of kangaroo rats in Chihuahua, exhibit a time-lag response of rainfall and plant productivity (Brown & Ernest, 2002). In addition, other factors, such as vegetation cover and structure, seed availability, and predator-prey dynamics, may play an essential role in driving small rodent population dynamics.

The interaction of rainfall and primary productivity in the Mediterranean region of Baja California is well documented and reportedly follows a general pattern on which vegetation cover increases during the rainy season (Cramer & Hofman 2015). Cover of herbaceous plants follows this linear pattern as these increase during the rainy season (Cramer & Hofman 2015). This ultimately leads to a stimulation of reproduction in rodents as water, nutrients, and hormones of green vegetation stimulate reproductive status in Heteromyid rodents (Chew & Butterworth, 1964; McClenaghan, 1987; Reichman & Van De Graaf, 1975; Soholt, 1977; Van De Graaf & Balda, 1973).

It has been documented that *D. gravipes* tends to occupy areas with sparse vegetation with <10% plant cover and shrubs <0.5 m of height and in level lands <10° (Best & Lackey, 1985; Andrade et al., 2024). However, the influence of these habitat characteristics and other environmental traits such as rainfall, on the species abundance and reproductive status remains to be investigated. This study aims to document the temporal and spatial variation of the abundance and describe the breeding cycle of *D. gravipes* and to explore relationship of precipitation and vegetation structure and cover. The study hypothesized that greater abundance is expected to be found at flatter sites, with vegetation cover of no more than 10% and with low and scarce shrubs and after the emergence of herbaceous plants, a greater proportion of juveniles and ultimately an increase on the species abundance.

4.2 Methods

4.2.1 Study area and sites

Our study area corresponds to the entire known distribution range of *D.gravipes* (Andrade et al., 2024). The area is a transitional zone between the Mediterranean and the Sonoran Desert regions (Nelson, 1922; Brown & Lowe, 1980; Mellink, 1996). Most of the study area is within the coastal plains of San Quintin, which extends from approximately 30.3 ° to 30.8 °N along the Pacific coast (Aguirre-Muñoz et al., 2001) and gradually encroaches to its narrowest point at El Campito, on which mesas and rolling hills approach to the shore (Nelson 1922). Vegetation corresponds to Californian coastal sage scrub (sensu Kirkpatrick & Hutchinson 1977) which is characterized by low growing aromatic shrubs including California sagebrush (*Artemisia* californica), Goldenbush (*Isocoma* menziessi), coastal prickly pear cactus (*Opuntia sp*), and others. The climate is dry in the northern portion and very dry in the southern portion (Garcia, 2004). It ranges from 15.2 mm average annual precipitation and 18.6°C average annual temperature to 16.7 mm and 16.6 °C in the north. Maximum temperatures are 28.7°C and 22.5 °C in the summer and 14.8°C and 11.7°C in the winter, respectively (http://clicom-mex.cicese.mx). Minimum temperatures are 15.8 °C and

15.8 °C in summer and 8.2°C and 3.1 °C in winter, respectively. All rainfall occurs during the winter from March to December.

For this study three sites were selected (Fig. 16) based on habitat and climatic characteristics, year-round accessibility, and landowner permissions. These sites are arranged along a climatic gradient, from rainier in the north to less rainy in the south (Fig. 17), and from Mediterranean vegetation in the north to central Baja California desert elements in the south (Fig. 18).

1) The plot on Monte Ceniza was cleared in 2018 but was not farmed. The soil texture is loamy sand. The vegetation cover is dominated by native plants representative of the coastal sage scrub community including the Red sand verbena (*Abronia maritima*), the invasive common ice plant (*Mesembryanthemum crystallinum*) and annual plants such as a smallseed sandmat (*Euphorbia polycarpa*). There were no shrubs in the sampling plot. Non-cleared land surrounding the sampling plot had coastal sage scrub including California sunflower (*Helianthus californicus*). The higher inclination of the sampling plot is <5°

2) The plot on El Malvar was an abandoned agricultural field on an alluvial plain of arroyo San Vicente, with silty-clay soil, was last cultivated in 2013. Currently, domestic livestock grazes on it. This vegetation was dominated by perennial herbs including the invasive common ice plant (*Mesembryanthemum crystallinum*) and cheesweed (*Malva parviflora*) although short shrubs were present including Baja desert thorn (*Lycium brevipes*). During the rainy season annual herbs emerged including smallseed sandmat (*Euphorbia polycarpa*). The plot is adjacent to hills with slopes covered by coastal sage scrub including the Baja desert thorn (*Lycium brevipes*).and desert vegetation including the Mexican giant cardon (*Pachycereus pringlei*). The higher inclination of the sampling plot is <5°.

3) The plot on El Campito was an abandoned agricultural field that was last farmed in 2003. It is located at the base of a coastal sand dune. The soil texture of the site is silty loam. The most abundant perennial herbaceous plants was the invasive common ice plant (*Mesembryanthemum crystallinum*) intercepted with some short shrubs, like Palmer’s seaheat (*Frankenia palmeri*) and Cliff spurge (*Euhorbia misera*). Annual herbs appeared during the rainy season including smallseed sandmat (*Euphorbia polycarpa*). The higher inclination of the sampling plot is <5°.

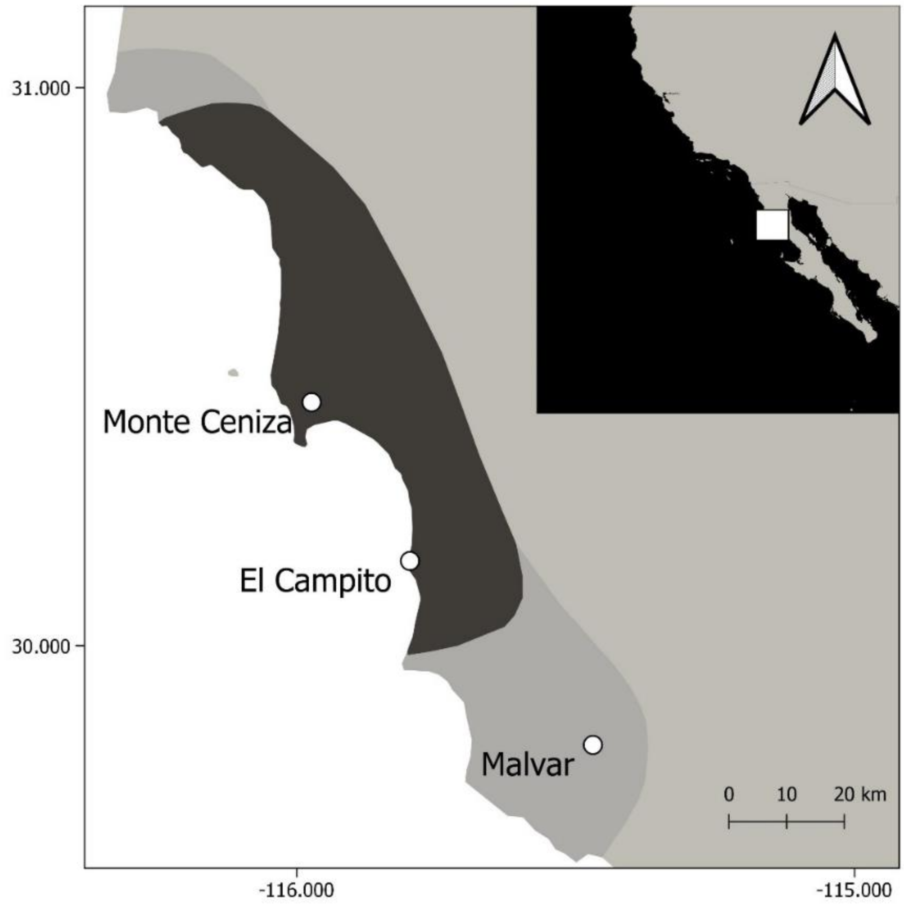

Figure 16. Study area and the three study sites in the known distribution range of *Dipodomys gravipes*. Dark gray polygon corresponds to historical distribution range and light gray to current limits which ranges from Colonet to southern El Rosario at Baja California, México (Andrade et al., 2024).

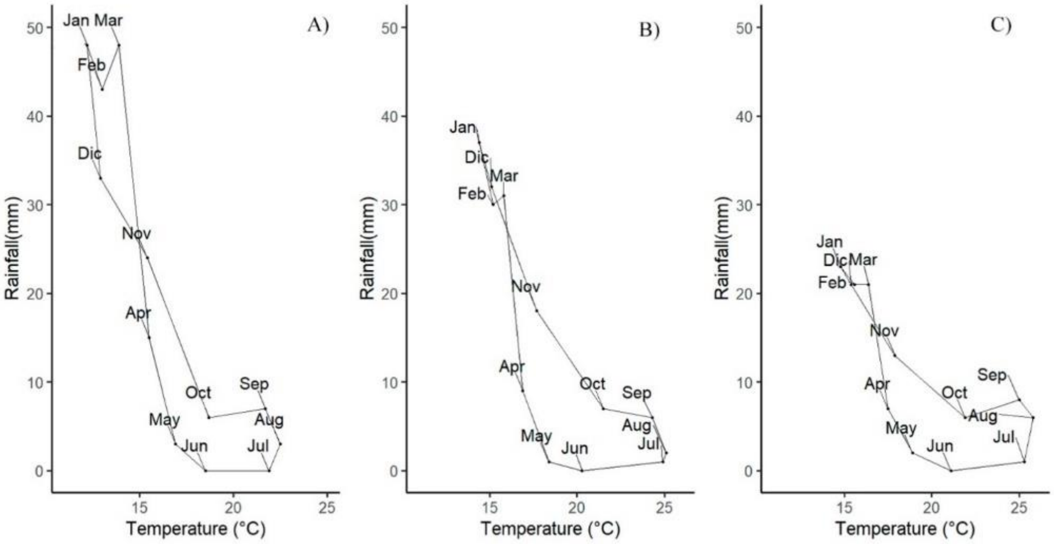

Figure 17. Climographs of study localities; A) Monte Ceniza, B) El Campito and C) El Malvar from clicom.mx. All data are the average of each month per year.

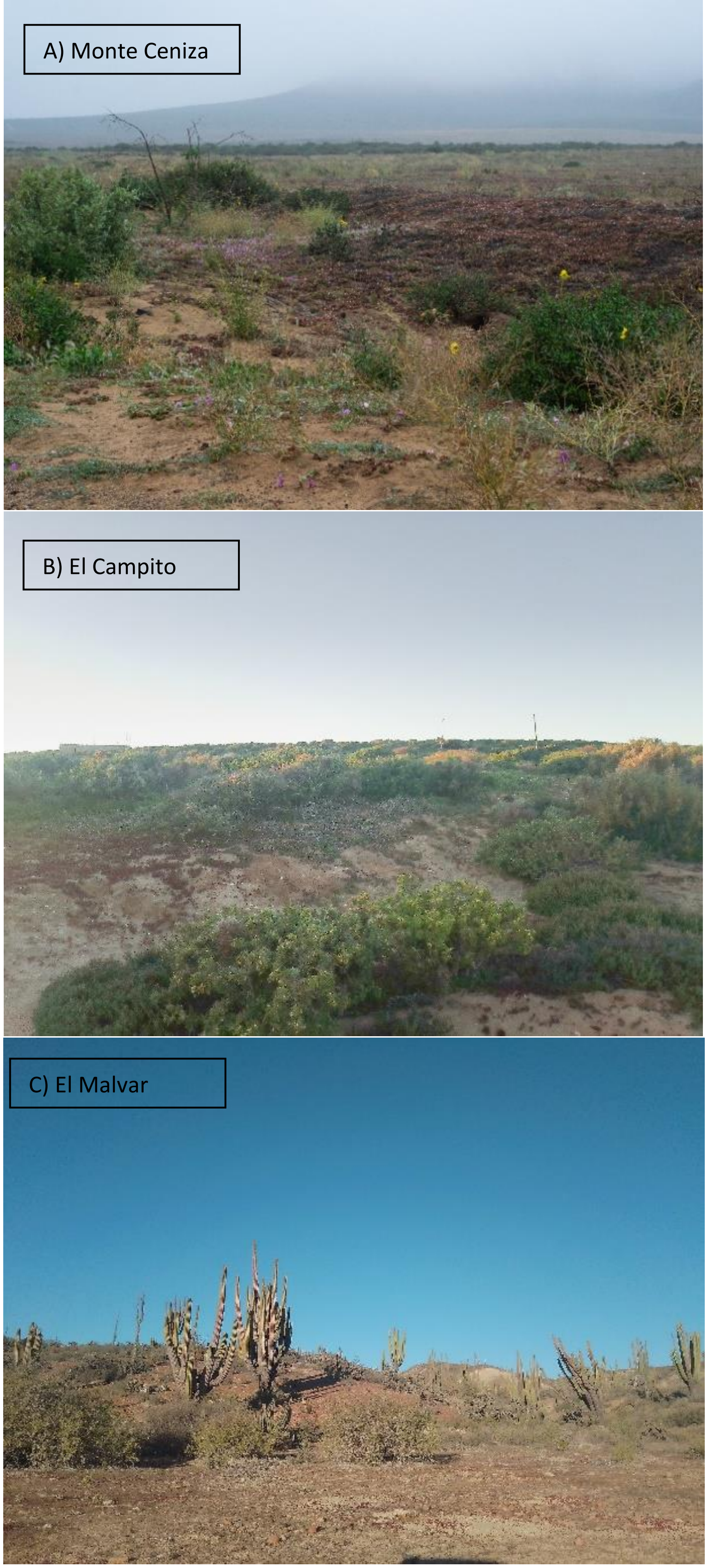

Figure 18. View of study sites. From north to south: A) Monte Ceniza with coastal sage scrub community. B) El Campito with coastal sage scrub C) El Malvar with an admixture of the coastal sage scrub and the central desert species.

