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Invasion of Mexico by Two Dung Beetles Previously Introduced into the United States

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ABSTRACT

Following the Australian CSIRO strategies, the United States Department of Agriculture introduced several dung beetle species as a biological control to decrease the dung accumulation and proliferation of different pest fly species therein. Of these, two species have been very successful: *Digitonthophagus gazella* and *Euoniticellus intermedius*. They have expanded from their release sites in the United States, and quickly invaded Mexican territory and dispersed rapidly. Here we report on 27 new capture sites in several Mexican states from 1994 to 1996 and discuss invasion routes as well as ecological conditions.

KEYWORDS: Scarabaeinae, introduced dung beetles, invasion of Mexico, unsaturated guilds.

INTRODUCTION

Introduction of exotic species and their eventual establishment and expansion present opportunities for ecological analysis. One is the chance to study the dynamics of the invasion. Another is to investigate if and how native populations react to the newcomer both initially at first contact and later on after competitive or other interactions had time to develop.

We gathered information on the invasion of Mexico by two species of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) previously introduced into the United States to remove cattle dung from the surface. The spread of *Digitonthophagus gazella* (F.) and *Euoniticellus intermedius* (Reiche) in different areas and along different routes is discussed under ecological and biogeographical aspects.

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RESULTS

Relationships between localities of *D. gazella* in Mexico and its release points in United States have been published recently (Kohlmann, 1994; Barbero & López-Guerrero, 1992). For *E. intermedius* this information is presented here for the first time.

Introduction into America of *E. intermedius* and *D. gazella*

The original distribution of *E. intermedius* is Ethiopian (Balthasar, 1963). It was introduced into Australia from South Africa in March 1971 and rapidly became established, obtaining an “explosive” success comparable to that of *Digitonthophagus gazella* (F.) (Bornemissza, 1976) and *Sisyphus spinipes* (Thunberg) (Doube et al., 1991). It has also been introduced into Hawaii and Puerto Rico (Fincher, 1986) and into New Caledonia (Rougon, 1987: 181). The first specimens for subsequent release in America came from Hawaii and were reared at the University of California, Davis, in 1974 (Anderson & Loomis, 1978). The founding Hawaiian material was obtained from CSIRO in Australia, originally collected in South Africa (USDA-ARS, 1992, 1993, 1994; G.T. Fincher, pers. comm.). Fincher (1986) pointed out that *E. intermedius* was released in California, but it has not been possible to determine where, when, or how many times releases took place. The most probable release date is 1978, a year before the California beetle introduction program was terminated (R. Moon, pers. comm.). Using material obtained in 1977 at the University of California, Davis, the USDA-ARS Veterinary Toxicology and Experimental Research Laboratory in College Station made the first of a series of releases in 1979 in six Texas counties (USDA-ARS, 1992, 1993, 1994; G.T. Fincher 1995, pers. comm.). *E. intermedius* was also introduced in Georgia in 1984 (Fincher, 1986).

The present distribution of *E. intermedius* in the United States is not accurately known. According to Blume (1984) and Fincher (1986), it has become established in California and Texas. In a study made in August 1991 in Cochise County, southeastern Arizona, *E. intermedius* was not collected among the 18 dung beetle species found at six sampling stations (Dajoz, 1994). While information about *E. intermedius* is limited, much is known on the present distribution of *D. gazella* in the United States (for information about the introduction of this species see Barbero & Lopez-Guerrero, 1992; Kohlmann, 1994). In 1981, *D. gazella* was found in several counties in California, in southern and southeastern Texas and in parts of Arkansas, Louisiana and Georgia. Its fastest expansion was to the south and east of Texas rather than to the north (Fincher et al., 1983). Hunter and Fincher (1985) reported finding this species in some parts of Oklahoma, Mississippi, Alabama and Florida, bringing the total to nine U.S. states where *D. gazella* was found. Kohlmann (1994) reported more recent records of *D. gazella* in Arizona and New Mexico; these sites make up the meeting point of the populations originating in California with those from Texas. There is little known about its expansion to the north, but its advance to the northeast has been shown by the collections in some sites in North Carolina (K. Vulinec, pers. comm.).

Expansion in Mexico

Locality data for *E. intermedius* and new data for *D. gazella* in Mexico (Figures 1 and 2) are based on our collections as well as those of colleagues. Voucher specimens were deposited in several collections. Without the record from 1992, all localities for *E. intermedius* are being published here for the first time.

1992: State of Durango: Mapimí and La Michilía Biosphere Reserves (Montes de Oca et al., 1994).

1994: State of Baja California Sur; State of Hidalgo: Tlanchinol; State of Tamaulipas: Los Cedros Biological Station, Gómez Farías, El Cielo Biosphere Reserve.

