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Chapter 15

SEED REMOVAL BY HETEROMYID RODENTS IN THREE HABITATS OF TROPICAL MEXICO

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Abstract

We analyzed the feeding patterns among species of heteromyid rodents in rain forest, deciduous tropical forest, and sarcocaule desert habitats. All of the heteromyids have the ability to select seeds for their nutritional content and the presence of toxic substances. The seeds are stored in burrows, and those not consumed before the next rainy season may germinate. *Heteromys* removal decreases in the open areas and increases in covered areas in the rain forest. Removal of seeds by *Liomys* is unaffected by the cover patterns in the deciduous tropical forest. In the desert, the microhabitat is important for removal of seeds, with a relation between method of movement of the species and removal. The bipeds (*Dipodomys*) use open areas and the quadrupeds (*Chaetodipus* and *Perognathus*) closed or covered areas. Deforestation has a different effect on different genera of heteromyids. It is prejudicial for *Heteromys* in the rain forest, probably is good for *Liomys* in the deciduous tropical forest, and the only effect in the desert is the substitution from one species for other.

Resumen

Se analiza la existencia de patrones en él habito de forrajeo entre los heterómidos (especies granívoras) presentes en tres diferentes tipos de ecosistemas: la selva húmeda, la selva baja caducifolia y el desierto sarcocaule. Se encontráron similitudes y diferencias entre los tres ambientes. Los heteromidos tiene la capacidad de seleccionar las semillas de acuerdo con el contenido de nutrientes y sustancias tóxicas que presentan en los tres hábitats, además de que las almacenán dentro de sus madrigueras, algunas de las cuales no son utilizadas y germinan en la próxima temporada de lluvias. En ambientes desérticos, un factor que influye dentro de la remoción, es la condición el microhábitat, que las diferentes especies utilizan, lo que se relaciona con su forma de desplazamiento, se observó que las especies bípedas (*Dipodomys*) utilizan las zonas abiertas y las cuadrúpedas (*Chaetodipus* y *Perognathus*) las cerradas. Para el caso de la selva húmeda (*Heteromys*) la intensidad de remoción se reduce en los sitios con menos cobertura vegetal y se incrementa en los de mayor. En la selva baja caducifolia, la remoción no parece ser afectada por la cobertura de manera importante, ya que el principal removedor (*Liomys*), no modifica su comportamiento, ni la intensidad de su actividad. La deforestación tiene efectos diferentes sobre las especies de heteromidos, así en las selvas húmedas en perjudicial (*Heteromys*), en la selva baja caducifolia no afecta y probablemente beneficia a las especies de *Liomys*, y para las zonas áridas, lo que sucede es la presencia de especie en función de la cobertura vegetal.

Introduction

Heteromyid rodents are the most important family of rodents in the arid lands of North America (Brown and Liberman, 1973; Mares, 1993). This group continuously stores seeds during the abundant season (Brown *et al.*, 1979; Einsenberg, 1963; Nikolai and Bramble, 1983) to be used in the dry and cold part of the year (Kenagy, 1973; MacMillen, 1983). The family is considered as the most relevant group of seed removers in the North American desert (Brown *et al.*, 1979; Janzen, 1970). The dental morphology and the musculature of these rodents are that of granivores, through these species also feed on parts of plants and on some types of insects (Reichman and Price, 1993).

The importance of the heteromyids in the removal and storage of seed is illustrated by *Dipodomys spectabilis*, which can store in its burrows more than five kilograms of seeds (Vorhies and Taylor, 1922). Many species of *Dipodomys* can manipulate the seeds to vary the relative humidity and avoid spoilage (Reichman *et*

al., 1985). This manipulation increases seed survival during the dry or cold part of the year. When the rainy season arrives, many of these seeds stored can germinate, increasing the reforestation of the areas. This group of rodents has specific morphological characteristics for their microhabitat, in which they harvest seed, affecting movement; bipeds for open areas and quadrupeds for closed. These rodents also have cheekpouches in which they can transport a great number of seeds, more than they can eat.