4.2.2 Field work

Field work was carried out from March 2022 to November 2023 and consisted in two main activities: Rodent livetrapping and habitat assessment. Bimonthly, we conducted rodent surveys at each site (see supplementary information 3, Table 7). As many rodent species that forage in the open ground restrict their activities during bright nights (Price & Heinz., 1984), we avoided nights the 7 days before and after a full moon, and all surveys had <19% moonlight intensity. At each survey period we placed 100 Sherman live traps (Model XLK; Sherman Traps, Tallahassee, Florida) on a 10 x 10 grid arrangement (10 –m spacing in both directions), baited with rolled oats, and left from dusk to dawn each of two consecutive nights. Due logistic problems trapping was not possible once at each of two localities (supplementary information 3, Table 7).

All rodents captured were identified to the specie level. Individuals of *D. gravipes* were marked with individual alphanumerical ear tags (Monel self-piercing tags, Model 1005-1, National Band & Tag Co., Newport Kentuchy). From each individual, we obtained its standard external measurements: body weight, total, tail, hindfoot, and ear lengths by means of conventional rulers and determined its breeding condition. Males were considered active if their testicles were fully scrotal. Female reproductively status was determined if one of the following traits was noticed: enlarged nipples, a copulatory plug, pubic symphysis aperture, pregnancy otherwise was considered inactive. For both cases, the percentage of reproductive statues was calculated. We used the minimum number known alive (Krebs, 1966) as a proxy to the abundance of *D. gravipes*.

We assessed the habitat by vegetation and soil attributes. We measured ground cover by plants within each grid of Sherman traps, based on 120 intercept points along six transects of 20 m (120-m). Intercept points were spaced 1 m to avoid autocorrelation between sampling points (Drezner & Drezner 2021). We recorded cover classes at each sampling point and classified these as open space (including bare ground, rock and litter), herbs (annual or perennial) and shrubs. We identified all plants to species level, based on our knowledge of the regional flora and Rebman & Roberts' (2012) field guide. Additionally, we collected plant specimens (leaves, seeds and flowers) for later identification when needed.

4.2.3 Statistical analysis

We estimated Pearson's correlation coefficients between total vegetation cover and herbaceous vegetation cover (annual and perennial separately) on the abundance and the reproductive status of *D. gravipes* to identify direction of the relationships. Shrub plant cover was depicted from analysis as only El Campito presented this vegetation cover and its cover do not change over time.

We also examined the relationship between photoperiod length and the reproductive status of females and males by means of Pearson's correlation to explore the direction of the relationship. To explore the influence of rainfall on the total vegetation cover and annual and perennial herbs we performed a correlation analysis based on Pearson's correlations at Monte Ceniza. We used only Monte Ceniza, as the rainfall precipitation pattern is similar to the other localities on amount of rain and due to climatic information available is from nearby climatic station from CONAGUA (smn.conagua.gob.mx). There are no climatic stations nearby the rest of the localities

To further examine vegetation cover changes across time and space, we plotted cover changes of the dominant plant species at all localities and performed a correlation analysis based on Pearson's coefficient. We defined seasons for all localities: Spring-Summer from April to October, and Fall-Winter from November to March. Our criterion was the increase/decrease in monthly rainfall and temperature. All analyses were performed in R (Ver. 4.2.1; R Development Core Team 2022). To further explore the influence of each cover class on the species abundance and reproductive status, we used generalized linear models. For all cases, we considered 5 environmental variables as fixed effects: Percent of total vegetation cover, of cover by annual herbs, of cover by perennial herbs, and length of daylight. We performed all possible combinations of models for all 5 variables and abundance and reproductive status as response variables. In all cases, locality was included as random effect.

All models were fitted by the functions glmer (package lme4) in R (Ver. 4.2.1; R Development Core Team 2022), considering Poisson distribution for all cases. Best models were selected with the Akaike information criterion for small samples (AICc), applying the principle of parsimony (Burham & Anderson 2004).

4.3 Results

4.3.1 Spatio-temporal variation on *D. gravipes* abundance

A total of 610 individuals of *D. gravipes* were captured during all sampling periods, in addition to 199 individuals of other 4 rodent's species: North-American deer mouse (*Peromyscus maniculatus*), San Diego pocket mouse (*Chateodipus fallax*), Western harvest mouse (*Reithrodontomys megalotis*) and little pocket mouse (*Chaetodipus arenarius*; supplementary information 3, Table 8; Figs. 35-38)

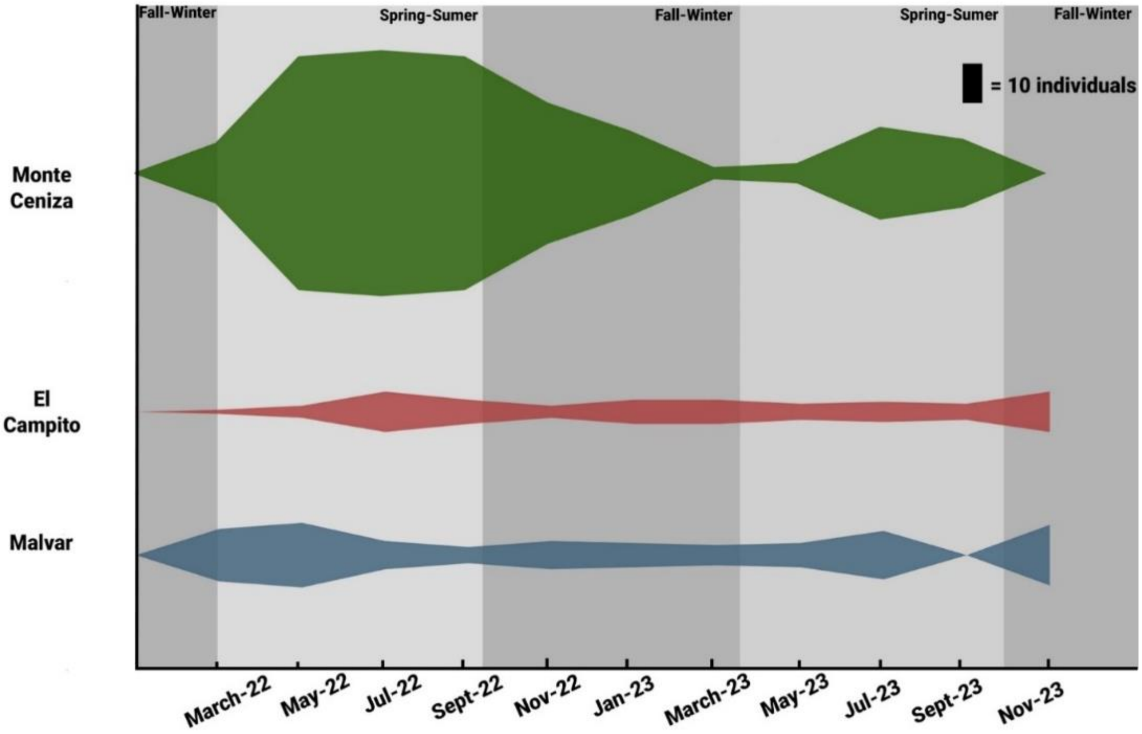

Figure 19. Seasonal and inter-annual abundance of *Dipodomys gravipes* in three study locations, in Baja California, 2021-2023.

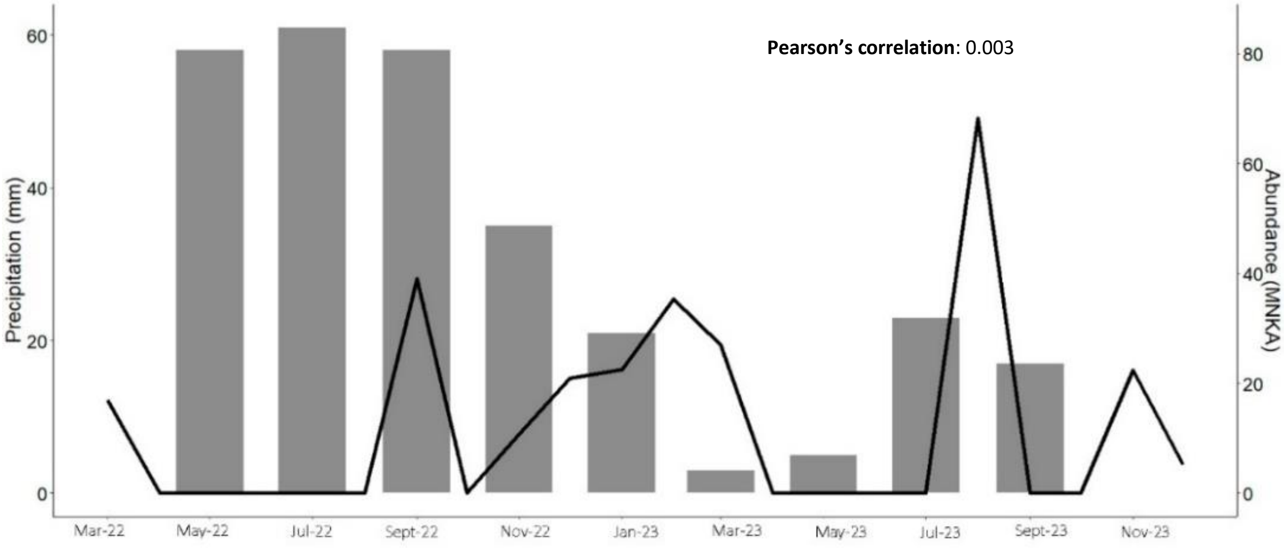

Figure 20. *Dipodomys gravipes* abundance across sampling period and cumulative rainfall in Monte Ceniza, Baja California, 2021-2023. Abundance estimator is minimum known number alive (MNKA).

The abundance of *D. gravipes* ranged from 3 to 61 individuals ($\bar{X}$ = 29.6 ± 6.69 individuals) in Monte Ceniza (Fig. 19), 1 to 15 individuals ($\bar{X}$= 5.7 ± 1.16 individuals) at El Campito and, 4 to 16 individuals ($\bar{X}$ = 8.6 ± 1.19 individuals) in Malvar.

The abundance of *D. gravipes* at all localities increased during the Spring-Summer and decreased during the Fall-Winter (Fig. 19). *Dipodomys gravipes* abundance at Monte Ceniza and rainfall do not exhibit a strong correlation (Pearson's correlation: 0.003) (Fig. 20).

4.3.2 Vegetation cover

Monte Ceniza was dominated by herbs and lack of shrub. Among the perennial herbs present, the Common ice plant (*Mesembryanthemum crystallinum*) was dominant across the study (Fig. 22). Other perennial herbs were also present and these includes the Cheeseweed mallow (*Malva parviflora*) and the Redstem stork's bill (*Erodium cicutarium*). This locality presents most annual plants diversity through the study, although as the rest of the sites were restricted to rainy seasons. Among these plants highlights the Smallseed sandmat (*Eupohrbia polycarcpa*) and the Seaside Calandrina (*Cistante maritima*) by its dominance during the Fall-Winter season. Some other annual were also present at a lower frequency such the Pink Sand verbena (*Abronia umbelata*) and the Postrate Spineflower (*Chorizante procumbens*). Herbaceous vegetation covers do not have a strong correlation to rainfall as both, annual and perennials, exhibits a Pearson correlation index of 0.201 and -0.294, respectively (Fig. 21).

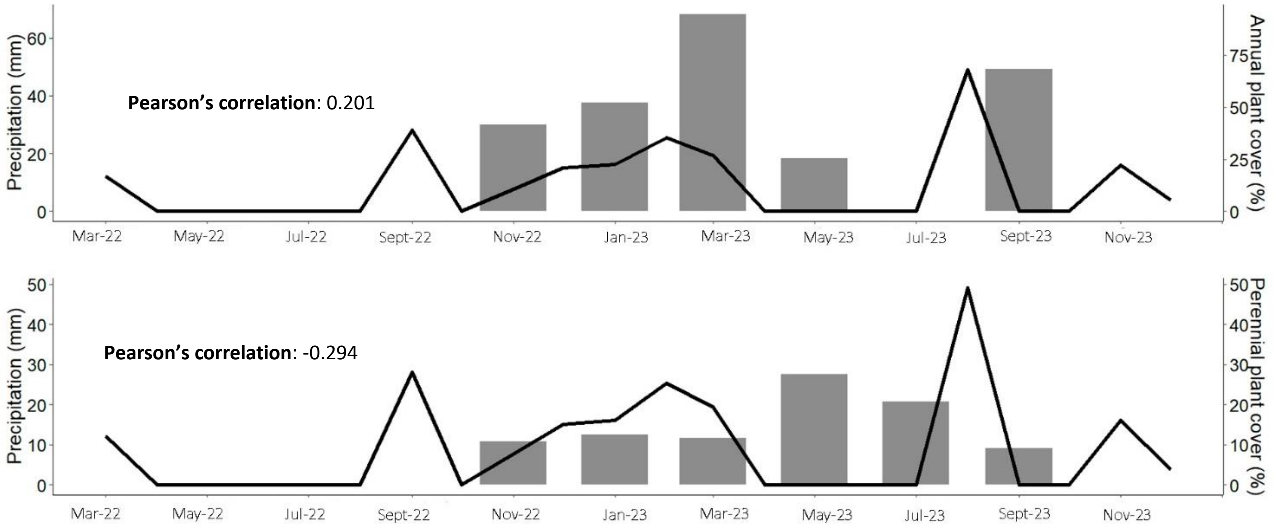

Figure 21. Vegetation cover across sampling periods and cumulative rainfall at Monte Ceniza, Baja California, 2021-2023. A) Cover by annual plants; B) cover by perennial plants. Black lines represents the cumulative rainfall per year.

El Campito was the only locality which exhibited shrubs across the sampling periods. Vegetative species of this life form documented were the Cliff Spurge (*Euphorbia misera*)*,* the Baja Desert-thorn (*Lycium brevipes*) and*,* the Common Saltwort (*Salsola sp*)*.* Perennial herbs was the dominant cover site with *Mesembryanthemum* crystallinum as the dominant species across the study (Fig. 22). However other plants such as the Palmer's Frankenia (*Frankenia palmeri*)*,* were present. Annual plants appeared during the rainy season and the dominant species of these group was *Lepidium sp* (Fig. 22).