1995: State of Durango: Durango City; State of Guanajuato: Sierra de Santa Rosa; State of Michoacán: Cerro Tzirate, Quiroga; State of Veracruz: municipalities of Alto Lucero, Actopan, Emilio Zapata, Jalcomulco and Xalapa.

1996: State of Chihuahua: Yepáchic, Cuauhtémoc; State of Jalisco: six municipalities on the Pacific littoral; State of Michoacán: Santa Fe El Chico; State of Sonora: San Carlos, Yécora; State of Veracruz: Cordoba.

1997: New localities for *D. gazella* in the state of Baja California Sur: Sierra de La Laguna; State of Chihuahua: Yepáchic, Cuauhtémoc; State of Sonora: Yécora.

Comparison of Expansion Routes of *E. intermedius* and *D. gazella*

If we compare the expansion of *E. intermedius* and *D. gazella* in Mexico (Figures 1 and 2), we find common routes and different ones beginning at introduction sites in the United States. *D. gazella* has avoided the Mexican Plateau and the surrounding mountains although there are penetrations in various points of the Plateau. One route follows the Pacific coast line, starting at the release sites in southern California, with a rapid expansion south into Mexico. By 1989 *D. gazella* had already reached the coast of Oaxaca but is known only from the southern tip of the Baja California Peninsula in Los Cabos (Kohlmann, 1994) and the Sierra de la Laguna (A. Tejas pers com). The other principal invasion route of *D. gazella* follows the Gulf coastal plain starting at the release sites in Texas, with a penetration into the northern part of the Mexican Altiplano (Figure 2).

E. intermedius also shows a Gulf of Mexico and Pacific expansion route, but its great success in colonizing the Altiplano Plateau has allowed it to extend to the south (Figure 1). Its colonization of Baja California has been wider than that of *D. gazella*. We regard the presence of *E. intermedius* in Sonora

Fig. 1. Dispersal of *E. intermedius* in Mexico after its introduction in the U.S.A. Collection sites are marked by stars and collection years are indicated to one side. See text for discussion about the presumed dispersal routes followed by *E. intermedius* into Mexico.

(San Carlos) as the result of its having successfully crossed the coastal desert. Its presence in Jalisco may be the result of an expansion southward along the Pacific coast (as happens in *D. gazella*) or to a rapid descent from the Plateau. We have no records from Sinaloa and Nayarit which would support the former hypothesis. *D. gazella* reached Guatemala in 1987 via Gulf of Mexico coastal plains (Kohlmann, 1994). *E. intermedius*, on the contrary, has just arrived (1995) to central Veracruz, an arrival date we consider accurate because central Veracruz is regularly and systematically sampled by Institute of Ecology personnel. On the Mexican Plateau *D. gazella* arrived at Mapimí in 1984 (a reliable first arrival date) and its southern penetration limit is in San Luis Potosí, achieved in 1987 (Kohlmann, 1994). *E. intermedius* arrived in Mapimí and La Michilia in Durango (1992) and southern to the states of Guanajuato and Michoacán.

The presence of *E. intermedius* in the state of Hidalgo near Tlanchinol results from an expansion inland from the Gulf coastal plains as a consequence of its greater ability to invade higher altitudes. *E. intermedius* is found in La Michilia (2600 m above sea level), in La Virgen ravine in the Sierra de Santa Rosa in Guanajuato (2430 m) and in Santa Fe El Chico (2160 m) and near the Cerro El Tzirate (2300 m); (these last two sites are in the Municipality of Quiroga in the State of Michoacán). *D. gazella* has not settled in La Michilía (only one specimen has been captured in a light trap in 1996 despite intensive samplings since 1995; S. Anduaga, pers. comm.) and the highest altitude where it has become established is just under 2000 m. Even though in Autlán, Jalisco, it has been recorded at 1150 m (Rivera-Cervantes & Garcia Real, 1991) new records of *D. gazella* at the inner part of the Western Sierra Madre (toward the Plateau) have been made at 1400 m (Yécora, Sonora), 1620 m (Yepachic, Chihuahua), 1650 m (countryside between the cities of Chihuahua and Cuauhtémoc, Chihuahua), and 1920 m (near Basaseachic, Chihuahua) (W.D. Edmonds and P. Reyes-

