HISTORICAL, BIOGEOGRAPHICAL AND ECOLOGICAL FACTORS EXPLAIN THE SUCCESS OF SOME NATIVE DUNG BEETLES AFTER THE INTRODUCTION OF CATTLE IN MEXICO

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SUMMARY

The introduction of different types of livestock following the Spanish conquest of Mexico generated notable changes in the landscape of the Mexican High Plateau and tropical regions of the country, replacing the mostly agricultural activities of indigenous populations with European-style livestock production. While the effects on native vegetation were significant, the dung produced by the livestock— mainly cattle, horses and goats—did not create the same degree of environmental problems that later occurred in Australia and New Zealand. This is explained because the dung beetles of Mexico—and that of the Americas in general—were capable of exploiting this exotic resource and incorporate it into the nutrient cycles of the tropical and temperate soils of the American continent. This ability to utilize an exotic resource can be explained by the evolutionary, biogeographic and ecological history of the species of beetles native to the American continent. Biogeographically, Mexican dung beetle species come from phyletic lines that originated in the Palearctic, Nearctic and Neotropical regions, arriving in Mexico in different waves during the Miocene and Pleistocene. During these epochs, the megafauna of Mexico included mammoths, mastodons, gomphotheres, horses, camels, glyptodonts, bison and antelope, among others. These animals produced dung that was similar to that of the livestock from Spain, especially that of cattle and horses. This made it possible for the native dung beetles to easily exploit the resource provided by the livestock introduced by the Europeans. In an anthropized landscape such as Mexico, we must focus not only on the conservation of the dung beetles that inhabit our temperate and tropical forests, but also on the species found in man-made pastures, both of which provide valuable ecosystem services such as incorporating dung into the soil nutrient cycle.

Key words: Mesoamerica, Scarabaeinae, New Spain , megafauna.

Bases de datos: http://polired.upm.es/index.php/pastos (España), AGRIS (Italia), CAB Abstracts (Reino Unido), CABI Full Text (Reino Unido), Catálogo LATINDEX (México), DIALNET (España), ICYT Ciencia y Tecnología (España)

INTRODUCTION

Mexico covers approximately 2 million km^2 and almost 62.5% of this area is used for the production of cattle, horses, sheep and pigs. Cattle production alone covers 58% of the country (INEGI, 2007) and there are more than 30 million heads of cattle in Mexico, (http://www.mitecnologico.com/Main/GanaderiaEnMexico).

Each cow defecates 15 to 20 times per day and its dung can cover one square meter per day (De Elias, 2002). The total weight of dung produced daily ranges from 20 to 30 kg per animal, though this varies with the breed of cattle and local climate conditions (Bavera and Peñafort, 2006). At an average weight of 25 kg of excrement per bovine/day, the 30 million heads of cattle in Mexico produce a total of 7.5 x 10^8 kg of dung daily; a substantial amount, and one that does not even take into account the dung produced by horses, sheep, goats and pigs. In ecological terms, however, this huge deposition of dung has not created any substantial problem for the country. This is because a considerable part of this resource is consumed by dung beetles that are abundant throughout Mexico, and in the temperate and tropical regions of the Americas in general.

The dung produced by Eurasian livestock represents an exotic resource for the American dung beetles, and one with which they have been in contact for approximately 500 years, dating back to when the Spanish began to transport animals and plants from one continent to another. Hernán Cortés brought cattle to Mexico for the first time in 1521, the same year the Spanish conquered Mexico-Tenochtitlan.

There is no doubt that the introduction of livestock in Mesoamerica after the European conquest was detrimental to the environment, but we must acknowledge that the indigenous people also had modified their surroundings to a notable degree (Simonian, 1999). Prior to the conquest, there was considerable exploitation of the environment in this region, albeit in a manner that differed from that of the Spanish farmers. For the indigenous cultures, the main productive activity was agriculture. On the arrival of the Spanish, Mesoamerica may have had a population of around 25 million people (Simonian, 1999). Efficient agricultural production, particularly in the tropical regions, implied that large areas of tropical forest had been transformed into agrosystems that, given cyclic management, could partially recover. Barrera-Bassols (1996) proposed that prior to the arrival of the Spanish 1.5 million hectares of land were managed for agricultural purposes, equivalent to 20% of the area of what is now the state of Veracruz. This is a very large area, and gives an idea of the scale of the alterations to the landscape. According to Simonian (1999), the anthropologist George A. Collier provides evidence that the inhabitants of the highlands of Chiapas made extensive use of fire to clear large areas of forest for agriculture before the Spanish arrived. Various pre-Hispanic governments, including that of Nezahualcóyotl, the tlatoani (monarch) of the city-state of Tezcuco, passed forestry laws, concerned by the excessive clearing and the effects of the uncontrolled use of fire on the forests and their fauna (see Simonian, 1999).

It is generally thought, however, that there was greater harmony between man and his environment in pre-Columbian America. Here is an example that clearly illustrates the lifestyle in Mexico-Tenochtitlan, as described by Escalante-Gonzalbo (2004): What did the 'Mexica' do with human waste? Did they throw it into the water, contaminating the lake in which their city was built? The answer is no, because people evacuated their bowels using latrines that were on bridges over canals. Container canoes below the latrines were used to transport the excrement to specific zones where it was processed and transformed to an agricultural fertilizer and raw material for tanning leather. Escalante-Gonzalbo (2004) states that this process, together with other systems of waste management and in the absence of cattle, resulted in a rather clean city.