The vegetation at El Malvar was dominated by perennial herbs trough the study period and *Mesembryanthemum* crystallinum and was the dominant species at all surveys, with *Erodium cicutarium* and *Malva palviflora* also present (Fig. 22). Annual herbs appeared during the rainy season, particularly plants such as *Eupohrbia polycarpa* and *Lepidium sp* (Fig. 22). The Common Mediterranean grass (*Schismus* barbatus), an annual grass was also present. There were no shrubs in the study plot, but *Lycium sp*. (< 1m of height) shrubs were adjacent to it.

Vegetation cover varied across the study at all localities. Total vegetation at Monte Ceniza varied between 0 and 50.8 %, at El Campito between 0 and 94.2% and at Malvar between 0 and 100%. Dominant species highlights the temporal variation of the vegetation coverage on which is plausible to identify a pattern; vegetation cover increases during the Fall-Winter and decreases during the Spring-Summer season (Fig. 22).

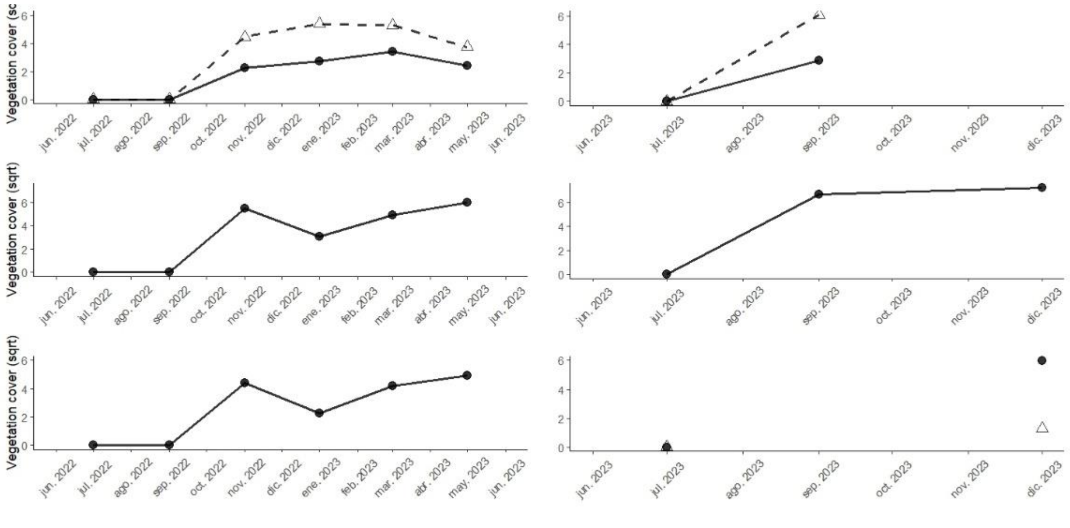

Figure 22. Temporal and spatial variation on vegetation abundances: A) Monte Ceniza; B) El Campito and; C) Malvar. Black lines with black dot represents a perennial herb, the common ice plant (*Mesembryanthemum crystallinum*) and punctuated line with triangle represents the annual plant, Smallseed sandmat (*Euphorbia polycarpa*). Shrubs are not shown as only El Campito presents shrubby vegetation.

Total vegetation coverage was negatively correlated to the abundance of the species (Fig. 23). Into detail, perennial herbs and annual herbs are negative correlated to the abundance of the species across localities with variations on the level of the influence. Perennial herbs at Monte Ceniza, Campito and Malvar exhibits Pearson's index values of -0.7, -0.3 and -0.4 respectively. Similarly, annual herbs and abundance at the same localities presents Pearson's index values of -0.6, -0.2 and -0.1, respectively (See supplementary information 3, Fig. 36).

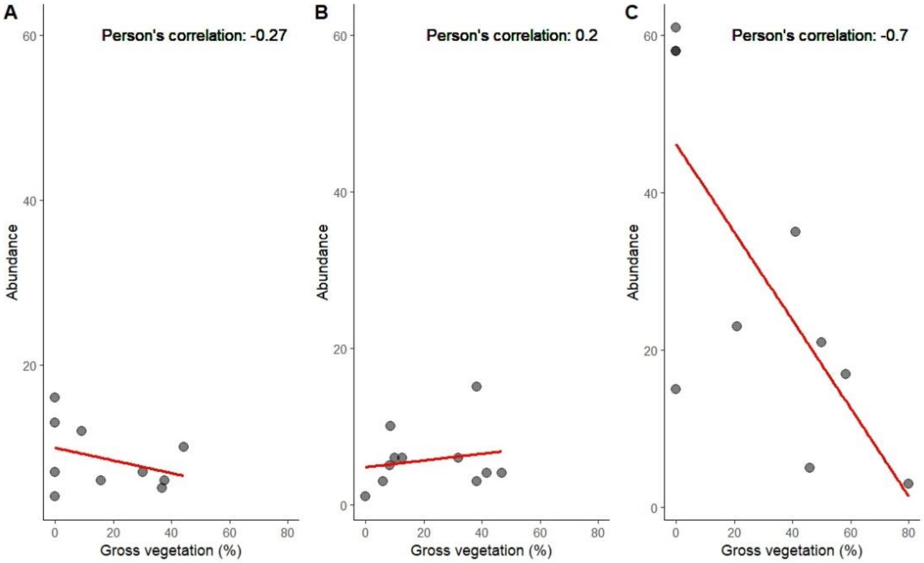

Figure 23. Correlation analysis of total vegetation cover and abundance of *D. gravipes*: A) Malvar; B) El Campito and C) Monte Ceniza.

The most parsimonious model that better explains abundance change includes total cover, perennial herb and annual herbs cover (Table 5). However, top competing models also included photoperiod as important variables (Supplementary information 3, Table 9).

Table 5. Fixed effects of the most parsimonious model for abundance of *D. gravipes*. Estimated and standard errors are provided as well p-values and significance.

	Estimate	Std. Error	Pr(>|z|)
(Intercept)	2.751453	0.474381	0.00000000663 ***
Total cover	0.02534	0.008953	0.00465**
Perennial herbs	-0.04829	0.009621	0.000000518***
Annual herbs	-0.047838	0.009852	0.0000012***

Significance codes: 0 '***' 0.001 '**' 0.01 '*'

4.3.3 Spatio-temporal variation on *Dipodomys gravipes* reproductive status.

Dipodomys gravipes reproductive status vary thorough time and localities without a clear pattern. Active male's percentage seems to vary from locality to locality with no distinguishable temporal pattern (Fig. 25). Similarly, percentage of reproductively active females vary from locality to locality also with no apparent temporal pattern (Fig. 25).

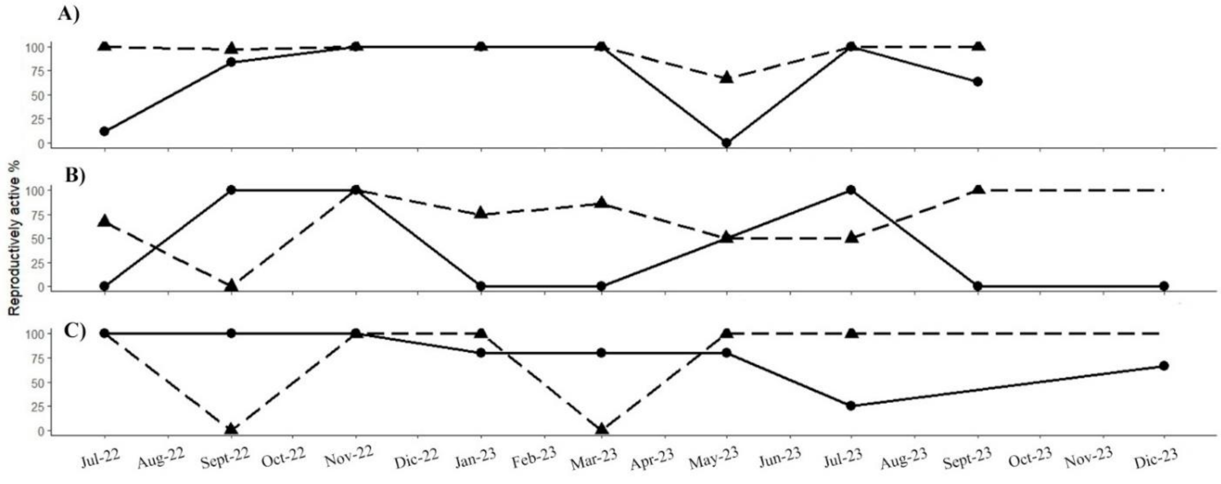

Figure 24. Spatio-temporal variation of reproductive status of both males and females of *D. gravipes* at three localities: A) is Monte Ceniza, B) El Campito and C) Malvar in Baja California, 2022-2023. Black circles with solid black line represents active males. Black triangles with dashed black line represents actives females.

The correlation of total vegetation cover and perennial and annual herbs on the reproductive status of females vary depending on the locality. In general terms, total vegetation cover and percentage of reproductive status in females is only positively correlated at El Campito whilst in the other localities is not (Fig. 25). Annual vegetation cover do not show a strong correlation with reproductive status of females (see supplementary information 3, Figs. 37, 38). Perennial vegetation cover exhibits a positive correlation with female reproductive status for Monte Ceniza and negative for El Campito (see supplementary information 3, Figs. 37, 38).

For males, total vegetation cover is not correlated with the percentage of descended testicles nor the cover of perennial herbs (Fig. 29). Annual vegetation cover does not show strong correlation with the percentage of descended testicles but for El Campito (Fig. 29).Linear mixed model for females' reproductive status, show that the only-intercept model is the best fit and total vegetation, annual nor perennial cover explain the variation of the response variable (see supplementary information 3, table 11).

However, total and annual vegetation are included in the top 3 competing models (see supplementary information 3, table 11). Likewise, for males the most parsimonious model is the only-intercept model, but top 3 competing model includes annual and perennial herb cover (see supplementary information 3, table 10).

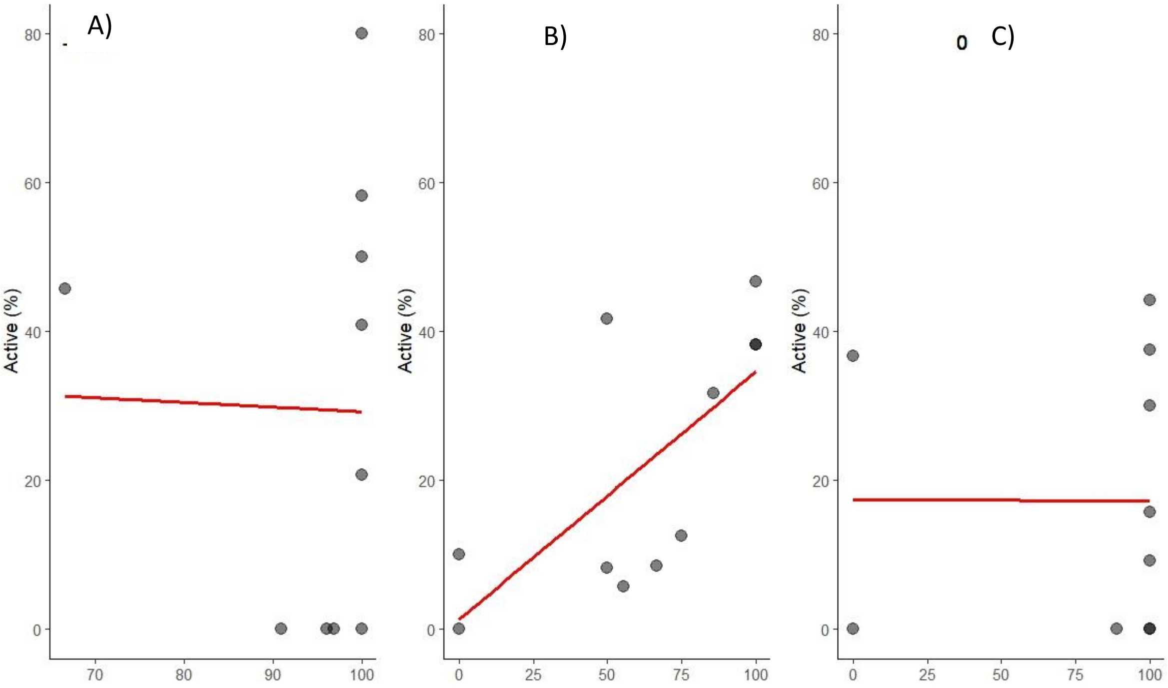

Figure 25. Female reproductive status and total vegetation cover correlation at each locality: A) Monte Ceniza; B) El Campito and C) Malvar. All coefficients are Pearson's correlation index.