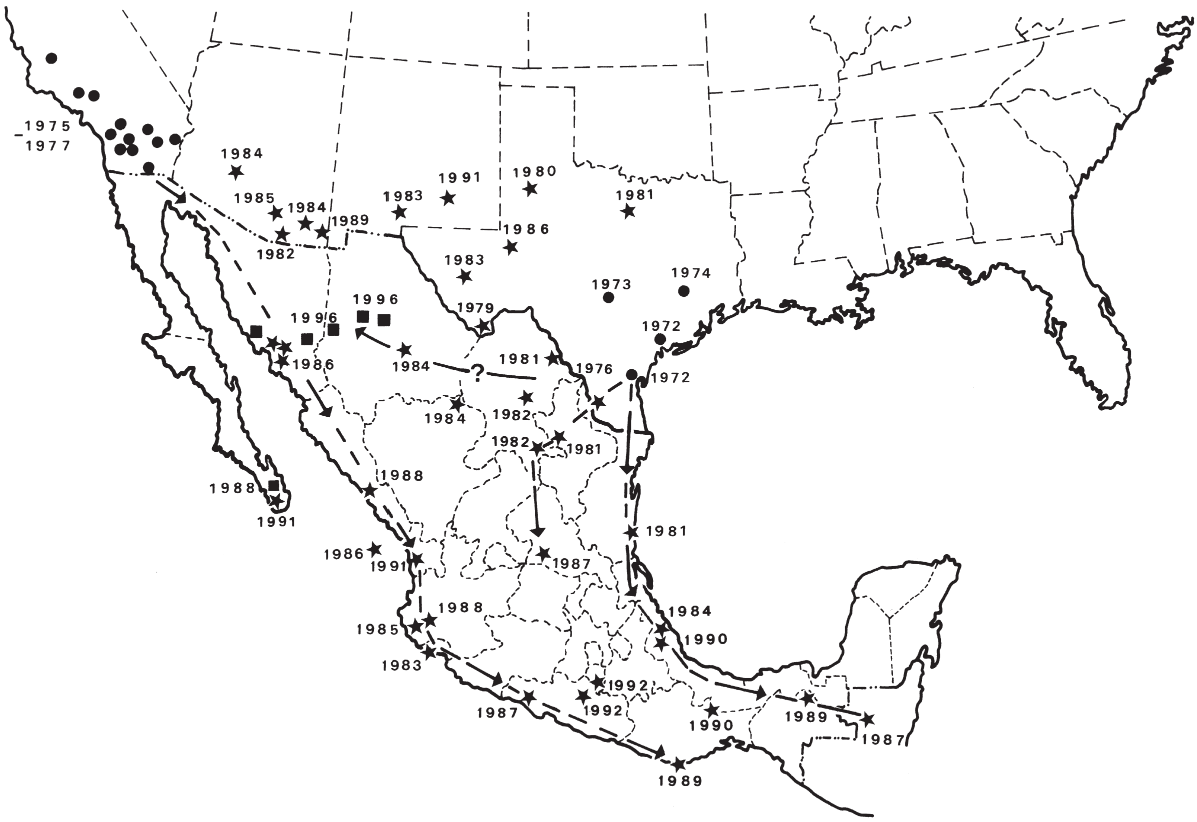

Fig. 2. Introduction and dispersal of *D. gazella* in North America. Original introduction sites are indicated by dots. Subsequent collection sites are marked by stars. Corresponding introduction and collecting years are indicated to one side. Squares indicate new records for *D. gazella* and those marked near the border between the states of Sonora and Chihuahua, in the inner part of the Sierra Madre Occidental, suggest a dispersal route across the northern part of the Mexican High Plateau from east to west. The other three dash/arrow lines represent the Atlantic, the Mexican High Plateau and the Pacific dispersal routes of *D. gazella*. (modified from Kohlmann, 1994).

Castillo pers. comm.). These represent the highest known altitude records for *D. gazella*. In central Veracruz Halffter et al. (1995) found that *D. gazella* does not go over an altitude of 1000 m even though it established itself at lower levels more than 12 years ago. On the contrary, *E. intermedius*, which arrived in this same area in 1995, has already reached an altitude of 1770 m starting its ascent through different routes toward the Transverse Neovolcanic Axis. *Euoniticellus intermedius* is at least as resistant as *D. gazella* to arid conditions (as the Baja California Peninsula colonization illustrated), and it has a greater capability for ascend mountains (and inferred ability to withstand lowest temperatures). Is it capable of colonizing a community at the other end of the ecological spectrum: the rain forest? Even though *D. gazella* has reached and proceeded southward around tropical forest areas (Los Tuxtlas, Veracruz; Palenque, Chiapas), it does not seem to penetrate it in spite of its great abundance in grasslands and disturbed adjacent areas. *E. intermedius* is still expanding toward southern Veracruz. For the record, neither *E. intermedius* nor *D. gazella* have been collected in African rain forests (Cambefort & Walter, 1991).

