

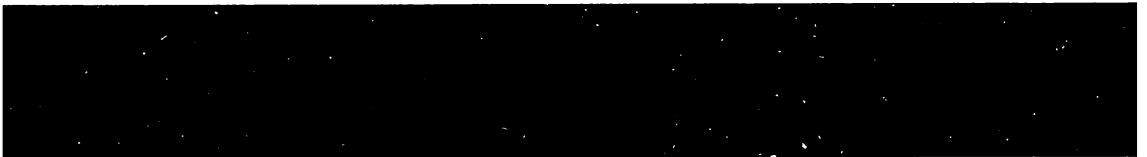
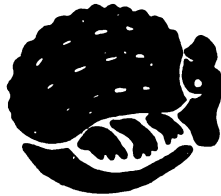
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**MEXICANA**  
*nueva serie*



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## ACAROFAUNA EN NIDOS DE AVES SILVESTRES EN MEXICO

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### RESUMEN

Se presenta un estudio preliminar de la fauna de ácaros de nidos de aves silvestres de las siguientes familias: Columbidae, Hirundinidae, Aegithalidae, Troglodytidae, Muscicapidae, Emberizidae, Fringillidae y Passeridae. Se identificaron 27 especies de ácaros pertenecientes a las familias, Acaridae, Ascidae, Bdellidae, Cheyletidae, Cunaxidae, Dermanyssidae, Ereynetidae, Glycyphagidae, Laelapidae, Macronyssidae, Penthalpidae, Pyroglyphidae, Raphignathidae, Tarsonemidae, Tetranychidae, Tydeidae y Uropodidae. Los ejemplares fueron colectados en los estados de México, Michoacán, Morelos, Oaxaca y Distrito Federal. Se cita por vez primera la presencia del macho de las siguientes especies, *Lasioseius penicilliger* Berlese 1916 y *Pellonyssus nidicolus* Baker, Delfinado y Abbatiello 1976.

**Palabras Claves:** Fauna, ácaros, nidos, aves silvestres, México.

### ABSTRACT

A preliminary study of the mites associated to the nest of birds of the families Columbidae, Hirundinidae, Aegithalidae, Troglodytidae, Muscicapidae, Emberizidae, Fringillidae and Passeridae. Twenty seven species identified belong to the following mites families: Acaridae, Ascidae, Bdellidae, Cheyletidae, Cunaxidae, Dermanyssidae, Ereynetidae, Glycyphagidae, Laelapidae, Macronyssidae, Penthalpidae, Pyroglyphidae, Raphignathidae, Tarsonemidae, Tetranychidae, Tydeidae and Uropodidae. They were recorded in Mexico, Michoacan, Morelos, Oaxaca and Distrito Federal. The males of the following species are described for the first time: *Lasioseius penicilliger* Berlese 1916 and *Pellonyssus nidicolus* Baker, Delfinado and Abbatiello 1976.

**Key Words:** Mites, nests, wild birds, Mexico.

### INTRODUCCION

El presente trabajo tiene como objeto conocer las especies de ácaros asociados a los nidos de diversas especies de aves. Este es el primer trabajo de este tipo que se realiza en nuestro país. Woodroffe (1953, 1954) fue el primero que estudió la importancia de los nidos de aves relacionados con los productos almacenados. Baker *et al.* (1976) estudiaron los ácaros en nidos de aves en Nueva York en donde reportaron 21 especies que pertenecen a 8 familias; los nidos estudiados se encontraron vacíos por lo cual los autores no pudieron identificar las aves a las que pertenecían.

## **METODOS**

Este trabajo se realizó gracias a la colaboración y apoyo del M. en C. Gonzalo Gaviño de la Torre quién, junto con sus colaboradores realizó la colecta del material de los nidos en el verano de 1985, primavera y verano de 1986, primavera y verano de 1988, así como la identificación de las aves que ocupaban los nidos.

La colecta de nidos se realizó en el campo y posteriormente fueron enviados al laboratorio en bolsas de papel de estraza. Estos se pusieron en embudos de Berlese por espacio de 24 a 72 horas y en algunos casos por más tiempo para extraer los ácaros y otros artrópodos. En las primeras 24 horas las poblaciones extraídas fueron abundantes, disminuyendo conforme iban transcurriendo las horas. Los ácaros se colocaron directamente en un portaobjeto con líquido de Hoyer como medio de montaje, se cubrieron con el cubreobjeto y se pusieron en una estufa a 40 °C por una hora aproximadamente.