INTRODUCTION OF LIVESTOCK TO MEXICO

Livestock was brought to Mexico soon after the conquest. Horses were a key factor in the conquest, and historians note the fondness of Hernán Cortés for bullfighting. The fall and virtual destruction of Mexico-Tenochtitlan occurred on the 13th of August 1521, and the first bullfight was held in Mexico City on the 24th of June 1526 to celebrate the return of Hernán Cortés from his arduous expedition to Honduras. On the 13th of August 1529, bullfights were held to venerate San Hipólito on the day that Mexico-Tenochtitlan had been conquered (Martínez, 1990). The first cattle to arrive in Mexico entered by the port of Villa Rica de la Vera Cruz. According to Barrera-Bassols (1996), this first herd gave rise to those of the central highlands of New Spain. In 1527, Nuño de Guzmán introduced cattle from Cuba and Hispaniola (Santo Domingo and Haiti). Cattle from the Guadalquivir marshes were brought to the tropics; extremely agile animals, they adapted well to life in the tropical forests and over time became feral cattle, of which there are still populations in Cuba today. In New Spain, by 1579, some northern ranches had herds of up to 150,000 head that doubled in population every 15 months (McClung de Tapia and Sugiyama, 2012). The average grazing density was one head of cattle per hectare, which is maintained to this day in some regions of the country.

It is estimated that there were 1 300 000 cows in the center of New Spain, but also 8 100 000 sheep and goats (McClung de Tapia and Sugiyama, 2012). Thus, cattle production was not the most widespread activity during the early stages of the colony; in fact the production of sheep dominated during this period. This was because sheep produced wool for exportation. Later, with the development of mining, cattle gained importance as a source of leather. Their meat was of much less importance, given the difficulties of preservation and transportation, which made trade in cattle particularly difficult in view of the small population of New Spain. The center of the country was more heavily populated, however the people there mainly consumed the meat of pigs, sheep and goats (G. Halffter pers. comm.).

Livestock production in Mexico radically transformed the original vegetation. The expansive prairies of the Mexican High Plateau, coupled with the lack of predators favored the growth of livestock populations to such an extent that many of these animals formed feral herds (McClung de Tapia and Sugiyama, 2012). Overall, the introduction of livestock to Mexico resulted in much deforestation, the appearance of new diseases and water contamination, although not to such a large extent during the initial stages (16^{th} and 17^{th} centuries). Indeed, following the conquest, there was actually a recovery in the forests as a result of the gradual change from a crop-based system to one that was predominantly livestock-based, leading to the abandonment of crop fields (Barrera-Bassols, 1996).

While there were severe changes to the environment with the introduction of livestock, the enormous quantity of exotic dung produced daily by the rapidly developing populations of Mexican livestock did not create an insurmountable problem for New Spain, or independent Mexico, or even modern Mexico, with the exception of certain specific cases. In Australia, the introduction of livestock, mainly cattle, was catastrophic because the dung of these animals was neither consumed nor incorporated into the soil nutrient cycle; however in Mexico, and tropical America in general, this was not a problem, owing to the native dung beetles. Through their feeding and reproductive behavior, dung beetles—mainly those of the subfamily Scarabaeinae—incorporate the excrement of mammals and other vertebrates into the soil. Their activities favor the recycling of nutrients in the ecosystem, which increases soil fertility and bioturbation (displacement and mixing of soils by animals or plants) and reduces the presence of parasites. Moreover, the dung beetles act as secondary dispersers of seeds (Andresen and Feer, 2005; Nichols *et al.*, 2008).

In Australia, the native dung beetle species are adapted to feed and reproduce mainly upon the dung of marsupials. When livestock were brought from the Old World to the Australian continent, a new type of dung was introduced that could not be utilized by the native dung beetles, with enormous economic consequences (Bornemizza, 1979). The partial solution has been the introduction of dung beetle species, mainly from Africa. Currently, Australia has 23 introduced beetle species that eat the dung of the livestock, and 437 known native species (Ridsdill-Smith and Edwards, 2011).

However, it was not necessary to bring in any new species of dung beetle for the livestock introduced to the Americas because the native fauna easily appropriated this new resource, leading to the efficient incorporation of dung, fertilization of the soil and prevention of the development of flies, among other environmental services. In a recent introduction of exotic dung beetle species, between 1972 and 1974, which took place mainly in Texas and California, *Digitonthophagus gazella* and *Euniticellus intermedius* were released. Both of these species are African and were introduced in order to recycle more efficiently the dung produced on cattle ranches (Anderson and Loomis, 1978; Fincher, 1986). While the effect of the expansion of these exotic species throughout Latin America has undergone various analyses, at least for Mexico (Montes de Oca and Halffter, 1998) there is no clear evidence that they have had a negative effect on the native populations. Perhaps this is because dung is not a saturated resource in open tropical regions, but I will return to this point later.

The expansion of livestock production is a process that began recently, between the 1940s and 1950s, as a result of the colonization of the tropics in order to exploit unused land. Prior to this, livestock production was an extensive activity, but one that was limited compared to the current situation. Thus, although initial livestock production caused noteworthy changes to the landscape, these were not as marked as those occurring under the current rate of livestock expansion.

Certain questions arise in relation to the interaction between the dung of the livestock introduced to America, and especially Mexico, and the native dung beetles: Which species utilize this abundant resource? Where did these species originate? How were they able to adapt to use a new, exotic resource so successfully? In this study, I explore the evolutionary, biogeographical and ecological reasons behind the successful appropriation of this exotic resource by the Mexican dung beetles, and identify the species that have exploited the dung of this livestock, which is mainly from cattle and horses.