Both species have very similar life histories (Table 1). They also have a similar biogeographic origin. They are both coprophagous species best adapted to cattle dung and open, sunny habitats. *E. intermedius* has been found in pastures as well as in open tropical deciduous, oak-pine and oak forests and in semiarid matorral dominated by *Acacia* and *Opuntia*. For *D. gazella*, a certain degree of plant cover represents a barrier; it has never been collected in closed forests.

The expansion rates in Mexico are similar for both species. By looking at the most reliable date of first arrival we conclude that it took *D. gazella* 12 years to move from Texas, where it was released in 1972,

TABLE 1. Comparison of some life history parameters of two species of dung beetles which recently invaded Mexico.

		Species	
		Euoniticellus intermedius	*Digitonthophagus gazella*
Dung relocation		burrower	burrower
Length (mm)		7–9	10–13
Weight (mg)	fresh	45	130
	dry	17	52
Activity		diurnal	crepuscular/nocturnal
Broods per nest		many	<45
Preimaginal development (days)		28	30
Fecundity		120	90
Overwintering		larvae + adults	larvae + adults
Generations		several	several
Longevity (days)		45	60

• After Doube (1991: 153), Cambefort (1991: table B 9(1) 390–391, Rougon & Rougon (1991: table B 13, 414) and own data.

to Mapimí, where it first appeared in 1984. *E. intermedius* was released in Texas in 1979 and was first recorded in Mapimí in 1992. The time elapsed in both cases is similar, about 12 years, and suggests a rate of expansion between central Texas and the Altiplano of about 50 km per year. Expansion time for both species to Tamaulipas was identical, nine years or about 56 km per year. However, the advance of *E. intermedius* south of Tamaulipas has been faster than *D. gazella*. Only one year after its capture in Tamaulipas, it was collected in Palma Sola and other localities of central Veracruz about 480 km to the south. It took *D. gazella* two to three years to travel this same distance (Kohlmann, 1994; Montes de Oca & Halffter, 1995).

In the literature there are several dispersion speed estimates for *D. gazella* but none for *E. intermedius*. Kohlmann (1994) estimated that *D. gazella*'s expansion speed above the plains of the Gulf of Mexico (Texas to Guatemala) was 103 km per year. It was even higher along the Mexican Pacific coast (220 km per year). These expansion speeds are much higher than those determined for Australia (50 to 80 km per year, Seymour, 1980) or the United States (58 km per year, Hanski & Cambefort, 1991). That *D. gazella* is a good flier is evidenced by its arrival at an Australian island situated 26 km off shore (Ridsdill-Smith, 1979) as well as its occurrence on Maria Madre and Maria Magdalena Islands approximately 45 and 27 km respectively off the coast of Nayarit in Mexico.

DISCUSSION

Biogeography of the Invasion

The invasion of Mexico and northern Central America by tropical species from the Old World introduced in the United States is an exceptional opportunity to analyze the historical biogeography of Mexican insects, specifically those that follow the Tropical Paleoamerican Distribution Pattern. According to Halffter (1976), the Paleoamerican pattern is followed by Old World genera or groups of species well adapted to warm or temperate-warm climates. Their arrival to America was ancient and probably via the Bering Strait. Their expansion to the Mexican Transition Zone (MTZ) is also ancient. Having speciated in the MTZ, they represent the groups of northern origin with the widest distribution in Mexico. Halffter et al. (1995) divided this pattern into four subdivisions. Of these, the Tropical Paleoamerican Pattern includes the groups that adapted to the tropical conditions of lowlands and sites of moderate altitudes where they coexist with elements of neotropical origin. Some of these species colonize mountains up to moderate altitudes as is also done by species of neotropical origin in response to favourable conditions: protected cliffs, local high humidity, infrequent frost, etc.

D. gazella and *E. intermedius* are expanding in the MTZ following a distribution very similar to the groups of native species that followed the Tropical Paleoamerican Pattern. There is, however, an ecological difference between the invading species and the native species exhibiting the Tropical Paleoamerican Pattern. In both cases they are distributed throughout Mexico's tropical lowlands, but among the native tropical paleoamerican lines there are several species that penetrate the tropical rain forest (for example, *Onthophagus* from the clypeatus group, and *Copris laeviceps* Harold). So far, neither invading species has entered the tropical rain forest in spite of having populated adjacent habitats (especially *D. gazella*). Conversely, they have had much success in colonizing very arid places (Baja California, Mapimí, northern Sonora) where there are none or very few native species that follow the Paleoamerican Tropical Pattern.