## **RESULTADOS**

Por la gran población de ácaros que se recolectaron, fue difícil hacer una estimación del número total de individuos. Se determinaron 17 familias, que a continuación se enlistan en orden alfabético dentro de sus órdenes respectivos: Orden Mesostigmata: Ascidae, Dermanyssidae, Laelapidae, Macronyssidae y Uropodidae. Orden Prostigmata: Bdellidae, Cheyletidae, Cunaxidae, Ereyetidae, Penthaleidae, Raphignathidae, Tarsonemidae, Tetranychidae y Tydeidae. Orden Astigmata: Acaridae, Glycyphagidae y Pyroglyphidae. Se observó que la población de ácaros varía de acuerdo con la edad del nido, cuando éstos son recientes, prácticamente no se encuentran ácaros, pero en cambio en nidos vacíos hay una diversidad y densidad mayor. Los ácaros encontrados son de hábitos diferentes, existen ectoparásitos cuyas poblaciones son las más abundantes, los depredadores, saprófagos y los que son más bien accidentales, como en el caso de las familias Penthaleidae y Tetranychidae cuyas especies son en general fitófagas. Los nidos con mayor número de especies de ácaros fueron los de *Hirundo rustica*, *Catharus aurentiirrostris* y *Passer domesticus*. (ver Apéndice)

Abreviaturas: Mpio. - Municipio. desv. - desviación. Cd. - Ciudad.

ORDEN MESOSTIGMATA

**Ascidae**

*Lasioseius penicilliger* Berlese

COLECTA: MICHOACAN: 10 km. desv. Uruapan-Anganocas camino Pancutus, *Catharus aurentiiostris* (Passeriformes: Muscicapidae), 27/6/88. Carretera 37, 10 km. desv. Angahuán *Pipilo fuscus* (Passeriformes: Emberizidae), 28/6/88. Carretera 37, 10 km. desv. Angahuán, *Pipilo erythrophthalmus* (Passeriformes: Emberizidae), 27/6/88. 3km. NW., Tingambato, *Catharus aurentiiostris* (Passeriformes: Muscicapidae), 30/6/88. Mpio. Tingambato (matorral de 1.20 m., área de huertas), *Pipilo fuscus* (Passeriformes: Emberizidae), 1/7/88. 3km. NW., Tingambato (bosque mixto), *Atlapetes pileatus* (Passeriformes: Emberizidae), 30/6/88.

La descripción de esta especie se realizó con hembras, por lo que el macho era desconocido. En las colectas realizadas, las poblaciones fueron abundantes y en ellas se colectaron varios ejemplares de machos. Se cita por primera vez a ésta especie para México, conociéndose a la fecha solo del estado de Michoacán.

MACHO: Largo del cuerpo 280  $\mu\text{m}$ , ancho 140  $\mu\text{m}$  (Fig. 1 y 2). El idiosoma está cubierto completamente por la placa dorsal, en la superficie tiene un patrón reticulado, igual que en la hembra. Las sedas dorsales con 36 pares, las sedas de la serie R están insertadas en la membrana interescutal lateral. La seda humeral r 3 sale del margen de la placa dorsal en forma recta. El tritosterno igual que en la hembra con 2 lacinias finas. La placa esternogenital es lisa con 4 pares de sedas. La placa ventrianal que ocupa todo el ancho del cuerpo y desde de las coxas IV hasta el borde posterior del cuerpo está reticulada con 5 pares de sedas. Gnatosoma esclerosado con los cornículos grandes. Como en otras especies de *Lasioseius* el dedo fijo del quelícero es multidentado, el espermadactil muy robusto de mayor tamaño que el quelícero.

*Lasioseius* sp.

COLECTA: MICHOACAN: Mpio. Zinapécuaro, km. 116.5 Carretera 126, tramo Maravatio-Queréndaro, *Junco phaeonotus* (Passeriformes: Emberizidae), 21/6/88. 10 km. desv. Uruapan-Anganocas camino Pancutus, *Catharus aurentiiostris* (Passeriformes: Muscicapidae), 27/6/88.

Por las características que presenta la placa esternal parece tratarse de una especie inédita.

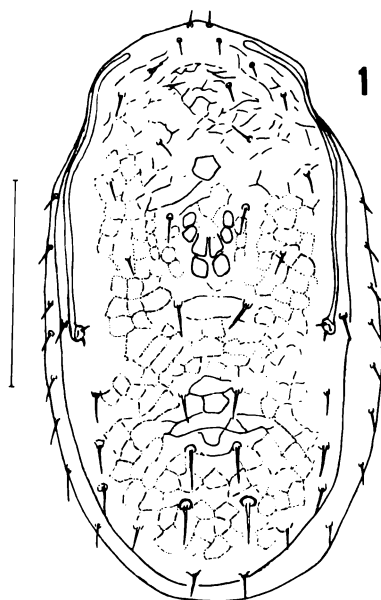


Figura 1

Macho de *Lasioseius penicilliger* Berlese vista dorsal del idiosoma. Escala de la línea 100 micras.