THE OROGRAPHY OF MEXICO

The complex orography of Mexico has favored the dispersal processes, vicariance and *in situ* speciation (mainly in the mountains) of plant and animal species. This combination of conditions has led Mexico to become one of the most megadiverse countries in the world. The Mexican High Plateau is extensive, and is highest at its southern end, close to the Trans-Mexican Volcanic Belt. As one advances northward, its elevation decreases. In the Valleys of Mexico and Toluca, the Mexican High Plateau reaches heights greater than 2300 m a.s.l. In the Chihuahuan Desert however, the elevation is only around 1000 m a.s.l. The northern limit of the High Plateau is located at the southern end of the Rocky Mountains. The Sierra Madre Occidental mountain range, delimiting the Mexican High Plateau on its western slope, runs parallel to the Pacific coast, from the border between the United States and Mexico to the state borders of Nayarit and Jalisco. Its total length is 1400 km and average width is 200 km. The eastern end of the Mexican High Plateau is the Sierra Madre Oriental, which consists of a series of elongated folds running in a NNW – SSE direction, from the north of the Texas Plateau southeastward, where it is interrupted by the Trans-Mexican Volcanic Belt, continuing SE, giving rise to the Sierra de Juárez mountains and terminating in the Isthmus of Tehuantepec. It is approximately 600 km long and an average of 80 km wide. The Trans-Mexican Volcanic Belt (or Neovolcanic Axis) is found between the 19th and 20th parallels and is some 950 km long and 50 to 150 km wide. At its eastern extreme, the Trans-Mexican Volcanic Belt has a discontinuity, but then continues as the Sierra de Los Tuxtlas mountain range, which is situated on the southern coastal plain of the Gulf of Mexico with a NW-SE orientation. The tallest peaks in this range are 640 to 1,680 m a.s.l. (Guevara *et al.*, 2004). The Sierra Madre del Sur mountains run parallel to the Pacific coast, from the state of Jalisco to the eastern part of the Isthmus of Tehuantepec. Between the Sierra Madre del Sur and the Trans-Mexican Volcanic Belt lies the Balsas Depression, the lowest part of which is located at 300 to 500 m a.s.l. The Central Massif and the Sierra Madre de Chiapas mountains are located in southeastern Mexico and constitute the northern projections of the Central American mountain system. The coastal plains run down the western and eastern sides of the country. East of Tabasco is the Yucatan Peninsula, which rose from the sea following the meteorite impact on Chicxulub at the end of the Mesozoic, ending the era of the dinosaurs. On the other coast of Mexico, the Baja California Peninsula is crossed from north to south by the Sierra de Baja California mountains.

This is the geographic landscape inhabited by the dung beetles, but it has not always been so; physiographic and tectonic changes have been, and still are, very intense in Mexico. Moreover, the dung beetles that presently inhabit Mexico have diverse biogeographic origins.

THE BIOGEOGRAPHIC ORIGINS OF THE DUNG BEETLES IN MEXICO

In biogeographical terms, Mexico is a very interesting country. It contains a zone of transition between the Nearctic and Neotropical regions (Darlington, 1957), which Halffter (1964) called the Mexican Transition Zone (MTZ). The biota of the Mexican High Plateau is fundamentally Nearctic and Palearctic in origin, while at the lower elevations of the southern regions and on the coastal plains, the biota is mainly of recent or ancient Neotropical origin.

The relationship between dung beetles and the expansion of livestock production in Mexico must be analyzed in the context of the biogeography of the country. The Mexican High Plateau is mainly populated by dung beetle species of Nearctic and Palearctic origins, as well as those that have evolved *in situ*, as has occurred with other animal groups. In the Mexican tropics, we find species of both recent and ancient Neotropical origins, and of Palearctic genera that have evolved *in situ*. The mountains host a mixture of species of diverse biogeographic origins, with a clear dominance of Nearctic species and those that have evolved *in situ*.

Halffter (1974, 1976) proposed several distribution patterns in the Trans-Mexican Volcanic Belt to explain the origin of the insects in this region and they apply to dung beetles. A distribution pattern refers to the current distribution of a group of organisms that originated in a given area; organisms which have coexisted over a long period of time and have a shared biogeographical history (Halffter, 1976).

The Paleoamerican Pattern

With origins in the Old World (Europe and Eurasia), the penetration of the insects with this pattern into America, and also therefore the MTZ, was from the north. The greatest diversity of insects at the supraspecific and specific levels in the Old World, compared to that of North America, suggests that the main center of evolution was the region comprising Europe and Eurasia. As with other insects exhibiting this pattern, beetle genera of Paleoamerican origin are ancient and widely distributed at the global level.

Onthophagus and *Sisyphus* are beetle genera of Paleoamerican origin. There are only two species of *Sisyphus* in the Americas (Halffter, 2003); however, at the species level, there is a notable diversification in *Onthophagus*, especially in warm and warm-temperate climates. Its penetration into the MTZ was likely to have occurred prior to the Miocene, when strong orogenic activity caused the uplift of the Mexican High Plateau and the Trans-Mexican Volcanic Belt and the definitive formation of the Sierra Madre mountain ranges of Mexico. The widespread distribution of *Onthophagus* in Mexico, from the Mexican High Plateau and the mountains to the tropical forests, suggests that they penetrated the MTZ before the existence of any large mountainous barriers. These same mountains influenced speciation, giving rise to endemic species that are found at different elevations, even in the foothills of the large mountain ranges. One example is *Onthophagus hippopotamus*, which inhabits mole tunnels in the high reaches of the Cofre de Perote Mountain in Veracruz. At the other extreme are the species of *Onthophagus* which inhabit the Mexican Desert. Pre-Pliocene fossils of *Onthophagus* and *Oniticellus* have been found in North America; the latter also belongs to the Paleoamerican Pattern. *Copris* is another genus of Palearctic origin with 24 species in the Americas, in addition to a fossil species (Matthews, 1962; Matthews and Halffter, 1968). In the United States of America this genus is found east of the 100th Meridian W, it is also found in Mexico and Central America, and there is one species in the Antilles.