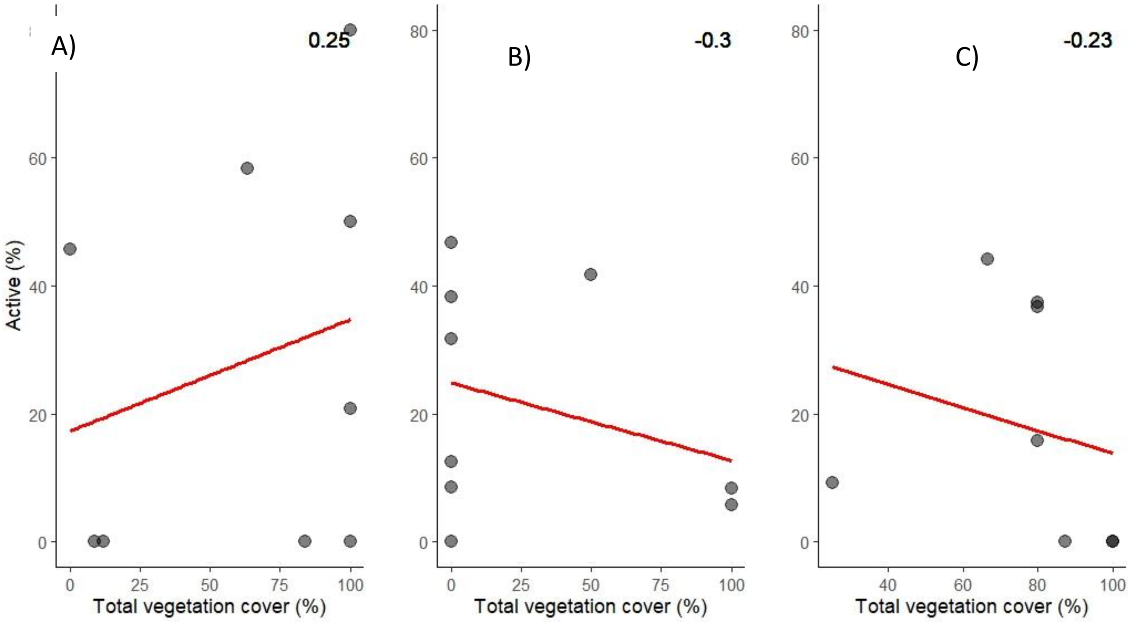

Figure 26. Male reproductive status and correlation with total vegetation cover at each locality: A) Monte Ceniza; B) El Campito and C) Malvar. All coefficients are Pearson's correlation index

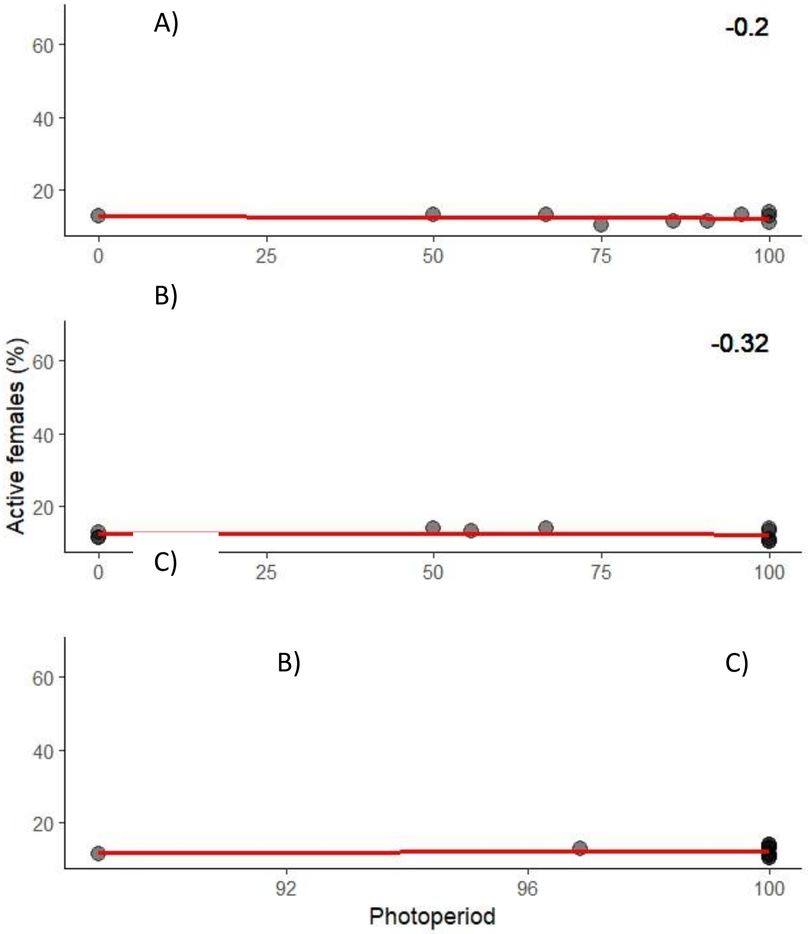

Figure 27. Female reproductive status and photoperiod correlation at each locality: A) Monte Ceniza; B) El Campito and C) Malvar. All coefficients are Pearson's correlation index.

Annual and perennial herbs cover are the variables most included in the most parsimonious model for each of reproductive status condition (Table 6; Annex t). Total vegetation cover is also included in the most parsimonious model but photoperiod (Table 6). Nonetheless, photoperiod appear in the top 3 models for explaining each of the response variables (Annex t).

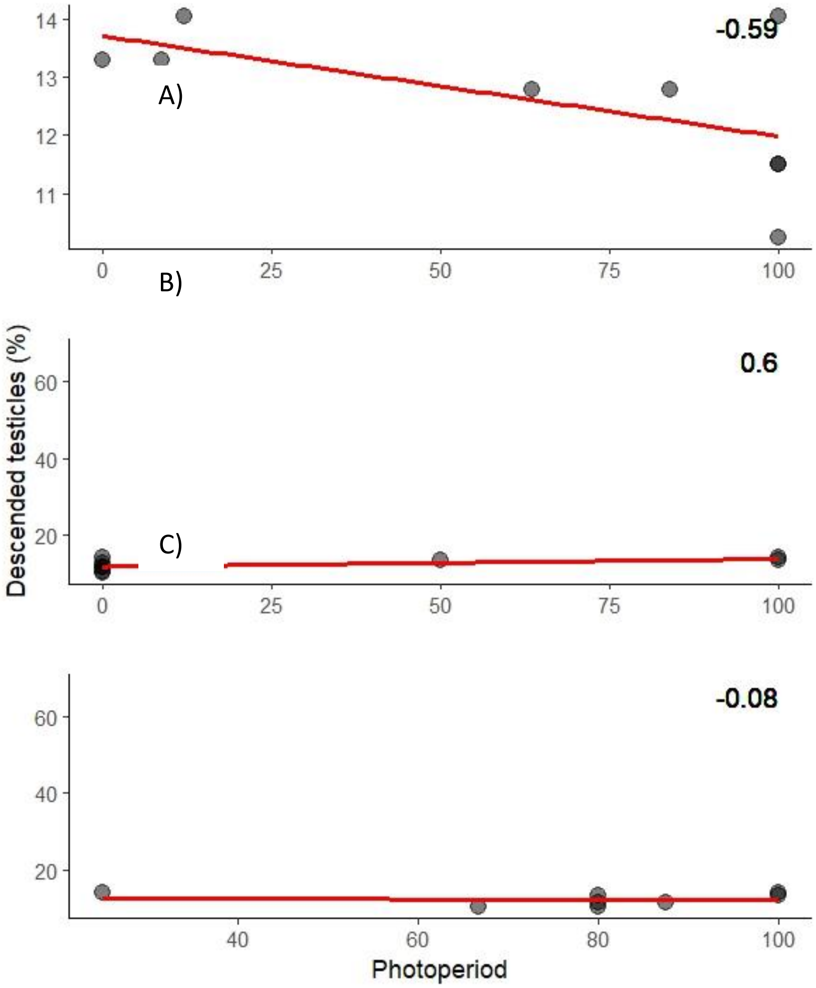

Figure 28. Male reproductive status and photoperiod correlation at each locality: A) Monte Ceniza; B) El Campito and C) Malvar. All coefficients are Pearson's correlation index.

4.4 Discussion

The abundance of *D. gravipes* vary across localities on which highlights Monte Ceniza with higher mean abundances (29.6 ± 6.69 individuals) in comparison to El Campito and Malvar ($\bar{X}$= 5.7 ± 1.16 individuals and 8.6 ± 1.19 individuals). The study hypothesized that greater abundances is expected to be found at flatter sites, with vegetation cover of no more than 10% and with low and scarce shrubs. When it comes about slopes inclination, all study plots exhibit an inclination below 10 °. Indeed, *D. gravipes* occupy flatter sites in comparison to its sympatric *D. simulans* which occupy sites with higher slope inclination (Price et al., 1991). Thus, this study endorses the importance of slope inclination for the species occupancy and underscores the range of suitable slope inclination for the species provided by previous works indicating a range between 0.5 to 9.7° (Andrade et al., 2023). Nonetheless the expectation regarding the role of slope inclination on its abundance are not conclusive due the similarities in the study plot’s inclinations. The response of abundance and other demographic parameters to a wide range of slope inclinations remains to be investigated.

Has been noted that *D. gravipes* occupy sites sparsely vegetated (Best & Lackey, 1985) below 10% cover of herbs and avoids shrubs taller than 0.5 m (Andrade et al., 2023). Habitat description for other species of kangaroo rats underscore a preference for open habitat with low vegetation cover, mainly by grasses and herbs and few scattered shrubs (Jones & Genoways, 1975; Bleich, 1977; Price & Heinz, 1984; Carter et al., 1985; Kelt, 1988; Best et al., 1989; Baumgardner, 1991; Intress & Best, 1990; Best, 1992). The study findings not only corroborate the latter for *D. gravipes* but complement it revealing a pattern on which the specie’s abundance vary accordingly with vegetation cover change. The study reveals that there is a negative correlation between vegetation cover and *D. gravipes* abundance (Figs. 23, 24). Furthermore, highlights a temporal pattern on which *D. gravipes* abundance decreases when vegetation increases during fall-winter season and increases total during spring-summer when vegetation cover drops (Figs. 19, 22). This temporal pattern has also been widely documented on other kangaroo rats (Reynolds, 1950; M'Closkey 1972; McClenaghan, 1983, 1984). This is an important pattern since remained unknown for *D. gravipes* until now.

Monte Ceniza, the locality with the higher mean abundance it is also the locality with the less vegetation cover at all surveys comparing with the other localities. This study corroborates that open ground or lower vegetation cover ultimately leads to an increase of *D. gravipes* abundance. First let’s consider that bipedal rodents such as kangaroo rats are able to forage in the open ground since can detect and avoid predator more effectively than quadrupled rodents (Eisenberg, 1963). Even though an increase of vegetation cover of herbs and/or grasses may increase predation risk (Reynolds, 1950). Similarly, it has been suggested agility of bipedal rodents is reduced under bushes (Rosenzweig, 1973) and an increase of vegetation cover may increase risk of predation (Reynolds, 1950). Thus, vegetation cover increase explains the temporal pattern in abundance reduction during periods with high vegetation cover and spatial differences on abundances between Monte Ceniza and the rest of the localities. Moreover, Heteromyd species activity varies seasonally, and during the fall-winter, they occupy nests and reduce metabolic expenditure (Kenagy, 1973). Even though this pattern is less apparent in larger heteromyds (> 56 g) (Kenagy, 1973).

Rodent abundance increase following precipitation events often occurs (Beatley, 1969; Chew & Butterworth, 1964; Brown, 1973; Whitford, 1976; Meserve et al., 1995; Hafner, 1977; Jaksic et al., 1997; Lima et al., 1999; Ernest et al., 2000; Letnic et al., 2005 Orland & Kelt, 2007). This also occur in desert communities including kangaroo rat species populations (Thibault et al., 2010). However, the increase of rodent abundance after precipitation events doesn't always occur (Reynolds, 1958; Ernest et al., 2000; Meserve et al., 2003; Brady & Slade, 2004; Gillespie et al., 2008) and in some extreme cases heavy rainfalls can cause populations to decline (Reynolds, 1958; Ernest et al., 2000; Meserve et al., 2003; Brady & Slade, 2004; Gillespie et al., 2008;). This is study suggest a time-lag response to the response of *D. gravipes'* abundance increase in response to the rise in precipitation. This type of response among kangaroo rats' abundance as a response to rainfall has been documented in previous studies (Kelt et al., 2009).

Heteromyd species activity varies seasonally, and during the fall-winter, they occupy nests and reduce metabolic expenditure (Kenagy, 1973). Even though this pattern is less apparent in larger heteromyds (> 56 g) (Kenagy, 1973) it is a plausible explanation for the decrease in *D. gravipes* abundance in the fall-winter. Breeding behavior is also necessary to consider regarding the seasonality of rodents' temporal abundance variations. Previous research suggests that natality peaks of *D. gravipes* occur during winter and spring with inter-annual births (Best & Lackey, 1985).

The study results provide an insight into the dynamics between the habitat and breeding strategy of the species. To start, the temporal variation of active status in males follows a similar pattern between annual vegetation cover, as it is one of the strongest predictors for reproductive active status for both females and males of the species. The increase in the cover of this type of vegetation increases the probability of active individuals. *Dipodomys* genus is considered to have a primarily granivorous diet; however, it is also well-documented that green vegetation is also part of its diet. In fact, water, nutrients, and hormones of green vegetation stimulate reproduction in this taxon (Chew & Butterworth, 1964; McClenaghan, 1987; Reichman & Van De Graaf, 1975; Soholt, 1977; Van De Graaf & Balda, 1973). Therefore, *D. gravipe's* breeding season is triggered by increased vegetation cover, particularly annual herbs that might provide estrogenic substances, as documented for other kangaroo rats (Beatley, 1969; Bradley & Mauer, 1971). Photoperiod is another climatic trait that is important for breeding regulation. Reproductive behavior is restricted to long-day periods in most non-tropical small rodents (Borniger & Nelson, 2017). Our data show this relationship is more evident for males than for males (Figures 20, 21). Our GLMM analysis does not include photoperiod in the most parsimonious models for each response variable but in the top 3 models for each (Table 7; Annex f). Then, the timing of reproductive activity is triggered by a complex of factors such as rainfall, temperature, and secondary vegetative compounds of green vegetation. The latter suggests an ecological coupling between food availability, breeding patterns, and species abundance.

So far, the study results have suggested an intra-annual temporal variation of *D. gravipes* abundances influenced by vegetation cover changes, which at the time responds to precipitation regimes. There is a plethora of research regarding long-term cyclic fluctuations of rodent populations at annual (Elton & Nicholson, 1942; Korpimäki & Krebs, 1996; Krebs & Myers, 1974; Norrdahl, 1995) on which inter-annual variations are highlighted. It is clear that changes in precipitation regimes indirectly influence the rodent's abundance. However, we advocate to continue the study of seasonal variation of demographic parameters for long-term to be able to confirm the seasonal variation and to begin to detect year-to-year and cyclic variations on these parameters.

Lastly, agriculturally driven land change is considered to have an influence on species occupancy and distribution (Andrade et al., 2023). This study proves that abandoned cropland meets the minimum habitat requirements for *D. gravipes* and sustains viable species populations. At the same time, highlights that Agriculture expansion and latter crop abandonment is important in increasing sparse, short herbaceous and lack of shrub habitat, which is important on increasing suitable habitat for *D. gravipes*. Despite differences across localities, patterns in demographic parameters are highlighted in the study and accentuate the importance of this transformed landscape. Therefore, government and non-profit conservation organizations should address the conservation value of abandoned cropland.