Studies of the ecology of the foraging of heteromyids in the cold desert (*Dipodomys*, *Microdipodops*, *Chaetodipus,* and *Perognathus*) are extensive (Brown *et al.*, 1979; Lawhon and Hafner, 1981; Reichman, 1975, 1977), however, there are only a few studies for the tropical and subtropical areas (*Liomys* and *Heteromys*) (Fleming, 1974; Sanchez-Cordero and Fleming, 1993). We believe the species of this family have general patterns in all the different habitats. In this chapter, we discuss some aspects of the removal, dispersal, and storage of seeds by the rodents of the *Heteromyidae* family in three different vegetation types of the tropical part of Mexico; rain forest, deciduous forest, and tropical desert. We will also consider the nutritional characteristics of seeds removed by heteromyids, their microhabitat preference, and management implications. The heteromyids are the only rodent species in these three habitats that remove seeds and they are considered great disperser. The other granivorous rodents eat the seed in situ and are not important seed dispersers.

Seed Removal, Dispersal, Storage

Different species of plants and animals coexist in a continuous interaction in any natural habitat. The production of fruit and seeds are a fundamental part of the ecosystem. Many authors have noted the importance of the heteromyids in their habitat, involving the removal and dispersal of seeds as part of their foraging (Brown *et al.*, 1979; Fleming, 1974; Janzen, 1970; Price and Heinz, 1984; Price and Reichman, 1987). Removal is defined by Fleming *et al.* (1987) as the transfer of seeds from one place to another. This process is one of two types; predispersion, where the plant has not released the fruit or seed and predators and scatterers take it directly, and postdispersion, where the fruit or the seed is released from the plant and taken by animals from the substrate or accumulation sites.

Fleming (1974) and Reichman (1977) noted that the removal of seeds by rodents is generally a function of the nutritional quality of the seeds, their density, and the microhabitat in which they are found in postdispersion removal. Janzen (1982) mentioned that the intensity of the removal is inversely proportional to the distance to the seeding plant, and is affected by the seed density. Price and Heinze

(1984) confirmed this, finding a relation between the number of seeds and removal, which relation is stronger as density increases.

The dispersion of seeds by rodents represents one of the more evident adaptations in the plant-animal relation. Many of the plants that are part of this relation have morphological and structural modifications that make them more attractive for dispersion. The most important removers in many habitats are heteromyid rodents, because they move many seeds to their burrows for storage, where they consume or select the seeds. These stores are not used in many instances, so the unconsumed seeds can germinate and help reforest the area.

The capacity of the cheekpouches directly influences the number of trips made by the rodent from its burrow to the seed patch, and the type and size of seeds collected. The population density influences behavior. The increase of the number of individuals within a defined area tends to modify their behavior (Fleming, 1974). Maza *et al.* (1973) emphasized that the area of heteromyid activity is modified when population density increases. Therefore, the home range is reduced so the intensity of the removal is increased at the supply sites.

Fleming (1974) noted that in many cases the seeds transported by rodents are highly toxic. Shaw (1934) and Monson (1943) said that heteromyids collect and constantly store a large amount of seeds when they are available, depositing them or protecting them in burrows where later they will be selected. They can also bury them in small deep places temporarily. Such behavior has been characterized by Reynolds (1958), Eisenberg (1963), and Vorhies and Taylor (1922). Martínez-Gallardo (1995) in the rain forest, Briones (1996) in the deciduous forest, and Gutiérrez-Ramos (unpublished data) for the sarcocaule desert found that the heteromyids remove the seeds that contain toxic compounds, at least in the first days after collecting the seeds.

General Habitat Relationships

General relation between heteromyid rodents, their seed removal, dispersal, and storage activities, and the habitats considered in this chapter are briefly summarized in the following section. Common species of heteromyids found in these habitats are also mentioned.

Rain Forest

The rain forest is a complex vegetation community in the tropical region where temperature and water do not limit resource development during the year (Dirzo, 1987). For that reason, the reproductive strategy of vegetal species can be

diversified because of the presence of seeds all year (Carabias-Lillo and Guevara-Sada, 1985).

Martinez-Gallardo (1988) found that *Heteromys desmarestianus* and *Peromyscus mexicanus* at Los Tuxtlas, Mexico, are the most important seed consumers, and depend on the presence of seed on the ground for stability of their populations. His results show that a low density of *H. desmarestianus* is related to low seed removal, and for *P. mexicanus* no relation between the density of rodents and seed removal was found, confirming the role of heteromyids as seed removers inside the forest. The main removers of scattered fruits and seeds in Los Tuxtlas, Veracruz, is *Heteromys desmarestianus*, and the removal occurs in different ways, depending upon the condition of the forest. When there is greater vegetal cover, the removal is more intense and vice versa. The seed density in each patch also influences the intensity as the vegetal cover does. The depredation risk is greater in clear areas, and consumers as *H. desmarestianus* try to avoid this type of microhabitat (Martínez-Gallardo, 1995).