Copris has a wide distribution, and more than 180 species with great diversification in tropical Asia and Africa, as well as in tropical America. Within the genus of *Copris*, one group of species (*fricator*) diversified in the mountains and another (*minutus*) has two complexes, one in the eastern United States of America and another (complex *incertus*) that is considered tropical. Various species of Paleoamerican genera certainly originated in the New World from Palearctic lineages.

The Nearctic Pattern

This is formed by Holarctic genera of relatively recent penetration (Plio-Pleistocene) that are restricted to the high reaches of the mountains of Mexico and of northern Central America in the MTZ. They correspond to genera that are ecologically associated with cold climates. Their habitat is mainly coniferous forest and high plains. In this pattern, there are Nearctic and Holarctic lineages. In the mountains of the MTZ, species with Nearctic affinities are generally found at a lower elevation than the Holarctic species are. The typically Holarctic boreo-montane elements of the MTZ have moved toward the south, exploiting the cold and humid conditions characteristic of the four glaciations during the Pleistocene and especially the periods immediately following these events.

Within the Nearctic Distribution Pattern, some representatives of the family Geotrupidae, the Geotrupini, are an example of an ancient group that has a sufficiently long history in the Americas to be reflected in the differences between species in the United States and those in the mountains of Mexico (Howden, 1964). *Geotrupes* and *Ceratotrupes* are found in the MTZ where *Ceratotrupes* is considered endemic, while *Geotrupes* is Holarctic and clearly related to the species of Asia and Europe (Howden, 1964). Both genera have numerous species endemic to Mexico.

The Mexican High Plateau Distribution Pattern

Formed by South American genera of ancient penetration into Mexico and Central America, with species endemic to the Mexican High Plateau of Mexico, Chiapas and Guatemala. They tend to dominate the Mexican High Plateau, and the high valleys of Oaxaca, Chiapas and Guatemala. They have penetrated the temperate forests of the mountains that border these geographic formations to a very limited extent. In terms of the species and individuals in the arid regions of Mexico, the canthonine species are generally the most numerous (Halffter, 2003). Species of the genus *Canthon* are found throughout Mexico, except in the high reaches of the cordilleras above 2500 m a.s.l (Halffter, 2003). According to the cladistic analysis done by Kholmann and Halffter (1990), a group of canthonine species found in arid formations, temperate pasture, pine,

pine-oak and temperate deciduous forest originated in an expansion during the Miocene. The species of this expansion belong to the genus *Canthon (C. humectus, C. pilularius, C. imitator, C. vigilans, C. chalclites and C. obliquus)*, the subgenus *Boreocanthon* and to the genus *Melanocanthon* (Halffter, 2003). With the exception of *Canthon obliquus*, a species endemic to the Sierra de la Laguna mountains on the southern tip of the Baja California Peninsula (Halffter, 2003), each of these species rolls a ball of dung, on which they feed or reproduce.

Canthon humectus Say is considered one of the most successful species of the Mexican High Plateau. It is distributed throughout the high valleys and plateaus of Oaxaca, Chiapas and the northeastern and eastern Mexican High Plateaus, especially in Jalisco and the warm dry areas of the Balsas River Basin, the valleys of Tehuacán-Cuicatlán and Guatemala (Halffter *et al.*, 2012). The Mexican High Plateau has been inhabited by this species for a very long time and eight subspecies are recognized (Halffter and Halffter, 2003). Its presence on the Mexican High Plateau suggests that this species of *Canthon*, of Neotropical origin, arrived there during the Miocene prior to the elevation of the Trans-Mexican Volcanic Belt (Halffter, 1976, 1987; Kohlmann and Halffter, 1990). Within the genus *Canthon*, the pilularius lineage is also of old Neotropical origin and four of its species inhabit the plains of the United States of America, with one reaching the High Plateau: *Boreocanthon puncticollis*, which is a canthonine of ancient origin.

One characteristic of the dung beetles on the High Plateau is the low number of species and the dominance of some of these species as a result of recent anthropogenic changes. For example, the extensive current distribution of *Canthon humectus* in the High Plateau is considered a direct consequence of the introduction of livestock by the Spanish, and also of the intense deforestation associated with the expansion of this productive activity (Verdú *et al.*, 2007; Halffter *et al.*, 2012). Cattle produce an abundant amount of dung, which is the most important source of food for *C. humectus* and deforestation has resulted in the high light intensity that is favorable to most of its subspecies, though some subspecies mainly live in the relatively shady conditions of the High Plateau forests (Halffter *et al.,* 2012). While it seems contradictory, the introduction of livestock has favored some Mexican species. A similar process occurs in parts of South America; Alfaro et al. (2008) describes how, in the coastal dunes of the Atacama and Coquimbo regions in Chile, the presence of herds of donkeys ensures the availability of food for *Megathopa villosa*. What did *Canthon humectus* and *Megathopa villosa* feed on before the introduction of livestock? Were they as abundant as they are now?