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Chapter 5. General discussion

Contemporary coastal landscapes at the southern end of California Floristic Providence are the result of decades of human activities, and consequently none pristine habitat is left. Yet, this southern portion still is a stronghold for the San Quintín Kangaroo Rat (*Dipodomys gravipes* Huey, 1925) as several localities had been recently rediscovered within and beyond the traditionally accepted distribution range as this study proves. Most of the localities, whether new or historical, are within abandoned farmland. Already in 1985 Troy Best, a recognized mammalogist, stressed the influence of agricultural expansion on the presence and abundance of *D. gravipes* as well the risk of extirpation of localities and ultimately the extinction of the species. Despite these early warning numerous agricultural practices continued to grow at an alarming rate and consequently the species' populations declined. Considering the lack of further captures in 1990s (Mellink, 1996), the species was declared potentially extinct in the wild (DOF, 1994). Later, Tremor et al., (2019) rediscovered the species within an agricultural-dominated landscape. Elapsed time between its last record before its rediscovery, lead to a substantial knowledge gaps on the species biology and ecology. It is not known how the species survive after a dramatic population decline due to agriculture expansion. In the vein of the main chapter of the thesis we first elaborate on the species correct identification and later on the influence of agricultural-dominated landscape on *D. gravipes* occupancy and distribution. Lastly, we address the species ecology to further understand the species-habitat relationship.

Accurate species identification is the cornerstone of biological research, serving as the foundational step across various fields (Galan et al., 2012). Without precise identification, drawing conclusions regarding the ecology and conservation of any species becomes unattainable, posing a fundamental pre-requisite for research and conservation efforts (Kürzel et al., 2022; Galan et al. 2012). Rodents, with the diverse shapes and forms, present a unique challenge in identification, especially given the striking similarities in shape and size among species. Traditional methods, such as visual identification and the measurements of external and internal traits, have long been employed for species identification. Yet, rare, cryptic and endangered species often necessitates supplementary data for validation. While external body measurements by experts can result in accurate identification, advanced techniques such as Next-Generation sequencing, including barcoding (short sequences mitochondrial DNA), have increasingly prevalent for species identification. These modern approaches offer enhanced precision on the confirmation of species and contribute to enlighten genetic variation across the species' ranges.

In chapter 2 we provide a formal verification of the rediscovery of the species based on multiple and inclusive datasets: cranial morphometric and mitochondrial DNA analysis. Moreover, measures for the robustness and congruence of the analysis were provided. The results provided a sound and robust confirmation of the presence of the species in the wild. Considering the species is categorized as potentially extinct in the wild by the Mexican government (DOF, 1994), the sole confirmation of the specie's rediscovery is a cornerstone for its conservation. Lastly, it provides certainty to the following research, particularly corresponding to chapters 3 and 4 of this thesis.

Dipodomys gravipes extended its range north and southward surpassing two historically active watercourses. Considering the coarse-scale scenopoetic variables (*sensu* Hutchinson, 1957), the species now occupy climatically similar sites at the northern and southern expanded ranges (Fig. 12; Chapter 3). Therefore, we can argue that the species range was constrained by non-climatic or scenopoetic variables and was able to reach and occupy localities beyond both ends once a natural barrier was eliminated: the arroyos at both ends.

The spatial distribution of suitable environmental (or climatic) conditions for the species are important to consider to further discuss. Typically, temperature and moisture are the broad-scale limiting factors for the species' distributions. In this regard is crucial to understand how these climatic characteristics are distributed within *D. gravipe*s current distribution. The species' range has been described as a transitional zone of two ecoclimatically distinct areas: the Mediterranean zone and the desert zone (Nelson, 1922; Brown & Lowe, 1980; Mellink, 1996). Climatically, the species' range is classified as dry with three distinct subtypes; dry-temperate for the northern localities, very dry-temperate for center whilst the southern end is classified as very dry-warm (Garcia, 2004). The range expansion of both ends, implies that the species moved to climatically similar areas; from the center of the distribution of the species to the extremes the temperatures and rainfall regimes gradually change and two climatic subtypes appears.

Nonetheless, *D. gravipes* has a wide array of ecological traits that enables the species to cope with the novel environment on the expanded range. To start is a homeotherm capable of regulate his temperature. Moreover, behavior adaptations enable it to avoid high temperatures (burrower and nocturnal) (See introduction for details on this). The latter upholds the niche conservatism hypothesis which in general terms state that the species and clades tend to retain their niches and related ecological traits over time (Wiens et al., 2011). Then, all ecological adaptations of the species allowed the species to occupy sites beyond traditional boundaries once can reach these. Moreover, these sites meet the habitat requirements of the species as seen in the chapters 3 and 4. The physiological stress imposed by "novel" environment and the abundance-centered hypothesis are being put into questioning. How far south and north can the species eventually reach? This question is as old as ecology as a science itself. From a physiological perspective, should reach a point where the species experience physiological stress. An ecological experiment that tests the physiological tolerance of the species is needed to determine it.

Ecological interactions such as competition, predation, and mutualism can significantly influence the species' ability to persist and expand in these new environments. For instance, competition with other rodent species for food and burrowing sites might limit the southern and northern boundaries of *D. gravipes*. Similarly, predation pressure, which could vary across its range, may also play a role in determining its abundance and distribution. Mutualistic relationships, such as those with specific plants providing cover or food resources, could facilitate its range expansion by creating favorable microhabitats.

These interactions may either support or challenge the abundance-centered hypothesis by demonstrating that factors beyond physiological tolerance and habitat suitability—such as biotic interactions—can also constrain or enable range expansion. Therefore, while physiological stress is a critical factor, understanding the role of ecological interactions is equally essential to predict how far south or north the species might eventually reach. An ecological experiment testing not only physiological tolerance but also the effects of competition, predation, and mutualism across its range would provide a more comprehensive understanding of the factors limiting or promoting the range expansion of *D. gravipes*.

Other factor at different spatial scale should be taking into account; source-sink dynamics and the resource-interaction component at a finer scale. Moreover, negative effects of less suitable habitat at the range limits can be exacerbated by assortment of interspecific interactions, including predation, competition, mutualism, and parasitism and diseases. This interactions should be examined within each location at a finer scales.

The chapter 3, suggests that the species is currently subject to metapopulation dynamics (*sensu* Hanksi & Gilpin, 1991) given observed colonization and recolonization of habitat patches in ecological time frame. Considering the theory, range boundaries can be formed through metapopulation dynamics of colonization and extinction (Holt et al., 2005). In the source-sink dynamics, typical of a metapopulation, a substantial proportion of the total population can be found residing in the so-called marginal habitat that cannot provide the resources to maintain a species' life history (Pulliam 1988). Interpsersion of source populations in a patchy landscape may sustain species presence in otherwise neighboring habitat (Pulliam & Danielson, 1991). Then, abandoned farmland enhanced the colonization of new sites beyond the traditional boundaries of the former specie's distribution and thus, the populations at the range edge of both ends act as peripheral sinks that 'absorbs' individuals from central or nearby source habitats as observed for other species (Guo et al., 2005; Holt et al., 2005). Thus, climatic suitability at coarse-scale should not be taken as the sole influence for the species distribution and range edges but rather consider the source-sink dynamics of the populations of *D. gravipes* particularly at the range edges.

If climatic suitability decreases from center to the distributional edges, demographic parameters such as abundance, survival and breeding success should also decreases. Traditional population ecology thinking has upheld this hypothesis for several decades. However, contrary to the dominant paradigm (abundance centered model), peripheral populations, in some cases, exhibit similar demographic parameters or higher of those of the center such as survival and breeding success (Kanda et al., 2009). As consequence, a substantial proportion of the total population may be found residing in marginal habitat. Therefore, it should be highlighted that source-sink dynamics should be taken into account for describing distributional edges of the species distribution. Our data, particularly the outlined in the chapter 4, constitutes empirical evidence of this phenomena. Malvar, is a peripheral population and sustain a population of *D. gravipes* and its temporal variation on its abundance and reproductive status are similar of those of Mone Ceniza, a center population. However, the outlined data is not conclusive since year-to-year variation must be considered. Rather the results incentives a long-term monitoring on this matter.

The chapter 4 of the thesis highlights that vegetation attributes are a meaningful driver of seasonal variation of abundance and reproductive status. As described for other species of kangaroo rats an increase of vegetation cover implies a decrease on *D. gravipes* abundance. This is part of a seasonal pattern that of course also vary from year to year. However, the description of this pattern on *D. gravipes* is crucial as it had not been provided.

When it comes to successional stages on abandoned cropland it is possible that occupy sites can eventually reach unsuitable vegetation cover for the species. Then a sound management strategy, based on the conclusion of the chapter 3 and 4, for *D. gravipes* colonies is vegetation cover reduction. Shrub cover also should be avoided within *D. gravipes* colonies. Therefore, shrub control should be considered as an important component of the strategy of vegetation removal. Similar shrub control actions have been experimentally tested with promissing results for *D. stephensi* (Price et al., 1994). Of course, it is important to consider a sound experimental design based on which the vegetation removal success can be quantitatively examined.

The long-term viability of *D. gravipes* as species, must be managed as non-isolated part of a subdivided population interconnected via gene flow covering a small geographic area within patchy habitat. A more comprehensive analysis on the metapopulation dynamics should be carried out to determine which population's functions as sources or sinks as well the degree of connectivity between these. Moreover, a comprehensive genomic distribution analysis as well the connectivity between sites based on nDNA data is of critical importance.

The majority of the confirmed sites are not protected by any conservation strategy whilst only a minority of these lies on areas under a conservation scheme. The un-protected localities are within abandoned cropland and are, presumably, privatelly-owned. In consideration of this, a wide-range management and conservation plan for the San Quintin Kangaroo Rat, necessitates a comprehensive approach that considers the various land tenure use across its range.

It is essential to consider the various approaches taken in the conservation and management within each protected area. The Federal Reserve, APFF's cornerstone is the engagement of the private owners and ejidos in the conservation and management of natural resources. Therefore, in order to design management and conservation strategies for the San Quintin Kangaroo Rat, landowners should be involved in the decision-making process. Similarly, the privately-owned reserves are allowed to create a specific management plan. Moreover, the owner of this private natural reserves are managed by non-profit conservation organizations. Conservation and management plans of these private reserves should account strategies and actions oriented towards the conservation of the species within its reserves. Therefore, it would be plausible and highly likely to include these private reserves on a broad spatial scale conservations strategy.

The challenges come with managing the vast majority of the species' localities that lies under privately-owned properties with the potential of latter cultivation. Most logic answer is to prevent the agricultural development. From a legal perspective it is plausible due to according with the specie's status on the Mexican Federal environmental regulation, damage a single individual is sanctioned with one to nine years or an economic equivalent of 300 to 3000 labor days with potential additional sanction of three additional year if the crime is performed within a natural reserve (Código Penal Federal; CPF). Then, technically all individuals of the species within privately-owned abandoned cropland are protected by the law. However, when it comes to the application of the law this sanctions rarely occurs. Under this context is absolutely necessary to work with local producer.

Then a second group of tasks is collaborate with local producers towards a farming scheme that meet both, the producers objectives and conservationist as well. However, as a complex socio-economic phenomena the latter will be time consuming with potential unsuccessful attempts. It is likely that producers are no willing nor open to change is ways of produce.

Chapter 6. General conclusions

The chapter 2 of this thesis uncover a simple, yet important question regards *Didipomys gravipes:* Was certainly rediscovered? Morphometic and molecular data proves that the species is certainly not extinct. Considering the national and international importance of the species, the sole confirmation of its rediscovery provides optimism for the species conservation.

Throughout the chapter 3, the thesis highlights that *D. gravipes* is not only not extinct but there are 19 confirmed localities of the species. Of the latter, 2 at the north and 4 at the south constitutes a range expansion of ~10 km and ~50 km, respectively.

With all data outlined in chapter 3 and 4, is parsimonious to state that abandoned cropland at early successional stages meet the habitat requirements for the species. Moreover, current species distribution suggests the species is subject to metapopulation dynamics largely due to anthropogenic activities. Then, future research and conservation efforts must be framed on the context of agriculture development, as well under metapopulation approach.

Dipodomys gravipe's abundance and reproductive status, follows general seasonal pattern of other kangaroo rats. This constitutes a valuable information of the specie's life history as uncover an important knowledge gap after ~32 after its last record.

Vegetation cover is a meaningful trait influencing abundance; an increase in total vegetation cover follows a population decline and vice versa. A seasonal variation on these relationships has been covered in the chapter 4 on this thesis. It is necessary to document a year-to year variation on the latter. However, results so far allow to suggest a sound management for *D. gravipes* habitat: Vegetation cover control to increase abundances. This type of management has been already proven to be successful in other kangaroo rats which show the same relationship between vegetation cover and abundance (Shier, unpublished). Robust experimental design based on which the vegetation removal success can be quantitatively examined is also strongly suggested.

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Supplementary information

Supplementary 1

Figure 29. PCR amplification products from 7 individuals using primers primers L8618 and H9323 (Riddle, 1995). The bands correspond to Cox3 (mtDNA) fragment of with an expected product size of 680 bp

Supplementary 2

Table 6. Physical characteristics of the sites.