### *Proctolaelaps* sp.

COLECTA: DISTRITO FEDERAL: Delegación Iztapalapa, Santa Martha, *Carpodacus mexicanus* (Passeriformes: Fringillidae), 21/6/86.

Por las características que presenta, parece tratarse de una especie no descrita.

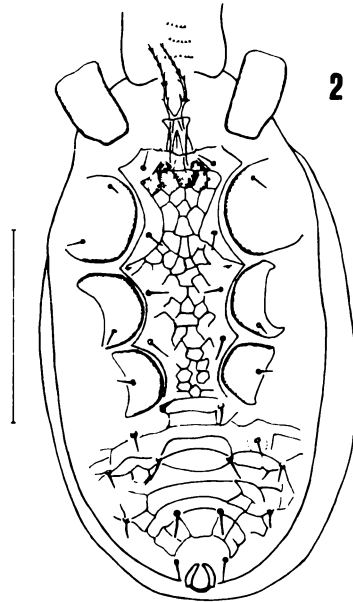
### **Dermanyssidae**

#### *Dermanyssus gallinae* (de Geer)

COLECTA: MEXICO: Mpio. Temamatla, Temamatla, *Hirundo rustica* (Passeriformes: Hirundinidae), 11/8/85.

Los nidos se localizan generalmente en zonas habitadas en pórticos y debajo de tejados. Son ectoparásitos de pájaros y se encuentran comunmente en los nidos. Se alimentan principalmente durante la noche; en el día se observan numerosos individuos saliendo del nido e invadiendo la pared. Varios estudios lo asocian en la transmisión de virus; no solo parasita a gallinas sino también a pájaros domésticos. Su distribución es mundial (Baker *et al.* 1956).





**Figura 2**  
Macho de *Lasioseius penicilliger* Berlese vista ventral. Escala de la línea 100 micras.

## **Laelapidae**

### *Tur lativentralis* (Fonseca)

COLECTA: MICHOACAN: Mpio. Zinapécuaro km. 116.5, Carretera 126, tramo Maravatio-Queréndaro (zona de pinos), *Junco phaeonotus* (Passeriformes: Emberizidae), 21/6/88.

Se cita por vez primera para México. Se conocen pocos datos de esta especie.

### *Androlaelaps (Haemolaelaps) fahrenheitzi* (Berlese)

COLECTA: DISTRITO FEDERAL: Delegación Iztapalapa, Santa Martha, *Passer domesticus* (Passeriformes: Passeridae), 21/6/86.

Son ácaros ectoparásitos hematófagos que no solo utilizan a aves como transporte sino que posiblemente son sus propios parásitos. Esta especie es frecuente en roedores de los géneros *Peromyscus* y *Microtus* con una amplia distribución en la República Mexicana. Strandmann (1949), cita al género *Haemolaelaps* en siete familias de aves silvestres en los Estados Unidos de América entre las que se encuentra a *Passer domesticus*.

*Echinolaelaps* sp.

COLECTA: MICHOACAN: Mpio. Zinapécuaro, km. 116.5, Carretera 126, tramo Maravatio-Queréndaro (zona de pinos), *Junco phaeonotus* (Passeriformes: Emberizidae), 21/6/88.

**Macronyssidae**

*Ornithonyssus sylviarum* (Canestrini & Fanzago)

COLECTA: MEXICO: Mpio. Temamatla, Temamatla, *Hirundo rustica* (Passeriformes: Hirundinidae), 25/8/85. MORELOS: Mpio. Huitzilac, 1 km. NE Fierro del Toro, *Phencticus melanocephalus* (Passeriformes: Emberizidae), 28/5/88. Mpio. Huitzilac (bosque mixto), 1 km. NE Fierro del Toro, *Catharus occidentalis* (Passeriformes: Muscicapidae), 3/6/88.

Es una especie hematófaga muy abundante en los nidos en donde fue colectada, de amplia distribución en las regiones templadas. Se cita por vez primera para estas especies de aves en México. Micherdzinski (1980), reporta a esta especie en *Hirundo rustica* y en diferentes especies de *Turdus*.

*Ornithonyssus sylviarum utrechtensis* Micherdzinski

COLECTA: MORELOS: Mpio. Huitzilac, 1 km. NE Fierro del Toro, *Turdus migratorius* (Passeriformes: Muscicapidae), 28/5/88.

La población de esta subespecie fue escasa.