The Typical Neotropical Pattern

This pattern includes South American genera and species that have entered the MTZ in relatively recent times, following the low lying tropical regions and with minimal taxonomic separation from the South American forms. The northern limit of penetration of these elements is formed by the Mexican coastal plains covered in tropical forest, although these taxa can reach the southern and even eastern United States. The Canthonini tribe is very well represented in the Americas, and comprises a large number of species.

Canthonine species are roller beetles. These beetles, as described previously, are named for their ability to make a food ball out of dung, roll and bury it a certain distance away. The female modifies this food ball into a nesting ball, covering it with earth and laying an egg in the ball (Halffter and Matthews, 1966). Within the Mexican canthonines, there are strictly coprophagous, copronecrophagous and strictly necrophagous species (Halffter, 2003). In the tropical forest, there are a considerable number of species, but the relative number of individuals in open areas is greater than that found within the forest. *Canthon indigaceus* (a species typical of pastures), *C. cyanellus* and *C. morsei*, as well as species of the subgenus *Glaphyrocanthon*, form the group that expanded from South America in a second Pleistocene wave, and are associated with tropical ecosystems; while the *viridis* group specialized in Mexico to the south of the Trans-Mexican Volcanic Belt (Halffter, 2003). The ecological equivalent of the Coprini tribe in the Neotropical fauna is the tribe Dichotomiini, the ecological role of which is very similar to that of the Coprini, but with an area of evolution that is Gondwanian, specifically American.

The Mesoamerican Montane Pattern

Its origin is in the montane Central American Nucleus, from where expansion could have taken place to the north and south. The majority of its elements have an ancient South American affinity.

NATIVE MEXICAN VERTEBRATES CURRENTLY EQUIVALENT TO THE INTRODUCED LIVESTOCK

Animals heavier than 44 kg are classified as megafauna, therefore cows, horses and donkeys can be considered part of this group, although the term is more commonly used in the context of extinct animals. Arroyo-Cabrales et al. (2008) state that there are currently only four large native species in Mexico: the pronghorn (*Antilocapra americana*), the mule deer (*Odocoileus hemionus*), the white-tailed deer (*O. virginianus*) and the bighorn sheep (Ovis canadensis), although in relatively recent times there has also been the bison, which was reintroduced in northern Mexico. In the tropical regions of Mexico, we could also include the tapir which is 70 cm to one meter in height and weighs 180 to 300 kilos. Its feces are quite similar to those of the horse, but contain a greater quantity of fibrous material (Elizondo, 1999). However, unlike cattle, the tapir lives mainly in the tropical forest and on the banks of rivers. It is therefore difficult to imagine that the shift by Mexican dung beetles from using native animal dung to that of the introduced livestock can be explained by the similarity between their dung and that of the current native vertebrates. It is also clear that, given the complex orography of the country and the biogeographic history of the Scarabaeinae, we cannot easily explain the success of this group of insects in terms of the appropriation of a food resource that is apparently new to them.

THE MEGAFAUNA

How do we explain the fact that the introduction of livestock to Mexico and to America in general, has not created a serious ecological problem in terms of the recycling of dung? I suggest that the explanation lies in the type of resources used by the beetles in past eras. I refer mainly to the dung of the megafauna that began to disappear ten thousand years ago. The greatest diversification of dung beetles is associated with the spread of herbivorous mammals in the Mesozoic (Davis *et al.*, 2002; Arillo and Ortuño, 2008). Fifty million years ago, in the Miocene, the continents were populated by more than 150 genera of megafauna, but by the end of the Pleistocene, 10 000 years ago, 97 of these had disappeared (Barnosky *et al.*, 2004). In the case of Mexico, and the MTZ in particular, the successful penetration of the South American Scarabaeinae species in the Miocene and Pleistocene must have occurred thanks to the presence of a mammalian fauna and megafauna that provided abundant food resources for the dung beetles. We can say the same for the dung beetles of Holarctic and Nearctic origins.

In Mexico, the Miocene and Pleistocene mammal communities were more diverse than those of today. Some 10 000 years ago, Mexico had a wide diversity of medium-sized and large mammals with at least 61 large species of mammals during the Pleistocene, the majority of which were herbivores. These include animals weighing more than a ton, such as the mammoths (*Mammuthus* sp.), the American mastodon (*Mammut americanum*), the gomphotheres (*Cuvieronius*, *Stegomastodon*) and the ground sloth (*Glossotherium*, *Eremotherium*), as well as glyptodonts, horses, camels, llamas, bison and antelope. These lived alongside similarly large predators such as wolves, lions, saber-toothed tigers and bears, among others (Arroyo-Cabrales *et al.*, 2008; Pérez-Crespo *et al.*, 2012). Even Baird's tapir, *Tapirus bairdii*, currently distributed from Tehuantepec to the coast of Ecuador, also lived in northern Mexico and the southern United States (from California to Florida) during the Pleistocene, where it died out 10,000 years ago. In addition to these, rhinoceros (*Teleoceras*) remains have been found in Miocene sites in northern, central and southeastern Mexico (Carbot-Chanona *et al.,* 2009).