Deciduous Tropical Forest

This ecosystem is characterized by the presence of a distinct rainy season in which flowering and fruiting occurs (Rzedowski, 1981). Flowering occurs at the end of the first rains, followed by the fruiting, which depends on the amount of rain. The fruiting process represents an event to the associated organisms because there is variation in seed production. Studies have mentioned that *Liomys* is one of most important genera as a remover of fruits and seeds in dry forests in much of North America (Janzen, 1982; Fleming and Brown, 1975). Janzen (1982) found that *Liomys salvini* can remove 93% of the seeds under a productive tree. Studies in Chamela, Jalisco, have shown the form in which the rodents participate in the removal process (Briones, 1991, 1996; Collet *et al.*, 1975; Martinez-Gallardo, 1988; Perez, 1978; Sánchez-Rojas, 1993). *Liomys pictus* is considered the main remover of seeds in the deciduous forest in this region. There is an inverse relation between the amount of vegetal biomass and the number of species inhabiting this type of habitat (Briones, 1991; 1996).

Sarcocaule Desert

This vegetal community is characterized by dry-tropical elements. In comparison with other environments, flowering is more-or-less continuous most of the year (Carabias-Lillo and Guevara-Sada, 1985); this suggests that the bank of seeds is constant. Vegetal behavior is related to the rainfall at the time of flowering (León de la Luz *et al.*, 1996).

There are four heteromyid species, *Dipodomys merriami*, *Chaetodipus arenarius*, *C. baileyi,* and *C. spinatus*; two Muridae, *Peromyscus eva* and *Neotoma*

lepida; and one Sciuridae *Ammospermophilus leucurus* in the sarcocaule desert near Bahía de La Paz (Cortés-Calva and Alvarez-Castañeda, 1997). When the vegetal cover decreases, population dynamics of these species are modified and with it the intensity of removal of seeds. Presence of the species is related to the distribution of habitat components (Cortes-Calva, 1997).

Our study shows that the use of the seeds is different for different species. *Dipodomys merriami* feeds in the open areas, *C. baileyi* inhabitats areas with scarce vegetation, and *C. arenarius* and *C. spinatus* live in the areas with dense vegetation; *C. arenarius* inhabits sandy soils and *C. spinatus* rocky soils. There is greater heteromyid activity in open areas, which are associated with the presence of a greater number of species of rodents. The occurrence of annual plants in this environment also plays an important role in the intensity of the seed removal zones (Brown *et al.*, 1979; Cortes-Calva, 1997). This has important consequences in seed removal by *Dipodomys merriami*, a common species in the Sonoran desert, and contributes to an increase in the distribution of vegetal species. In agreement with Brown *et al.* (1979), the interaction between the seeds and consumers has two important effects on the structure and function of the desert ecosystem; as predators, the consumers influence distribution and abundance of vegetal populations, and as prey they provide food for carnivores.

One of the basic resources in the sarcocaule desert is the availability of water. Organisms living in the desert have morphological and physiological adaptations to subsist in habitats where little water is available. Heteromyids also have kidneys that facilitate nitrogen excretion and the osmotic balance in a diet that contains little free water (Eisenberg, 1963). These rodents do not drink water directly, but take water from foods by metabolism (Schmidt-Nielsen (1964, 1972).

Nutrititonal Value of Seeds Removed

Studies made in desert ecosystems in general show that the heteromyids have the capacity to select seeds with high nutritional values and high water content, excluding those with minor nutritional value or toxic compounds (Price, 1978; Reichman and Price, 1993). The selected seeds are low in proteins, which requires great water investment, and high in carbohydrates and fats, which results in high metabolic water production (Reichman and Price, 1993). Heteromyids in the sarcocaule desert have a preference for seeds with high concentrations of lipids and carbohydrates.

The preference for feeding in certain microhabitat types, taking advantage of existing seed patches and density conditions has been emphasized in studies of seed removal by rodents in desert ecosystems (Brown *et al.*, 1979; Price, 1978;

Price *et al.*, 1984; Reichman, 1975). Similar results were obtained by Martínez-Gallardo and Sánchez-Cordero (1993) for *H. desmarestianus* in the tropics. The distribution of seeds directly influences the way by which seed removal occurs in the rain forest, and is independent of the density and the successional status of the forest (Martínez-Gallardo, 1995). For the deciduous tropical forest, Briones (1996) found that *Liomys pictus* removes all types of seed, but notes a preference for those with high nutritional content.