In Baja California Sur the very poor Scarabaeinae fauna consists of an endemic mountain species from Sierra La Laguna (*Canthon obliquus* Horn), *Onthophagus cartwrighti* Howden and, dominating the lowlands, *Canthon (Boreocanthon) puncticollis* LeConte. Of these three species, the two *Canthon* are of clear neotropical affinity, even if they are endemic species, one to southern Baja California and the other to northern Mexico and the United States. *Onthophagus* is of paleoamerican affinities but does not belong to the lines with tropical paleoamerican distribution. In Mapimí (State of Durango), a very arid region in the northern Mexican Plateau, the native scarabaeinae fauna comprises *Canthon imitator* Brown, C. (*Boreocanthon*) *praticola* LeConte and *C.* (*B.*) *puncticollis* LeConte. These three species are characteristic of northern Mexico and the United States and have neotropical affinities at the generic level. The paucity of coprophagous beetle fauna in a cattle-raising area like Mapimí is even more evident when we extend the list to include all Scarabaeoidea. To the three autochthonous species of Scarabaeinae mentioned before (of which only *C. puncticollis* is frequently collected) and two invaders, we only have to add three Aphodiinae species: *Aphodius* (*Labarrus*) *lividus* Olivier, *Aphodius* (*Otophorus*) *haemorrhoidalis* (L.), and *Aphodius* (*Nialaphodius*) *nigrita* Fabricius. The first two (perhaps all three) were recently introduced into America (Lobo, 1996). Thus, from a very poor present pool of eight Scarabaeoidea species, four (maybe five) have recently expanded following introduction into the United States. These figures are even more impressive if we consider that already in 1993, 96% of the individuals (and a great proportion of biomass) in Mapimí corresponded to *D. gazella* and *E. intermedius*. In ecological terms, Mapimí was practically empty of coprophagous Scarabaeoidea before the very recent arrival of the two new invading species. This was the observation of 15 years ago, judging by the number of unworked dung pats on the ground (Halffter, pers. obs.). The known importance of invading species in arid zones is widened by collections from the coastal plain of Sonora where, aside from *D. gazella* and *E. intermedius*, only *C.* (*B.*) *puncticollis* is found.

The Scarabaeinae fauna of the most arid places of northern Mexico is made up of paleoamerican elements (but not tropical paleoamerican) and genera of neotropical affinity, such as *Canthon*, which have species adapted to xeric conditions. Why have *D. gazella* and *E. intermedius* been so successful in places where, during the Cenozoic, no Old World elements arrived that were adapted to extreme arid conditions? The explanation seems to be in the ecological characteristics of the Old World phyletic lines that arrived in North America during the Cenozoic. Their places of origin are located in temperate conditions and the species closest to the American ones are today in eastern Asia (as happens with the species related to the *Onthophagus chevrolati* group (Zunino & Halffter, 1988). Or, in the case of the lines that follow the Tropical Paleoamerican Pattern, their relatives are in the tropics of the Old World but not in arid conditions. For example, the non-American species most closely related to the *Onthophagus clypeatus* group are located in southeast Asia (Zunino & Halffter, unpublished). What does seem clear is that no species with the ecological and biogeographical characteristics of *D. gazella* and *E. intermedius* arrived in America from the Old World during the Cenozoic. Introduction of *D. gazella* and *E. intermedius* into America has jumped the climatic barriers that would have otherwise prevented their immigration.

Unsaturated Niches and Their Relationship with the Success of Invading Species

Invasion would not have been so fast if cattle dung had not been a new food source in Mexico (16th century to now) that supported an unsaturated beetle guild. This is true particularly for the small and medium sized burrowing species like *D. gazella* and *E. intermedius*. Halffter et al. (1995) pointed out that, under the tropical conditions of central Veracruz, the number of Scarabaeinae species found in grasslands with cattle is always lower than in tropical forests, even though in the forests available dung is much less. If we compare the case of Veracruz with the Scarabaeinae fauna found in Africa in places with open vegetation and wild mammal dung, the differences are notable. In a central Veracruz grassland, Montes de Oca & Halffter (1995) recorded 18 native scarabaeine species of which 11 are burrowers. In the same geographic area under similar conditions and at other points, 9 to 14 species were found of which 6 to 8 are burrowers (Halffter & Arellano, unpublished data). For African communities, the numbers are much greater: 120 species (Doube, 1991), 123 species (Cambefort, 1991) and with a preponderance of burrowers. In arid sites with cattle dung available, the difference is more striking: three native species in Baja California Sur and three in Mapimí, of which only one species from Baja California is a burrowing beetle. For comparison, in Africa (Niamey) under similar conditions there are 21 species, of which 19 are burrowers (Rougon & Rougon, 1991). All Mexican and African communities we compared (tropical grasslands or arid places) include either or both *D. gazella* or *E. intermedius*.