Additionally, in the state of Oaxaca, in southeastern Mexico, there are records of *Mammuthus columbi*, the Columbian mammoth, and of another two proboscidean species of the family Gomphoteriidae: *Rhynchotherium praecursor* and *Cuvieronius tropicus* (Pérez Crespo *et al.,* 2008). For Oaxaca, these authors describe finding fossil evidence of *Bison* sp. *Bison* fossils have even been found in Nicaragua. In the river basins of Oaxaca, the remains of megafauna from the Tertiary have been found, dated at 2 to 3 million years old. These include the camel *Camelops*, horse *Equus*, elephant *Elephas*, cow Bos and the pronghorn *Antilocapra*.

MEGAFAUNA AND THE DUNG BEETLES

The successful appropriation by dung beetles of the dung of introduced livestock in Mexico, and in America in general, was possible because they had been in contact with the dung of prairie mammal herbivores that certainly shared the properties and characteristics of the dung of current livestock. This is true mainly for cattle, mules and horses but also for sheep and goats, the dung of which is similar to that of deer. During the Miocene, pastures similar to savannas appeared in North and South America as a consequence of global cooling and the progressive increase in the aridity of the climate. Using biogeochemical markers, Pérez-Crespo et al. (2012), conclude that the Columbian or prairie mammoth (*Mammuthus columbi*), should be more appropriately named the pasture mammoth, after these pastures that resembled the savannas of Africa and had trees that allowed the animals to enjoy a mixed diet from grazing on the grass and browsing the trees. Such a diet would certainly have generated dung similar to that of present day cattle.

What quantity of dung was produced by the extinct megafauna? We cannot say, but it would have been enormous. Consider the fact that that one elephant produces approximately 200 kg of dung every day. If the 30 million head of cattle in Mexico were elephants, they would produce a total of 60×10^8 kg of dung, daily. Something had to remove such a huge amount of mega-dung in the past or an ecological collapse would have occurred very quickly. The natural candidates for this task are the dung beetles of that epoch.

However, this megafauna declined significantly during the Pleistocene due to various factors including changes in the environment and in human activity (Arroyo-Cabrales *et* *al.*, 2008). These authors state that, of the Mexican pleistocenic paleomastofauna, one order (Notoungulata), six families (20.9%), 29 genera (19.9%) and 77 species (28.1%) died out, including two of the three families of the order Proboscidea (Gomphotheriidae and Mammutidae), and three of the six families of the superorder Xenarthra (Glyptodontidae, Megatheriidae and Mylodontidae). The Proboscidea disappeared completely from Mexico and the rest of the Americas. Some families did not suffer worldwide extinction, but others, such as Antilocapridae, Bovidae and Equidae, lost most of their species. Of 78 extinct species of large mammals, 62 were herbivorous. This suggests that the dung beetles associated with those herbivores also suffered a notable reduction in species. A good indication of this is the low number of dung beetles species on the Mexican High Plateau, and the success and expansion of *C. humectus* with the introduction of livestock by the Europeans. All of this suggests that this species, or its ancestors, were very well adapted to consuming the dung of the megafauna present from the Miocene to the Pleistocene. Such a quantity and diversity of types of dung must have sustained a great number of dung beetle species that are now extinct. Another element that suggests that there was a more diverse beetle fauna in the past is the fact that cattle dung is not fully exploited in the grasslands of Mexico and the rest of the Americas. It has been explained that this is a consequence of an ecological semi-vacuum (Halffter *et al.*, 2008), but what has not been explained is why this vacuum exists.

I propose that this ecological vacuum is the result of the extinction of many dung beetles species that consumed the dung of the megafauna that started dying out during the Miocene, and mostly disappeared during the Pleistocene. The disappearance of a significant number of megavertebrates must have produced a cascade effect that also caused the loss of many species that depended on their dung. Dung beetle species number more than 150 in African savannas (Cambefort, 1991) and are supported by the dung of the big mammals such as elephants, rhinoceros, giraffes and impalas, among others. According to Davis et al. (2002), two principal ecological factors influence the present tribal, generic and species distribution patterns of Scarabaeinae dung beetles around the world: climate suitability and the number of types of dung. There is a relationship between dung diversity and the biogeographical and evolutionary history of mammals. Regions with low dung diversities (mostly comprising pellets and small omnivore/ carnivore droppings) feature low taxonomic diversification and high proportions of ball rolling taxa (Davis *et al.*, 2002). However, regions with higher dung diversities, comprising the dung of large herbivores, have greater taxonomic diversification, and one that is numerically dominated by tunneling taxa (including endocoprids and kleptocoprids). If that is true for the recent dung beetles, the same rule is likely to have applied in the past. Thus, a high species diversity of dung beetles (perhaps 50 to 100 species, or more) could have existed in the past on the Mexican High Plateau and in the tropical regions of the country. If this high dung beetle diversity did not exist, then the few species present at that time would have been hyperabundant in terms of the number of individuals.

CURRENT SCARABAEINAE SPECIES IN THE CATTLE PRODUCTION AREAS AND LIGHT-FILLED ENVIRONMENTS OF MEXICO

Table 1 lists the species that consume livestock dung present in the pastures and open areas of the Mexican High Plateau, as well as in tropical regions and mountains, according to a bibliographic search and interviews with some Scarabaeinae experts. Most of the taxa are species, but some are subspecies. I will consider all of them as species in this analysis. This list should be considered preliminary and will be expanded and refined with the support of colleagues and as more specific studies of dung beetle diversity in areas of livestock production in Mexico become available. Many species found in pastures are not on the list as they were considered to be unrepresentative of these environments; however, future studies may well modify this point of view. Open, light-filled environments—suitable for heliophilous organisms—are characterized by herbaceous plants and grasses, ranging from open prairies to semi-wooded and wooded savannas that allow sunlight to enter relatively shady sites.