Locality	Latitude	Longitude	Captured	Condition	History	Cover	Slope	Adjacent	Herbs	Shrubs >0.5m	Soil	Slope	Rugg	Elev
Jaramillo	30.9195	-116.1105	1	Fallow	Historic	<10	<10%	Crops	Yes	No	Xerosol	2.52	1.63	72
San Ramón	30.7015	-116.0272	3	Fallow	Historic	<10	<10%	Crops-Urban	Yes	No	Xerosol	0.78	0.38	7
Agua Chiquita	30.5399	-115.8571	17	Fallow	Historic	<10	<10%	Shrubs	Yes	No	Planosol	5.25	2.38	60
Punta Azufre	30.411	-115.9296	3	Never farmed	Historic	<10	<10%	Marsh	Yes	No	Solonchak	1.44	1.25	6
El Socorro	30.3365	-115.8271	4	Fallow	Historic	<10	<10%	Dune	Yes	No	Xerosol	3.44	1.75	9
San Jacinto	31.0446	-116.2175	1	Fallow	New	<10	<10%	Crops	Yes	No	Fluvisol	6.17	2.50	28
Mesa Agua Chiquita	30.5522	-115.8814	2	Fallow	New	<10	<10%	Crops	Yes	No	Xerosol	8.46	2.63	103

Monte Ceniza	30.4362	-115.9731	6	Fallow	New	<10	<10%	Sage	Yes	No	Regosol	4.96	2.13	22
Valle Tranquilo RN	30.1825	-115.7564	2	Fallow	New	<10	<10%	Sage	Yes	No	Regosol	3.50	2.50	96
El Consuelo	30.1517	-115.7968	2	Fallow	New	<10	<10%	Dune	Yes	No	Xerosol	2.47	1.00	17
Mesa militares	30.0857	-115.7387	7	Fallow	New	<10	<10%	Sage	Yes	No	Planosol	0.70	0.50	251
Parcela 91	30.1724	-115.7558	1	Never farmed	New	<10	<10%	Sage	Yes	Few	Regosol	6.18	2.50	120
Mesa Sur	30.0556	-115.7095	2	Fallow	New	<10	<10%	Crops	Yes	No	Fluvisol	4.86	1.75	49
Colonet	31.0294	-116.285	5	Fallow	North	<10	<10%	Crops	Yes	No	Planosol	2.24	2.75	82
Arroyo San Telmo	31.0446	-116.2175	3	Fallow	North	<10	<10%	Crops	Yes	No	Fluvisol	6.17	2.50	28
San Vicentito	29.9	-115.561	7	Fallow	South	<10	<10%	Sage	Yes	No	Regosol	8.09	3.13	147

Las Pintas	29.8975	-115.4078	4	Fallow	South	<10	<10%	Sage	Yes	Few	Xerosol	0.78	2.25	234
Malbar	29.822	-115.4687	15	Fallow	South	<10	<10%	Shrubs	Yes	Few	Xerosol	4.21	1.63	153
San Carlos	29.6214	-115.4976	3	Never farmed	South	<10	<10%	Shrubs	Yes	No	Xerosol	7.38	3.00	21
Arroyo San Telmo (a)	31.0151	-116.237	0	Fallow	Potential	<10	<10%	Crops	Yes	No	Fluvisol	5.15	2.13	24
San Telmo	30.944	-116.0185	0	Fallow	Potential	<10	<10%	Crops	Yes	No	Fluvisol	4.54	1.88	128
Jaramillo north	30.9323	-116.0994	0	Fallow	Potential	<10	<10%	Crops	Yes	No	Xerosol	9.71	1.88	128
Jaramillo east	30.9195	-116.1105	0	Fallow	Potential	<10	<10%	Crops	Yes	No	Xerosol	2.52	1.63	72
San Jacinto Sw	30.8601	-116.1429	0	Fallow	Potential	<10	<10%	Crops	Yes	No	Xerosol	1.11	1.50	10
Agua Amarga	30.5752	-115.8307	0	Fallow	Potential	>10	<10%	Shrubs	Few	No	Regosol	3.51	1.88	108

Desalination plant	30.4958	-116.0379	0	Fallow	Potential	<10	<10%	Sage	Yes	No	Solonchak	6.91	2.63	67
San Quintín S.R.	30.4695	-116.0346	0	Never farmed	Potential	>10	<10%	Sage	Few	Yes	Solonchak	1.11	2.00	13
Punta Mazo	30.4362	-116.0276	0	Never farmed	Potential	>10	<10%	Dune	Yes	No	Solonchak	3.51	1.88	14
Punta Mazo dunes	30.4219	-116.0127	0	Never farmed	Potential	>10	<10%	Dune	Yes	No	Solonchak	2.24	1.88	14
San Simón	30.4591	-115.9099	0	Never farmed	Potential	>10	<10%	Shrubs	No	Yes	Xerosol	4.08	2.13	14
Punta Azufre south	30.4135	-115.9313	0	Never farmed	Potential	<10	<10%	Marsh	Yes	No	Solonchak	5.00	2.00	10
Socorrito	30.317	-115.8242	0	Never farmed	Potential	<10	<10%	Marsh	Yes	No	Xerosol	2.47	2.00	11
Arroyo hondo	30.222	-115.7854	0	Never farmed	Potential	>10	<10%	Shrubs	No	Yes	Xerosol	6.94	3.00	47

Onion fields	30.2183	-115.7728	0	Fallow	Potential	<10	<10%	Crops	Yes	No	Planosol	3.51	4.63	98
Valle Tranquilo (out)	30.1933	-115.7848	0	Fallow	Historic	<10	<10%	Shrubs	Yes	No	Xerosol	1.98	1.75	43
Valle Tranquilo inland	30.1809	-115.7413	0	Never farmed	Potential	<10	<10%	Shrubs	Yes	No	Regosol	2.45	2.25	120
Rancho Gonzalez	30.1374	-115.6303	0	Fallow	Potential	<10	<10%	Crops	Yes	No	Regosol	9.11	5.13	121
Arroyo El Rosario	30.1259	-115.6175	0	Fallow	Potential	>10	<10%	Shrubs	No	Yes	Fluvisol	0.50	0.50	73
Rosario dump	30.0917	-115.6572	0	Urban	Potential	<10	<10%	Urban	No	No	Fluvisol	4.55	2.88	92
Rosario south	30.0755	-115.6331	0	Never farmed	Historic	<10	<10%	Shrubs	No	No	Xerosol	4.21	1.13	158
Panteón inglés	30.4259	-115.9356	0	Fallow	Potential	<10	<10%	Marsh	Yes	No	Xerosol	0.50	0.50	7
Rosario riverbed	30.0957	-115.6653	0	Fallow	Historic	>10	<10%	Shrubs	No	Yes	Fluvisol	4.55	2.88	92

Supplementary 3

Table 7. Suvey dates at each locality

Survey	Malvar	El Campito	Monte Ceniza
1	2-3 March 2022	03/03/2022 to 03/04/2022	03/11/2022 to 03/12/2022
2	4-5 may 2022	05/06/2022 to 05/07/2022	05/08/2022 to 05/09/2022
3	08/06/2022 to 08/10/2022		
4	08/29/2022 to 08/30/2022	09/01/2022 to 09/02/2022	09/03/2022 to 09/04/2022
5	10/20/2022 to 10/21/2022	10/22/2022 to 10/23/2022	10/28/2022 to 1029/2022
6	01/25/2023 to 01/26/2023	01/27/2023 to 01/28/2023	01/29/2023 to 01/30/2023
7	03/23/2023 to 03/24/2023	03/25/2023 to 03/26/2023	03/21/2023 to 03/22/2023
8	05/20/2023 to 05/21/2023	05/22/2023 to 05/23/2023	05/28/2023 to 05/29/2023
9	07/20/2023 to 07/21/2023	07/22/2023 to 07/23/2023	07/18/2023 to 07/19/2023
10	Not done	09/18/2023 to 09/19/2023	09/20/2023 to 09/21/2023
11	12/07/2023 to 12/08/2023	12/09/2023 to 12/10/2023	Not done

Table 8. Abundance of *D. gravipes* and total counts of rodents species at two season and three sites at Baja California, Mexico.

Species	Total	Site			Season	
		El Campito	Malvar	Monte Ceniza	Spring-Summer	Fall-Winter
Dipodomys gravipes	610	93	105	412	305	305
Peromyscus maniculatus	152	96	55	1	61	91
Chaetodipus fallax	44	17	7	20	22	25
Reithrodontomys megalotis	2	0	2	0	0	2
Chaetodipus arenarius	1	0	1	0	0	1

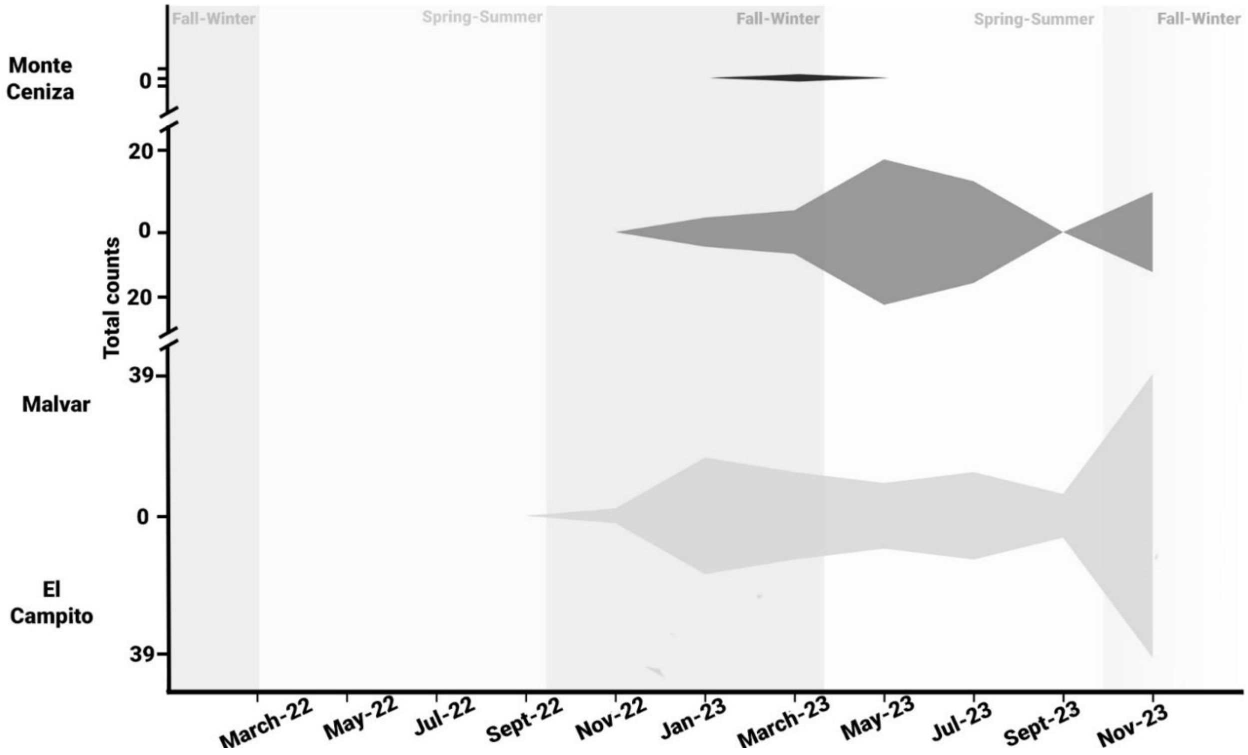

Figure 30. Seasonal and inter-annual abundance of *Peromyscus maniculatus* in three study locations, in Baja California

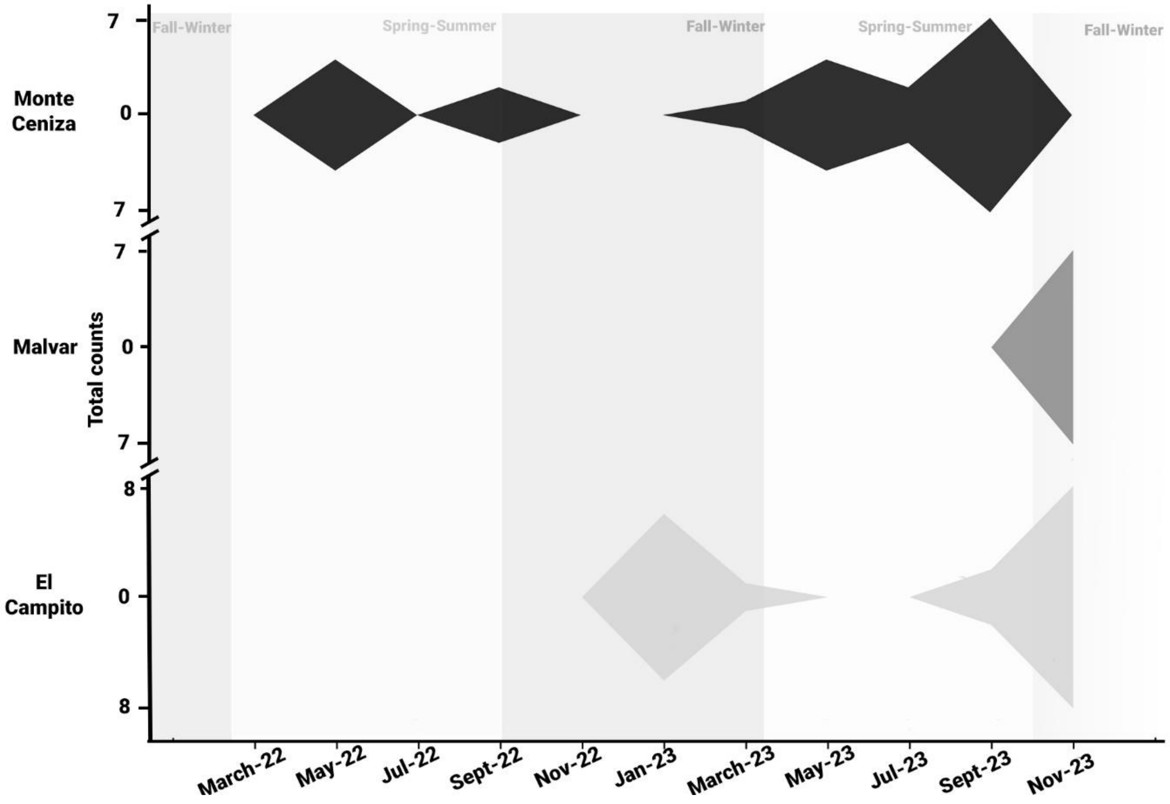

Figure 31. Seasonal and inter-annual abundance of *Chaetodipus fallax* in three study locations, in Baja California