Rich coprophagous scarabaeine faunas are not restricted to Africa. According to Martin-Piera and Lobo (1995), in the Iberian Peninsula "…any grassland of 100 m^2 may contain more than 40 species, and a single dung pat will easily provide a collection of 15 to 20 species." These figures approximate a scarabaeoid guild (Scarabaeinae, Geotrupinae and Aphodiinae) close to saturation (or saturated) in a grassland with abundant cattle dung. Ridsdill-Smith & Kirk (1981) estimated that in the Iberian Peninsula, 80% of the dung is removed by beetles. In Mexico, either in the hot Veracruz grasslands, or in the arid conditions of Mapimí or Baja California Sur, most of the dung pats were scarcely disturbed by the dung beetles before the arrival of *D. gazella* or *E. intermedius*.

In Mexico, induced tropical grasslands or the pastures in arid zones support a guild of dung beetles (in number of species and number of individuals) disproportionately smaller than available food would allow. The changes caused by humans have created suitable conditions for the rapid expansion of invading species. Deforestation establishes an uninterrupted sunny environment of grasslands and open formations where forests are reduced to patches. The subsequent establishment of cattle raising produces an unprecedented availability of food in a now highly unsaturated niche. The results are: 1) a demographic "explosion" that has accompanied the arrival in many places of the first invading species (for example, Central Veracruz and Mapimí). In many sites, a few years after its first record, *D. gazella* was the most abundant burrowing species of Scarabaeinae; 2) a high expansion rate of both invading species; 3) weak effect by invaders on native species, at least in the case of *D. gazella* (*E. intermedius* has only recently arrived in the study areas).

In Australia, *D. gazella* and *E. intermedius* have also expanded in unsaturated niches because most of the native Australian species do not utilize cattle dung and live in the forest (Matthews, 1972, 1974, 1976; Doube et al., 1991). As in Mexico, this is evident in the invading species' rapid success. Moreover, in Australia the number of individuals of both species captured by traps is higher than that collected under similar conditions in their area of origin (South Africa), where they compete with other native species (Box 15.3 in Doube et al., 1991).

We have cited as additional evidence of the lack of saturation in the niche the weak influence of the invasion on the native species. Even though *D. gazella* dominates in central Veracruz and is associated with the marginalization of the native species, *Onthophagus batesi* Howden & Cartwright (Montes de Oca, 1993, 1994; Montes de Oca & Halffter, 1995), evidence for concluding competitive exclusion is insufficient. There seems to be a spatial segregation by which *D. gazella* occupies places with full sun while *O. batesi* survives in partially shaded places (Lobo & Montes de Oca, 1994; Montes de Oca, unpublished). Howden & Scholtz (1986) pointed out that a possible result of the introduction of *D. gazella* into Texas is a population decline in *Onthophagus pennsylvanicus* Harold, *O. hecate* Panzer and possibly another *Onthophagus* species. However, there are no conclusive evidences to relate changes on native species to the presence of *D. gazella*, because they can be also associated to changes in rainfall or vegetation. Preliminary data from Australia (Doube et al., 1991) suggest that *D. gazella* has no perceptible effect on the native species.

Aside from taking advantage of favourable ecological conditions, *D. gazella* and *E. intermedius* have a series of characteristics that help to explain their success: a) their high biotic potential (Table 1), enhanced by being multivoltines; b) a preference for bovine dung, which is both very abundant and nutritionally rich; (c) an eurytopic environmental tolerance strategy (most Mexican species are very stenotopic). Both species colonize areas of grasslands, underbrush and open forest formations where they find ample food and sunlight. The only difference is that the capacity for occupying areas with some forest cover seems to be less in *D. gazella* than in *E. intermedius*, not only in Mexico but also in their original African habitats (Davis, 1987). In both invading species, the preference for cattle dung is present in their original areas (Doube, 1991: 147, Cambefort, 1991: 390–391, Rougon & Rougon, 1991: 414) as well as in places where they have been introduced. We have already commented that tolerance to extreme arid conditions seems to be greater in *E. intermedius*. Resistance is fostered by its ability to make two types of nest, a discovery made in the African Sahel (Rougon & Rougon, 1982; Rougon, 1987; Barkhouse & Ridsdill-Smith, 1986). One type, in which the brood masses are grouped closely together to conserve moisture, is constructed during the dry season. For the second type, constructed during more humid seasons, the female makes several tunnels placing separate brood masses in each one. This ability to vary nest architecture according to conditions of moisture contributes to reproductive success of this species (Barkhouse & Ridsdill-Smith, 1986). The ability of *E. intermedius* to build different nest types in response to variations in soil and moisture also has been observed in Mexico. In Mapimí, where there is a mosaic of soil types, this species constructs a variety of nest types. One type consists of a single brood mass constructed at a shallow depth; it is less complicated and built faster than other types. It may be a response to high population density per dung pat as occurs in Mapimí.