The highest diversity of heliophilous species in Mexico is found in the tropical regions. I have recorded 24 species, including three subspecies of *Canthon indigaceus* and one of *Phanaeus tridens*. Almost 83% of the species are tunnelers or resident and about 17% are rollers. *Canthon indigaceus chevrolati* is very abundant on the coastal plains of the Gulf of Mexico and in the Yucatan (Halffter *et al.*, 1992; Montes de Oca *et al.*, 1991; Basto-Estrella, 2012), C. *i. indigaceus* is found on the tropical Pacific slope, while *C. c. chiapas* is in southeastern Mexico. Species of *Phanaeus* are very abundant in the light-filled regions of the Mexican tropics, especially *Phanaeus damon*, which is widely distributed on both coastal plains (Deloya and Moron, 1994) and which has benefitted from livestock production. *Dichotomius colonicus* is a very aggressive species that quickly invades open territory and is found distributed throughout Mexico, except for the Baja California peninsula (Kohlmann, 2003). *Copri incertus* is another highly abundant species in tropical Mexico, as is *Onthophagus incensus* in certain areas. *Onthophagus landolti* is very abundant in the open regions of Chiapas (Zunino, 2003) and a recent study showed it to be the most abundant species in terms of numbers of individuals on the livestock ranches of the Yucatan Peninsula (Basto-Estrella, 2012). *Digitonthophagus gazella* and *Euoniticellus intermedius* are introduced species.

TABLE 1

Preliminary list of dung beetle species that consume livestock dung and are present in pastures and open areas in Mexico.

Lista preliminar de escarabajos del estiércol que se alimentan de estiércol de Ganado y están presentes en pastizales y áreas abiertas de México.

Tropical regions
Ateuchus rodriguezi DeBorre, 1866
Canthon (Boreocanthon) ateuchiceps Bates, 1887
Canthon (Canthon) indigaceus chevrolati Harold, 1868
Canthon (Canthon) indigaceus chiapas Robinson, 1948
Canthon (Canthon) indigaceus indigaceus LeConte, 1866
Copris incertus Say, 1835
Copris sallei Harold, 1869
Dichotomius centralis Harold, 1869
Dichotomius colonicus Say, 1835
Digitonthophagus gazella Fabricius, 1787
Euoniticellus intermedius Reiche, 1848
Phanaeus (Phanaeus) amithaon Harold, 1875
Phanaeus (Phanaeus) damon Castelnau, 1840
Phanaeus (Phanaeus) daphnis Harold, 1863
Phanaeus (Phanaeus) nimrod Harold, 1863
Phanaeus mexicanus Harold, 1863
Phanaeus (Phanaeus) tridens Laporte & Castelnau, 1840
Phanaeus (Phanaeus) tridens pseudofurcosus Balthasar, 1939
Phanaeus (Phanaeus) furiosus Bates, 1887
Phanaeus (Phanaeus) scutifer Bates, 1887
Onthophagus batesi Howden & Cartwright, 1963
Onthophagus hoepfneri Harold, 1869
Onthophagus incensus Say, 1835
Onthophagus landolti Harold, 1880
Mexican High Plateau
Canthon(Canthon) humectus hidalgoensis Bates, 1887
Canthon(Canthon) humectus humectus Say, 1832
Canthon (Canthon) humectus incisus Robinson, 1948
Phanaeus (Phanaeus) adonis Harold, 1863
Phanaeus (Phanaeus) quadridens Say, 1835
Phanaeus (Phanaeus) vindex Macleay, 1819
Onthophagus mexicanus Bates, 1887
Mountains
Copris armatus Harold, 1869
Copris klugi Harold, 1869
Onthophaugus chevrolati chevrolati Harold, 1869
Onthophagus fuscus parafuscus Zunino & Halffter, 2005
Subfamila Geotrupinae:
Geotrupes (Megatrupes) cavicollis Bates, 1887
Geotrupes (Onthotrupes) herbeus Jekel, 1865
Geotrupes (Halffterius) rufoclavatus Jekel, 1865
Ceratrotupes bolivari Halffter & Martínez, 1962
Ceratrotupes fronticornis Erichson, 1847
Onthotrupes herbeus Jekel, 1865
Onthotrupes sallei Jekel, 1866

On the Mexican High Plateau, there are approximately seven species associated with open environments. Four of these are tunnelers and three are rollers, and they can be found on some mountains within their distribution area. Here, the genus *Phanaeus* of the *mexicanus* and *daphni* groups is formed by species that are undergoing expansion in central Mexico as a result of livestock production. *Canthon humectus* is a very successful heliophilous roller on the Mexican High Plateau and also owes its success to livestock production (Verdú *et al.*, 2007; Halffter *et al.*, 2012). In the Barranca de Metztitlán, Puebla, *C. humectus hidalgoensis* is the most dominant species. The frequency of this heliophilous roller is high on the Mexican High Plateau, as is that of the other subspecies *C. humectus humectus*, and *C. humectus sayi* in similar agroecosystems (Halffter *et al.*, 2012). Verdú et al. (2007) propose that an alternative food source for *C. humectus hidalgoensis* could be the decomposing fruit and plant matter provided in Metztitlán, Puebla by the widely cultivated species of *Agave* and *Opuntia*. If this is the case, it is very likely that their populations would have been considerably smaller before the conquest than they are now, thanks to the abundance of the dung produced mainly by donkeys.