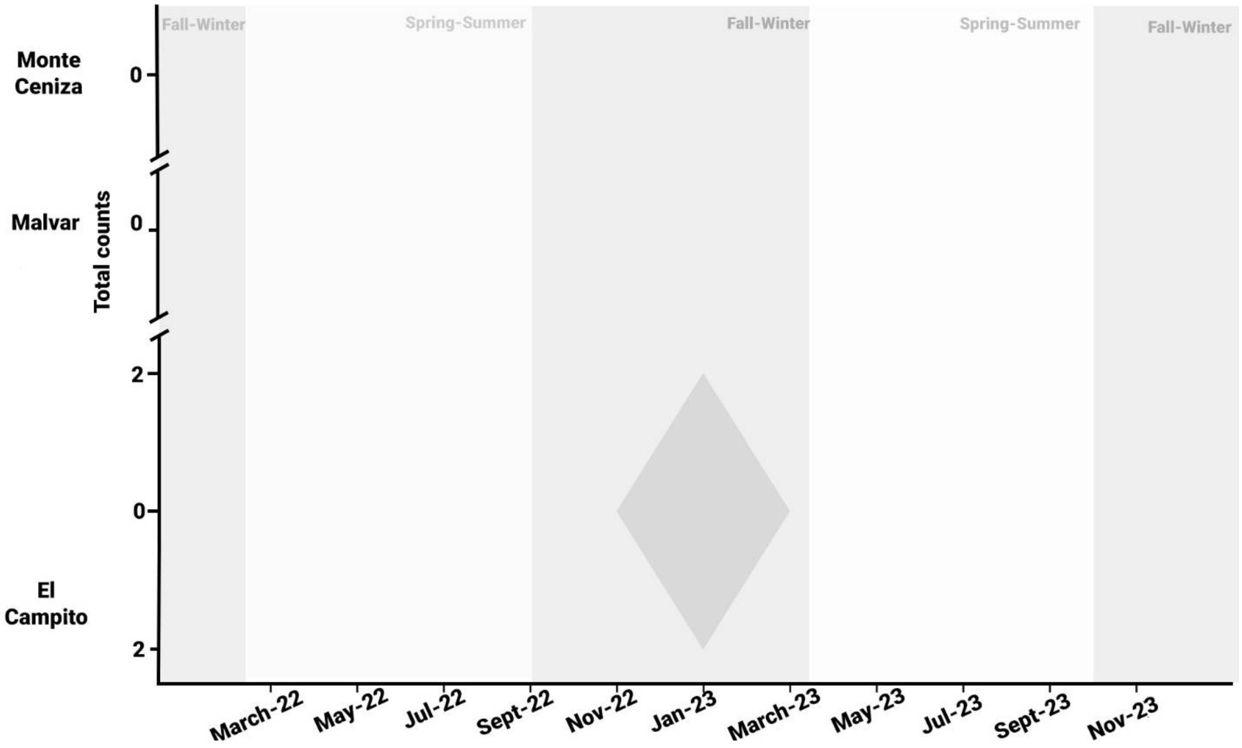

Figure 32. Seasonal and inter-annual abundance of *Reithrodontomys megalotis* in three study locations, in Baja California

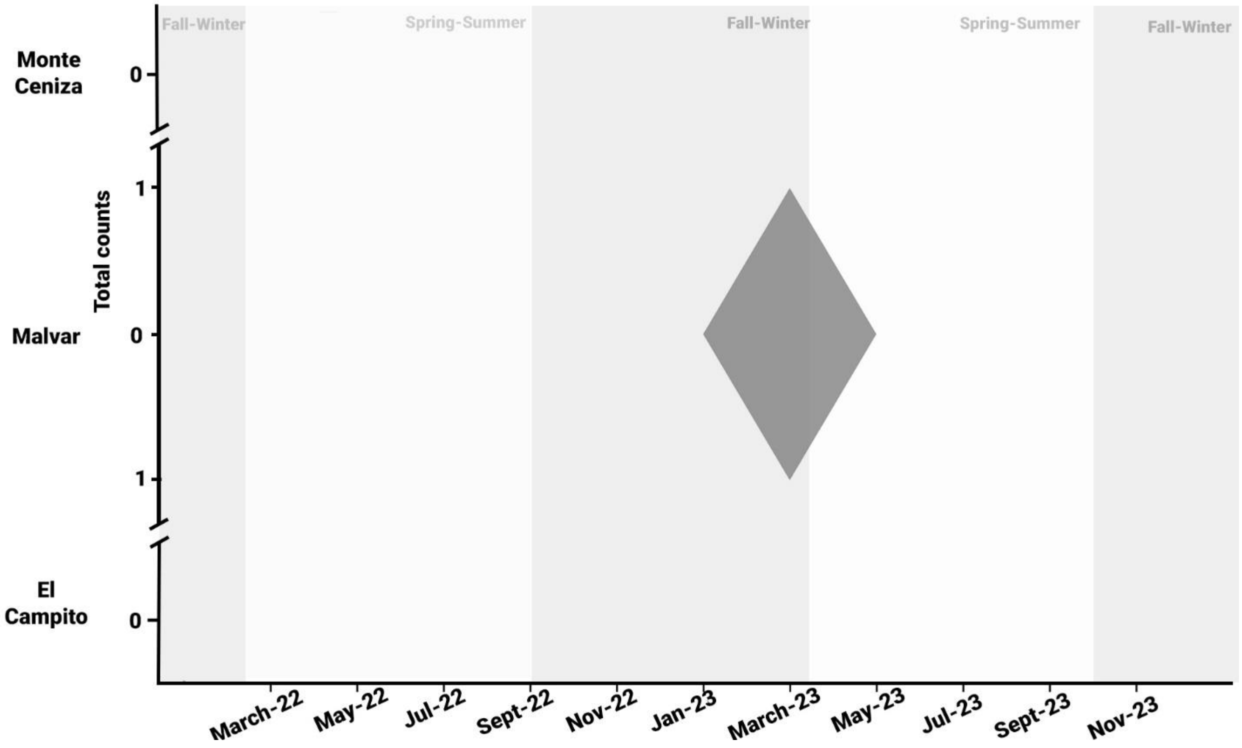

Figure 33. Seasonal and inter-annual abundance of *Chaetodipus arenarius* in three study locations, in Baja California.

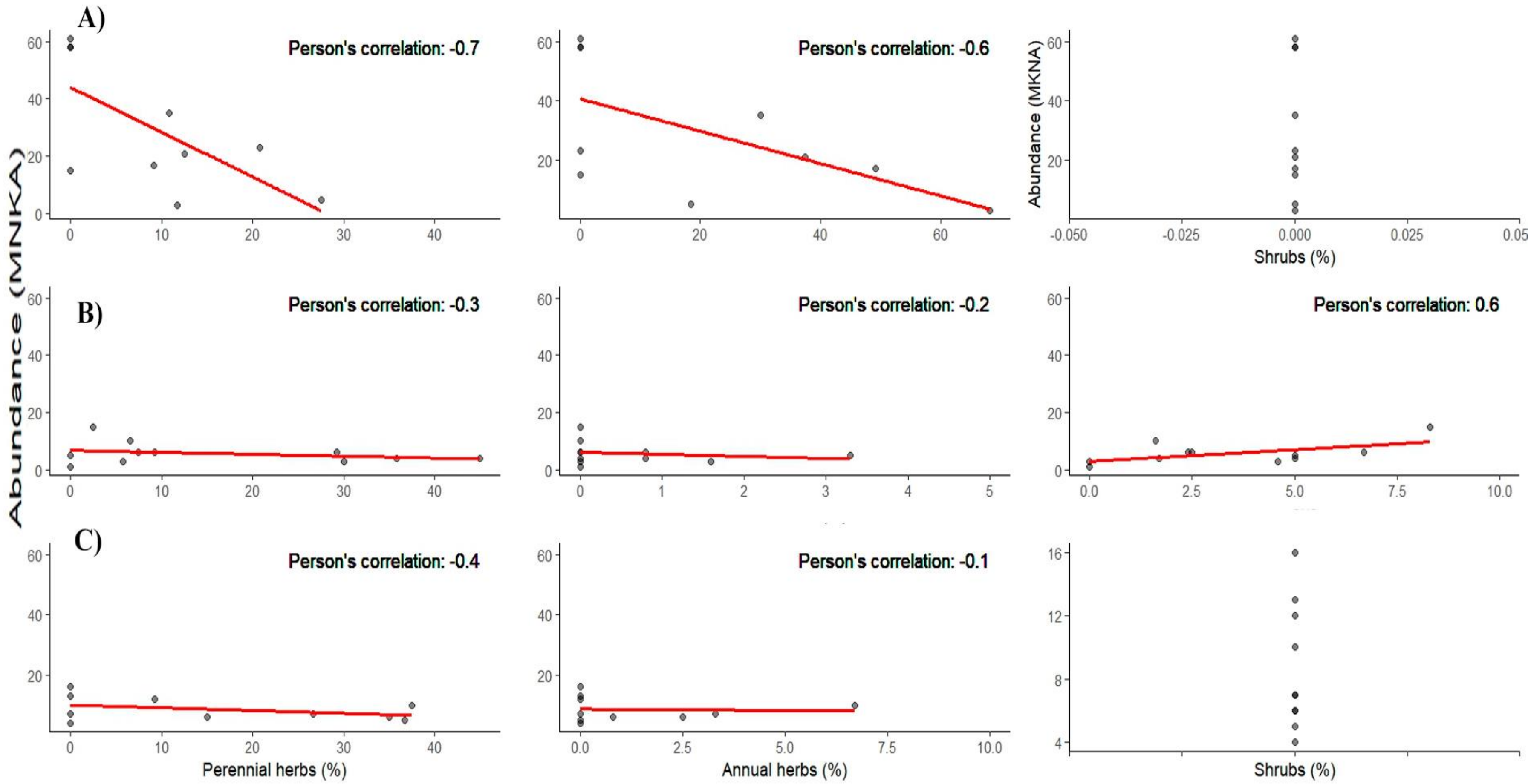

Figure 34. Regression analysis of vegetative components as independent variables on *D. gravipes* abundances. Each row represents a plant type and each column represent a locality.

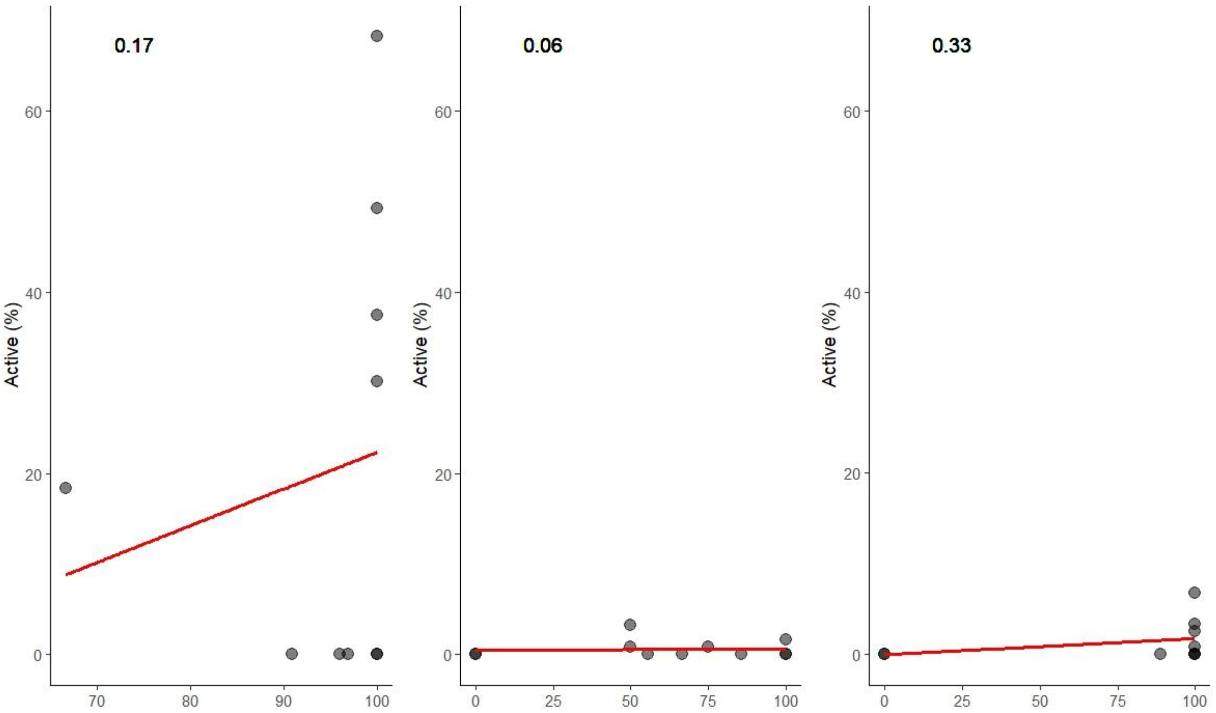

Figure 35. Female reproductive status and annual vegetation cover correlation. Each column represents a locality and each row represents a status of breeding. All coefficients are Pearson's correlation index.