Fazit

This report gives a picture of the actual spread of two introduced dung beetles in Mexico. As pointed out in the discussion, all new world habitats providing cattle dung can be regarded as sites favourable for future invasion of these old world dung beetles. Consequently, a continuation of their invasion into more areas of cattle ranching can be predicted.

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REFERENCES

Anderson JR, Loomis EC (1978): Exotic dung beetles in pasture and range land ecosystems. *California Agriculture (Febr):* 31–32.

Balthasar V (1963): *Monographie der Scarabaeidae and Aphodiidae der Palaearktischen und Orientalischen Region.* Vol. 2. Coprinae (Onitini, Oniticellini, Onthophagini). Tschechoslowakischen Akademie der Wissenschaften, Praha. 627 pp. 16 plates.

Barbero E, Lopez-Guerrero Y (1992): Some considerations on the dispersal power of *Digitonthophagus gazella* (Fabricius 1787) in the New World (Coleoptera Scarabaeidae Scarabaeinae). *Trop Zool 5:* 115–120.

Barkhouse J, Ridshill-Smith TJ (1986): Effect of soil moisture on brood ball production by *Onthophagus binodis* Thunberg and *Euoniticellus intermedius* (Reiche) (Coleoptera: Scarabaeinae). *J Aust Ent Soc 25:* 75–78.

Blume RR (1984): *Euoniticellus intermedius* (Coleoptera: Scarabaeidae): Descriptions of adults and immatures and biology of adults. *Env Entomol 13:* 1064–1068.

Bornemissza GF (1976): The Australian dung beetle project, 1965-1975. *Australian Meat Research Committee Review 30:* 1–30.

Cambefort Y (1991): Dung beetles in tropical savannas. In: Hanski I, Cambefort Y, eds., *Dung Beetle Ecology.* Princeton University Press, New Jersey, pp. 156–178.

Cambefort Y, Walter P (1991): Dung beetles in tropical forests in Africa. In: Hanski I, Cambefort Y, eds., *Dung Beetle Ecology.* Princeton University Press, New Jersey, pp. 198–210.

Dajoz R (1994): Les coléoptères coprophages du sud-est de l'Arizona (États-Unis). Composition spécifique, biogéographie et structure des peuplements. *Ann Soc Entomol Fr (N.S.) 30 (2):* 159–167.

Davis ALV (1987): Geographical distribution of dung beetles (Coleoptera: Scarabaeidae) and their seasonal activity in south-western Cape province. *J South African Entomol Soc 50:* 275–285.

Doube BM (1991): Dung beetles of southern Africa. In: Hanski I, Cambefort Y, eds., *Dung Beetle Ecology.* Princeton University Press, New Jersey, pp. 133–155.

Doube BM, Macqueen A, Ridsdill-Smith TJ, Weir TA (1991): Native and introduced dung beetles in Australia. In: Hanski I, Cambefort Y, eds., *Dung Beetle Ecology*. Princeton University Press, New Jersey, pp. 255–278.

Fincher GT (1986: Importation, colonization and release of dung-burying scarabs. In: Patterson PA, Rutz DA, eds., Biocontrol of Muscoid Flies. *Miscell Publ Entomol Soc Amer 61:* 69–76.

Fincher GT, Stewart TB, Hunter III JS (1983): The 1981 distribution of *Onthophagus gazella* Fabricius from releases in Texas and *Onthophagus taurus* Schreber from an unknown release in Florida (Coleoptera: Scarabaeidae). *Coleopt Bull 37(2):* 159–163.

Halffter G (1976): Distribución de los insectos en la zona de Transición Mexicana. Relaciones con la entomofauna de Norteamérica. *Fol Entomol Mex 35:* 1–64.

Halffter G, Favila ME, Arellano L (1995): Spatial distribution of three groups of Coleoptera along an altitudinal transect in the Mexican Transition Zone and its biogeographical implications. *Elytron 9:* 151–185.

Hanski I, Cambefort Y (eds.) (1991): *Dung Beetle Ecology*. Princeton University Press, New Jersey, 481 pp.

Howden HF, Scholtz CH (1986): Changes in a Texas dung beetle community between 1975 and 1985 (Coleoptera: Scarabaeidae, Scarabaeinae). *Coleopt Bull 40:* 313–316.

Hunter III JS, Fincher GT (1985): Five new state records for the afro-asian dung beetle *Onthophagus gazella* (Coleoptera: Scarabaeidae). *J Entomol Sci 20 (1):* 24–25.

Kohlmann B (1994): A preliminary study of the invasion and dispersal of *Digitonthophagus gazella* (Fabricius, 1787) in Mexico (Coleoptera: Scarabaeidae: Scarabaeinae). *Acta Zool Mex (n.s.) 61:* 35–42.