In the mountains of Mexico, there are 11 heliophilous species that consume the dung of cattle and horses. Four of these species belong to the subfamily Scarabaeinae, and seven to the subfamily Geotrupinae. All of these are tunnelers: there are no roller species associated with the upper montane regions.

CONCLUSIONS

In an environment that is increasingly anthropized, the conservation policies that limit traditional human activities such as livestock production and agriculture can have a negative impact on the biota of certain regions by homogenizing the environment and reducing the rate of species exchange between habitats (Halffter *et al.*, 2012). The current trend is to favor silvopastoral systems that create a complex, but highly productive and economically beneficial environments, one that is also considered to be the most environmentally friendly. For the dung beetle, traditionally managed landscapes constitute a complex system that favors the interaction of livestock, grazing, vegetation structure and dung beetle community systems (Verdú *et al.*, 2007; Díaz *et al.*, 2010; Halffter *et al.*, 2012).

New paradigms in conservation biology propose that connectivity, via corridors of natural vegetation between patches of natural habitat, should be analyzed in the context of the agricultural or managed matrix. The objective is to achieve a matrix that is biodiversity friendly, and one that facilitates the movement of forest species between forest fragments (Perfecto and Vandermeer, 2008). Living fences appear to act as continuous habitat corridors and allow forest beetles to colonize other forest fragments (Estrada and Coates-Estrada, 2002; Díaz *et al.*, 2010). With dung beetles, however, we must also consider facilitating the movement of open area species between pastures: the high turnover of species between pastures and forest fragments shows that few forest species colonize the pastures and vice versa (Halffter *et al.*, 1992; Estrada and Coates-Estrada, 2002; Díaz et al. 2010). Connections between natural areas and managed landscapes can therefore help sustain biodiversity and the natural processes of ecosystems, in addition to transforming the unfriendly matrix into a more hospitable managed matrix (Bennett, 2003; Vandermeer and Perfecto, 2007; Perfecto and Vandermeer, 2008).

While the introduction of livestock has had a strong impact on the original ecosystems of the Americas, and Mexico in particular, livestock dung itself has not caused a problem. Nevertheless, the beetles that consume this dung now face new challenges that threaten their survival, and the environmental service of dung recycling where livestock is produced is therefore being affected. Currently, the most serious challenge is posed by the use of parasiticides and insecticides in livestock management and these can kill or reduce the populations of dung beetles (Martínez and Lumaret, 2006; Nichols *et al.*, 2008; Cruz, 2011; Cruz *et al.*, 2012). This practice could end up having a very costly impact on livestock production. The presence of introduced species may pose another threat to the survival of heliophilous dung beetles, but we do not yet have any specific studies on this topic. The view of the experts has been that the dung beetles are the guardians of the temperate and tropical forests; a vision of guardianship that is now justifiably widening to encompass the areas where livestock is raised.

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FACTORES HISTORICOS, BIOGEOGRÁFICOS Y ECOLÓGICOS EXPLICAN EL ÉXITO DE ALGUNOS ESCARABAJOS DEL ESTIÉRCOL NATIVOS DESPUÉS DE LA INTRODUCCIÓN DEL GANADO EN MÉXICO

RESUMEN

La introducción de diferentes tipos de Ganado después de la conquista de México por los españoles generó notables cambios en el paisaje del Altiplano Mexicano y de las regiones tropicales del país, al reemplazarse las actividades fundamentalmente agrícolas de las poblaciones indígenas por el estilo Europeo de producción ganadera. Aunque el efecto de esta actividad sobre la vegetación fue notable, el estiércol producido por el ganado, principalmente el proveniente de vacas, caballos y ovejas, no generó el mismo nivel de problemas ambientales que si se generaron con la introducción del ganado en Australia y Nueva Zelandia. Esta diferencia se explica porque los escarabajos del estiércol de México y de América en general fueron capaces de utilizar este recurso exótico e incorporarlo al ciclo de nutrientes de los suelos templados y tropicales del continente americano. La capacidad para utilizar un recurso exótico, como lo es el estiércol del ganado introducido en América, puede ser explicado por la historia evolutiva, biogeográfica y ecológica de las especies nativas de los escarabajos del estiércol del continente americano. Biogeográficamente, los escarabajos del estiércol de México provienen de líneas filéticas que se originaron en las regiones Paleárticas, Neárticas y Neotropicales, llegando a México en diferentes oleadas que ocurrieron durante el Mioceno y el Pleistoceno. Durante esas épocas, la megafauna de México incluía mamuts, mastodontes, gonfoterios, caballos, camellos, gliptodontes, bisontes y antílopes, entre otros. Estos animales producían estiércol que fue similar al del Ganado introducido por los españoles, principalmente el de vaca y caballo. Esta situación hizo posible que los escarabajos del estiércol nativos explotaran fácilmente el Nuevo recurso provisto por el Ganado introducido por los Europeos. En un paisaje tan antropizado como lo es actualmente México, debemos de enfocarnos no solo a la conservación de los escarabajos del estiércol que habitan nuestros bosques templados y tropicales, sino también tenemos que proteger a las especies encontradas en los pastizales ganaderos las cuales proveen valiosos servicios al ecosistema, tales como la incorporación del estiércol al ciclo de nutrientes, pero que se están viendo amenazadas por otras actividades humanas como el usos de desparasitantes e insecticidas para el ganado y por el cambio climático global.

Palabras clave: Mesoamérica, Scarabaeinae, Nueva España, megafauna.