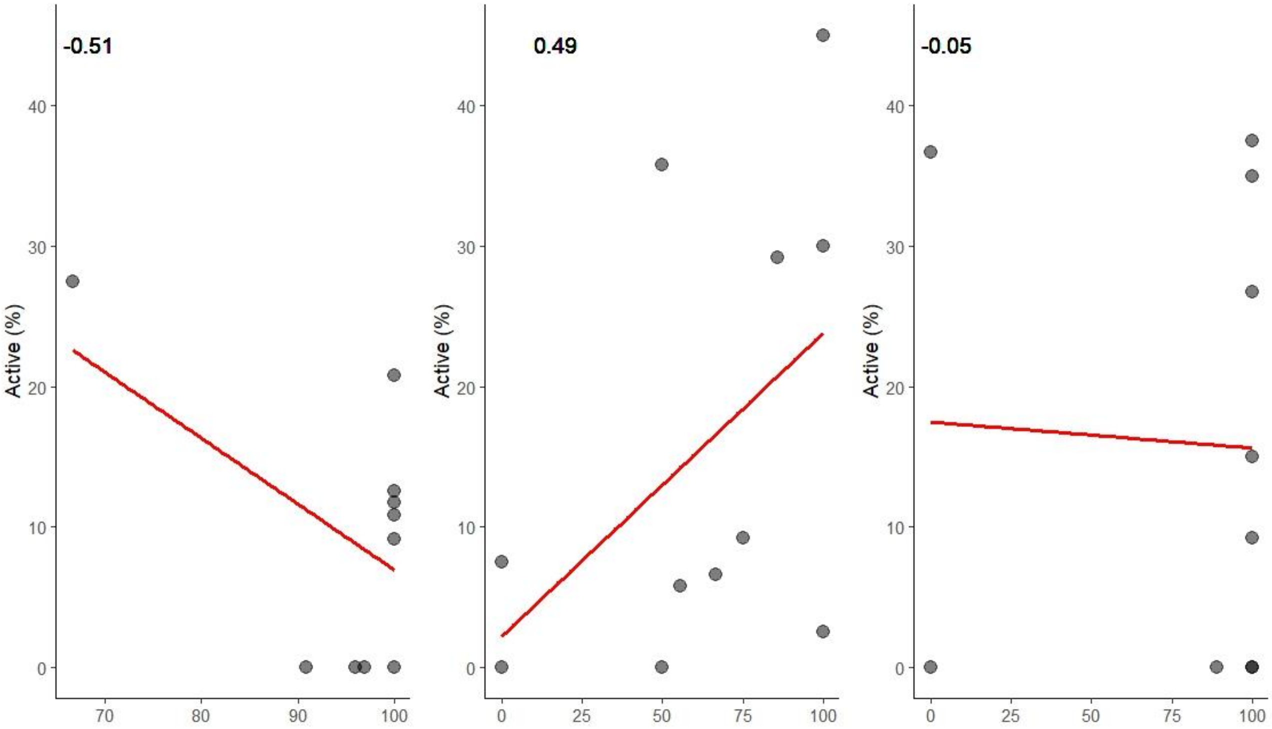

Figure 36. Female reproductive status and perennial vegetation cover correlation. Each column represents a locality and each row represents a status of breeding. All coefficients are Pearson's correlation index

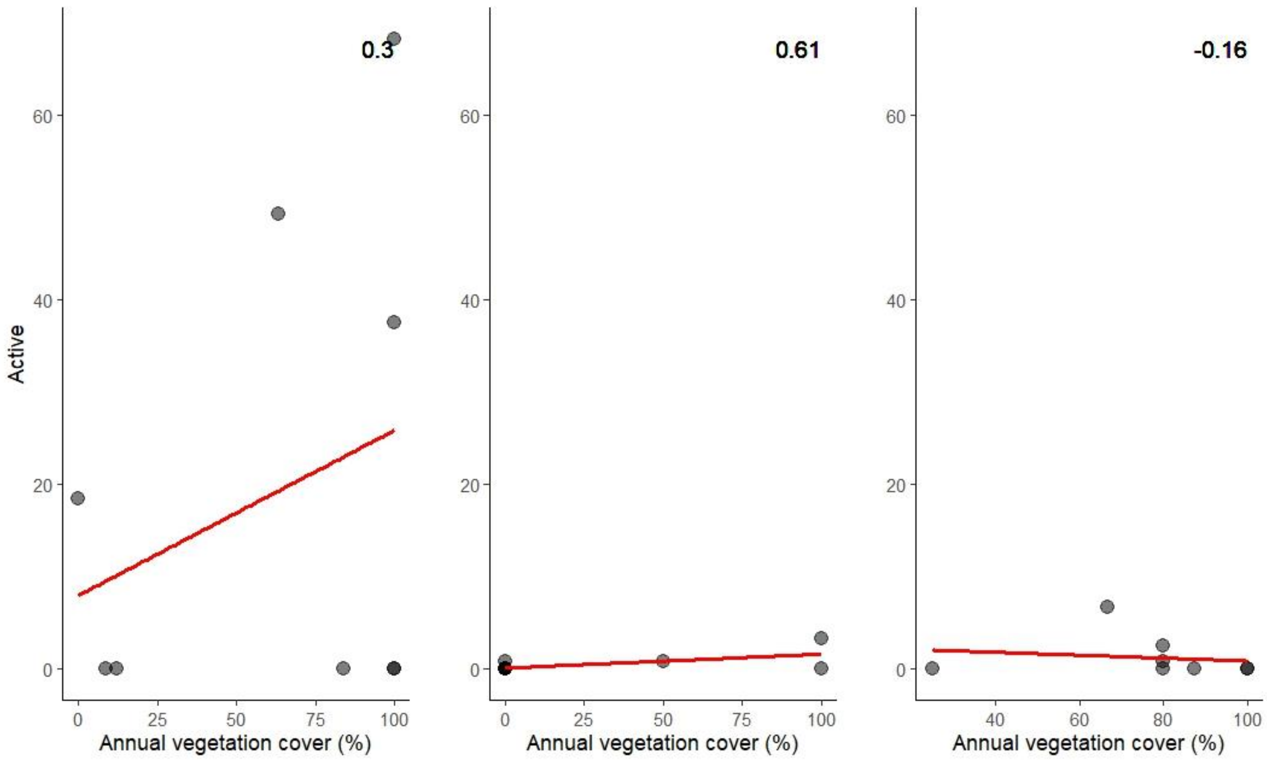

Figure 37. Male reproductive status and annual vegetation cover correlation. Each column represents a locality and each row represents a status of breeding. All coefficients are Pearson's correlation index.

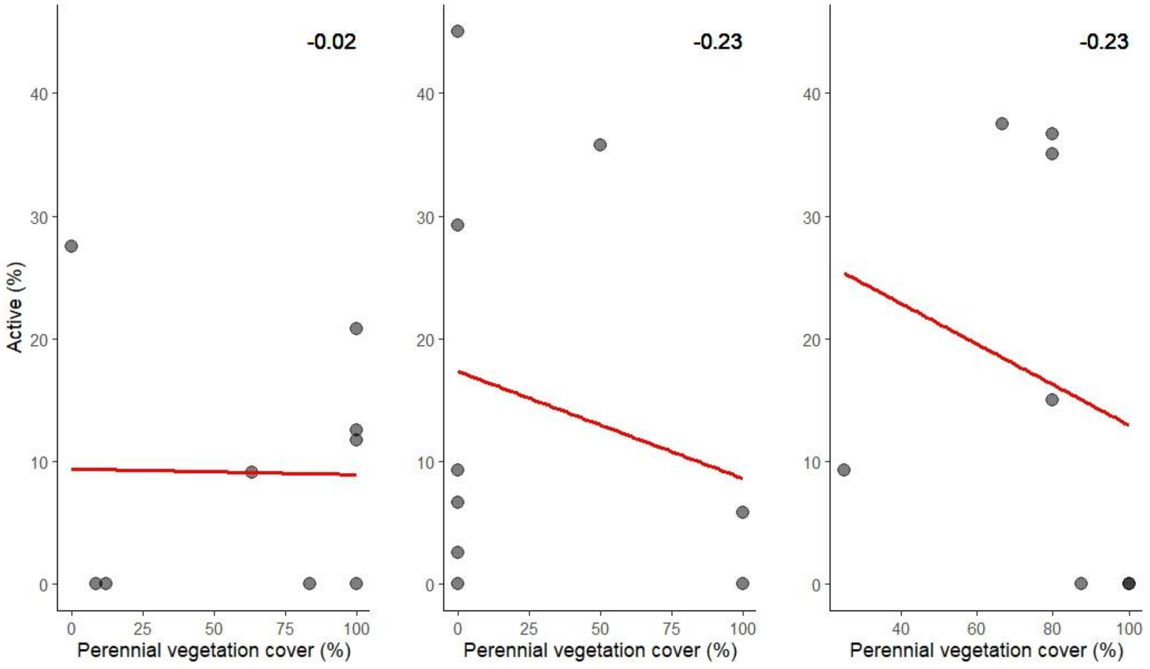

Figure 38. Male reproductive status and annual vegetation cover correlation. Each column represents a locality and each row represents a status of breeding. All coefficients are Pearson's correlation index.

Table 9. All models for abundance as reponse variables ranked by AICc

(Intercept)	Annual herbs	Perennial herbs	Total cover	Photoperiod	df	logLik	AICc	delta	weight
2.751453	-0.047838	-0.048290	0.025340	NA	5.000000	-101.990824	216.981647	0.000000	0.463164
1.672361	-0.051055	-0.053997	0.030873	0.084021	6.000000	-100.321097	217.063246	0.081599	0.444647
2.840506	-0.022186	-0.024429	NA	NA	4.000000	-105.475165	220.855091	3.873444	0.066777
2.255263	-0.020889	-0.024619	NA	0.046267	5.000000	-104.915241	222.830481	5.848834	0.024870
2.843859	NA	NA	-0.020824	NA	3.000000	-112.782517	232.655942	15.674295	0.000183
2.880403	NA	-0.009608	-0.017275	NA	4.000000	-111.742936	233.390635	16.408987	0.000127
2.805384	-0.007399	NA	-0.016548	NA	4.000000	-112.160645	234.226052	17.244404	0.000083
2.334156	NA	NA	-0.020159	0.039629	4.000000	-112.365553	234.635869	17.654222	0.000068
2.179270	NA	-0.011265	-0.015720	0.054929	5.000000	-110.979067	234.958134	17.976487	0.000058
2.393982	-0.006540	NA	-0.016507	0.032367	5.000000	-111.889744	236.779489	19.797842	0.000023
2.598988	-0.027794	NA	NA	NA	3.000000	-119.342031	245.774970	28.793323	0.000000
2.192111	-0.026835	NA	NA	0.032170	4.000000	-119.077339	248.059441	31.077794	0.000000
1.083953	NA	-0.033307	NA	0.137552	4.000000	-122.115973	254.136707	37.155060	0.000000
2.838778	NA	-0.035586	NA	NA	3.000000	-127.669191	262.429292	45.447645	0.000000
0.364225	NA	NA	NA	0.167471	3.000000	-147.775937	302.642784	85.661137	0.000000
2.468943	NA	NA	NA	NA	2.000000	-156.258124	317.037986	100.056339	0.000000

Table 10. All models for male reproductive status ranked by AICc

(Intercept)	Annual herb	Perennial herbs	Total vegetation	Photoperiod	df	logLik	AICc	delta	weight
78.3786363	NA	NA	NA	NA	3	-152.8548	312.598489	0	0.26887573
78.3421714	NA	NA	7.86042517	NA	4	-151.990934	313.520329	0.92183991	0.16958077
78.1379405	8.15145377	NA	NA	NA	4	-152.235679	314.009819	1.41133067	0.13276544
112.05088	NA	NA	NA	-2.73417196	4	-152.66283	314.864121	2.26563247	0.08661154
78.4202746	NA	3.71638341	NA	NA	4	-152.670167	314.878795	2.28030601	0.08597842
78.2856031	NA	-3.73913322	10.4619092	NA	5	-151.890994	316.181988	3.58349922	0.04481306
86.4252694	NA	NA	7.5185729	-0.65620952	5	-151.98108	316.362159	3.76367041	0.04095255
78.3099489	1.2303895	NA	7.08805587	NA	5	-151.985829	316.371658	3.77316935	0.04075851
78.1632667	7.88811272	2.44874292	NA	NA	5	-152.157036	316.714072	4.11558358	0.03434504
93.1446734	7.79061817	NA	NA	-1.21902666	5	-152.199965	316.799931	4.20144205	0.03290183
107.31209	NA	3.17622062	NA	-2.34653837	5	-152.529913	317.459826	4.86133768	0.02365514
78.4728698	-11.5698624	-10.7449954	22.6965977	NA	6	-151.746298	318.992595	6.39410663	0.01099231
82.8801623	NA	-3.65039745	10.2096099	-0.37289134	6	-151.887877	319.275753	6.67726441	0.00954118
86.0590014	1.12067612	NA	6.8308859	-0.62884013	6	-151.976869	319.453739	6.85525009	0.00872877
90.7492832	7.32511152	2.29359523	NA	-1.02041933	6	-152.133844	319.767688	7.16919942	0.0074607
79.0106842	-11.5432364	-10.716985	22.6372776	-0.04368774	7	-151.746254	322.362073	9.76358418	0.002039

Table 11. All models for female reproductive status ranked by AICc

(Intercept)	Annual herbs	Perennial herbs	Total cover	Photoperiod	df	logLik	AICc	delta	weight
78.3786363	NA	NA	NA	NA	3	-152.8548	312.598489	0	0.26887573
78.3421714	NA	NA	7.86042517	NA	4	-151.990934	313.520329	0.92183991	0.16958077
78.1379405	8.15145377	NA	NA	NA	4	-152.235679	314.009819	1.41133067	0.13276544
112.05088	NA	NA	NA	-2.73417196	4	-152.66283	314.864121	2.26563247	0.08661154
78.4202746	NA	3.71638341	NA	NA	4	-152.670167	314.878795	2.28030601	0.08597842
78.2856031	NA	-3.73913322	10.4619092	NA	5	-151.890994	316.181988	3.58349922	0.04481306
86.4252694	NA	NA	7.5185729	-0.65620952	5	-151.98108	316.362159	3.76367041	0.04095255
78.3099489	1.2303895	NA	7.08805587	NA	5	-151.985829	316.371658	3.77316935	0.04075851
78.1632667	7.88811272	2.44874292	NA	NA	5	-152.157036	316.714072	4.11558358	0.03434504
93.1446734	7.79061817	NA	NA	-1.21902666	5	-152.199965	316.799931	4.20144205	0.03290183
107.31209	NA	3.17622062	NA	-2.34653837	5	-152.529913	317.459826	4.86133768	0.02365514
78.4728698	-11.5698624	-10.7449954	22.6965977	NA	6	-151.746298	318.992595	6.39410663	0.01099231
82.8801623	NA	-3.65039745	10.2096099	-0.37289134	6	-151.887877	319.275753	6.67726441	0.00954118
86.0590014	1.12067612	NA	6.8308859	-0.62884013	6	-151.976869	319.453739	6.85525009	0.00872877
90.7492832	7.32511152	2.29359523	NA	-1.02041933	6	-152.133844	319.767688	7.16919942	0.0074607
79.0106842	-11.5432364	-10.716985	22.6372776	-0.04368774	7	-151.746254	322.362073	9.76358418	0.002039