Lobo JM (1996): Diversity, biogeographical considerations and spatial structure of a recently invaded dung beetle (Coleoptera: Scarabaeoidea) community in the Chihuahuan desert. *Global Ecology and Biogeography Letters 5* (in press).

Lobo, JM, Montes de Oca E (1994): Distribución local y coexistencia de *Digitonthophagus gazella* (Fabricius , 1787) y *Onthophagus batesi* Howden & Cartwright, 1963 (Coleoptera: Scarabaeidae). *Elytron 8:* 117–127.

Martin-Piera F, Lobo JM (1995): Diversity and ecological role of dung beetles in Iberian grassland biomes. In: McCracken DI, Bignal EM, Wenlock SE, eds., *Farming on the Edge: The Nature of Traditional Farmland in Europe.* Joint Nature Conservation Committee, Peterborough, pp. 147–153.

Matthews EG (1972): A revision of the Scarabaeinae dung beetles of Australia. I. Tribe Onthophagini. *Aust J. Zool, Suppl Ser 9:* 1–330.

Matthews EG (1974): A revision of the Scarabaeinae dung beetles of Australia. II. Tribe Scarabaeini. *Aust J Zool, Suppl Ser 24:* 1–211.

Matthews EG (1976): A revision of the Scarabaeinae dung beetles of Australia. III. Tribe Coprini. *Aust J Zool, Suppl Ser 38:* 1–52.

Montes de Oca E (1993): Comparación de la comunidad local de Scarabaeinae (Coleoptera, Scarabaeidae) de una zona de la región de Laguna Verde, Veracruz, después de 20 años. Memorias I Reunión de Investigadores sobre Fauna Veracruzana, pp.17–18.

Montes de Oca E (1994): Distribuciones temporal y espacial en las etapas iniciales de colonización del gremio de escarabajos coprófagos cavadores de un pastizal tropical (Coleoptera: Scarabaeidae, Scarabaeinae). M.Sc. Thesis, ENCB-IPN, México, D.F. 149 pp.

Montes de Oca E, Halffter G (1995): Daily and seasonal activities of a guild of the coprophagous, burrowing beetle (Coleoptera Scarabaeidae Scarabaeinae) in tropical grassland. *Trop Zool 8:* 159–180.

Montes de Oca E, Anduaga S, Rivera E (1994): Presence of the exotic dung beetle *Euoniticellus intermedius* (Reiche) (Coleoptera: Scarabaeidae) in northern Mexico. *Coleopt Bull 48:* 244.

Ridsdill-Smith TJ (1979): New dung beetles at work in Western Australia. *J Agricult Western Aust 20:* 34–47.

Ridsdill-Smith TJ, Kirk AA (1981): Dung beetles and dispersal of cattle dung. *Proc. Aust. Conf. of Grassland Invertebrate Ecology 3:* 215–219.

Rivera-Cervantes LE, Gargia-Real E (1991): New locality records for *Onthophagus gazella* Fabricius (Coleoptera: Scarabaeidae) in Jalisco, Mexico. *Coleopt Bull 45:* 370.

Rougon D (1987): Coleoptéres coprophiles en zone sahelienne: étude biocenotique, comportement nidificateur, intervention dans le recyclage de la matiére organique du sol. Sc. D. Thesis, Université d'Orleans, France, 324 pp.

Rougon D, Rougon C (1982): Le comportement nidificateur des Coléoptères Scarabaeinae Oniticellini en zone sahélienne. *Bull Soc Entomol Fr 87:* 272–279.

Rougon D, Rougon C (1991): Dung beetles of the Sahel Region. In: Hanski I, Cambefort Y, eds., *Dung Beetle Ecology*. Princeton University Press, New Jersey, pp. 230–241.

Seymour J (1980): Dung beetles get a little help from their friends. *Ecos 26:* 20–25.

United States Department of Agriculture (USDA)-Agricultural Research Service (ARS) (1992): Releases of Beneficial Organisms in the United States and Territories-1981. *Miscell Publ No* 1464.

United States Department of Agriculture (USDA)-Agricultural Research Service (ARS) (1993): Releases of Beneficial Organisms in the United States and Territories-1982. *Miscell Publ No* 1550 .

United States Department of Agriculture (USDA)-Agricultural Research Service (ARS) (1994): Releases of Beneficial Organisms in the United States and Territories-1983. ARS 131.

Zunino M, Halffter G (1988): Análisis taxonómico, ecológico y biogeográfico de un grupo americano de *Onthophagus* (Coleoptera: Scarabaeidae). *Mus Reg Sci Nat,* Torino, Monografía IX, 211 pp., figs.

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