Microhabitat Preference

The presence or absence of other rodent species can influence the use of a certain type of microhabitat (Larsen, 1986; Price, 1978). There is general similarity in study results obtained for different environments, where smaller number of species of rodents produces a reduction in the intensity of the removal of seeds (Brown, 1973; Price and Heinz, 1984). Martinez-Gallardo (1995) mentioned that when the population density of *H. desmarestianus* decreases, seed removal also decreases. The same phenomenon has been found in the sarcocaule desert as an effect of the home range of the species increasing, causing microhabitats to be used that had not been used before. Rosenzweig (1973) and Price (1978) stated that there is a preference for foraging in specific sites, or by the type of ground, quality of the seeds, and antipredator behavior, and an effect on the intra- and interspecies conformation of the population.

There is a relation between some species of heteromyids and certain vegetal species in some parts of the year (Cortés-Calva, 1997; Reichman and Price, 1993). The behavior of the species that use vegetation cover for rest and protection from predators or to maintain their body temperature, is often changed (Kotler, 1984; Lowe and Hinds, 1971). Martínez-Gallardo (1995) found that removal of seeds occurs to a lesser degree in clear areas within the rain forest, with seed removals increasing in those sites with good cover. In the deciduous tropical forest, seed removal in many cases was related to the type of seeds present and their specific characteristics, physical or chemical, and that the vegetation cover is not an important factor (Briones, 1996; Janzen, 1971). Our studies in the sarcocaule desert show an association between the rodents and vegetation patches (Cortés-Calva, 1997). Because there are species of heteromyids that used covered areas, *Chaetodipus arenarius*, *C. baileyi*, *C. spinatus*, and open areas, *Dipodomys merriami*, all of the habitats can be used by the rodents.

The removal of seeds in relation to habitat is also related to the specific species. Only *Heteromys* spp. remove seeds in covered areas within the rain forest. *Liomys* spp. are present in both the deciduous tropical forest and associated

grasslands, and, therefore, vegetative cover is not as important in the habitats. There are so many species of *Dipodomys*, *Chaetodipus*, *Perognathus*, and *Microdipodops* that all seeds in the different microhabitats can be used in sarcocaule desert habitats.

Management Implications

Deforestation is important in the dynamics of the habitats considered in this chapter, mainly by affecting dispersion of fruits and seeds, and decreasing the vegetal cover.

Deforestation in the rain forest influences the intensity of seed removal. The amount and quality of seeds are impacted and, as a consequence, vegetal diversity is altered (Martínez-Gallardo, 1995). Removal activity in deforested sites is lower than at sites with less alteration. Dynamics of rodent populations can be changed because there is limited resource for growth and reproduction (Sánchez-Cordero, 1993; Sánchez-Cordero and Fleming, 1993). With alteration of population compositions, abnormal fruit and seed removals are common. In the altered areas are found changes in the vegetal composition, predominantly of the annuals (Martínez-Gallardo, 1995). *H. desmarestianus* is a key species in the rain forest; when its population density is lowered, removal decreases. At the same time, the population of *Peromyscus mexicanus,* a opportunistic species, increases in number but does not substitute for the dispersal effect of *Heteromys.*

Alteration of habitats in the deciduous tropical forest does not affect seed removal by *Liomys pictus* (Briones, 1996). Our observations suggest that on those sites that originally supported deciduous forest and have been disturbed by the introduction of species of the family Gramindae, the population of *Liomys* increases. Effects of deforestation in desert ecoystems, which is generally less serve in its impact than in other habitats, can be mainly seen in the increase of open areas and presence of grasses. We observed a change in the composition of the heteromyid species in this situation, with increasing bipeds and decreasing quadrupeds. For the case of the sarcocaule desert, we found there was no change in the number of quadruped species but found one biped present. This phenomenon can be explained by the increase of grass species that cover extensive sites and produce more seeds than can be used by the heteromyids. However, these findings are opposite to those found by Munger and Brown (1981) and Heske *et al.* (1994).

Studies in these three habitats have demonstrated that disturbance can also promote the extirpation of rare species, cause drastic changes in the environment, and increase populations of opportunistic rodents by promoting immigration of species from other habitats (Briones, 1996). In some of these habitats, the same species of heteromyids can be considered as opportunistic species.

Anthropogenic disturbance influences the composition of mammals, in general, because of the sensitivity of some of species to the modification of their surroundings (Martínez-Gallardo, 1995). Modification of plant structures can either favor or reduce populations of various species depending largely upon the reaction of the specific rodent species to modified vegetal structures.

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