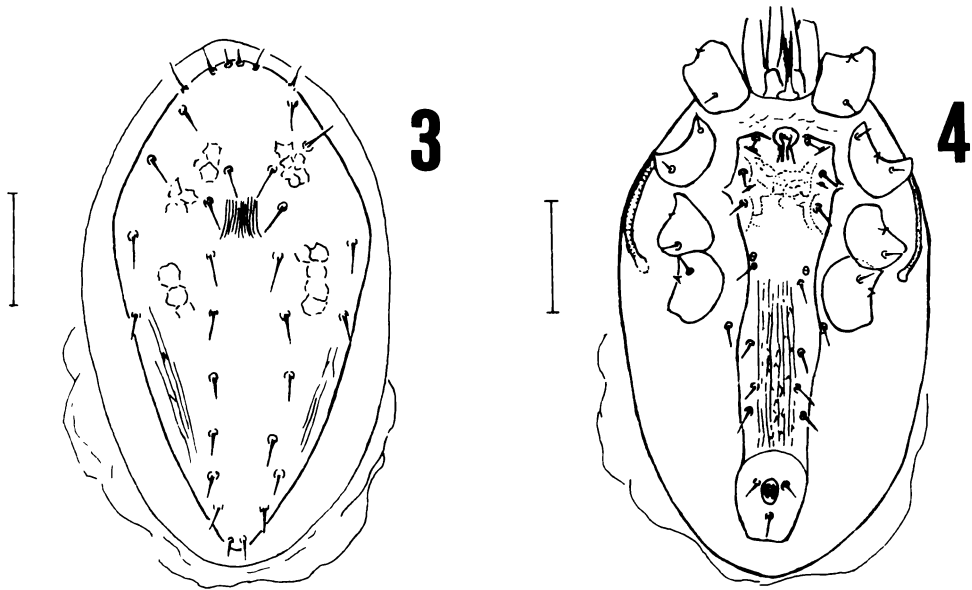
*Pellonyssus nidicolus* Baker, Delfinado & Abbatiello

COLECTA: MEXICO: Mpio. Temamatla, Temamatla, *Hirundo rustica* (Passeriformes: Hirundinidae), 11/8/85. MORELOS: Jonacatec, *Columbina inca* (Columbiformes: Columbidae), 20/2/86. Jojutla, Las Huertas, *Leptotila verreauxi* (Columbiformes: Columbidae), 6/4/86. 4 km. N Alpuyecá *Columbina passerina* (Columbiformes: Columbidae), 19/10/85. DISTRITO FEDERAL: Cd. Universitaria, *Passer domesticus* (Passeriformes: Passeridae), 28/4/86. MICHOACAN: Mpio. Zinapécuaro, km. 116.5, Carretera 126 tramo Maravatio-Queréndaro, *Campylorhynchus gularis* (Passeriformes: Troglodytidae), 21/6/88.

Se cita por vez primera para México tiene una distribución amplia y abundante. El macho hasta ahora desconocido fue colectado.

MACHO: Longitud del cuerpo 477  $\mu\text{m}$ , ancho 360  $\mu\text{m}$  (Fig. 3 y 4). Los queléceros muy largos y delgados. La placa dorsal cubre todo el cuerpo, a partir de la mitad se va reduciendo hacia la parte posterior, quedando en forma de cuña o lengüeta. Con 15 pares de sedas finas y cortas. Ventral. Placa holovenral reticulada en la región esternal, con 3 pares de sedas y 3 pares de poros; la región genital está estriada y nuevamente la región ventral se presenta reticulada. El

peritrema se extiende desde la coxa II hasta la mitad de la coxa IV. Patas. Igual que en la hembra con fórmula coxal de espolones 1-2-2-1.



Figuras 3-4

Macho de *Pellonyssus nidicolus* Baker, Delfinado & Abbatiello. Fig. 3. vista dorsal. Fig. 4. vista ventral. Escala de la línea 100 micras.

## Uropodidae

### *Trichouropoda* sp.

COLECTA: MICHOACAN: Mpio. Tingambato, (área de huertas, el nido en arbusto), *Catharus guttatus* (Passeriformes: Muscicapidae), 1/7/88.

Los uropódidos son en general habitantes de nidos y galerías. Se alimentan probablemente de detritos orgánicos y de hongos (Krantz, 1978).

ORDEN PROSTIGMATA

## Bdellidae

### *Bdella muscorum* Ewing

COLECTA: MICHOACAN: Mpio. Tingambato (matorral de 1.20 m., área de huertas), *Catharus guttatus* (Passeriformes: Muscicapidae), 1/7/88. Mpio. Zinapécuaro, km. 116.5, Carretera 126 tramo Maravatio-Queréndaro *Campylorhynchus gularis* (Passeriformes: Troglodytidae), 21/6/88.

Es una familia de ácaros activos, corredores, de color rojo, café o verde, depredadores de pequeños artrópodos o huevecillos. Se encuentran en hábitats forestales. *Bdella lignicola* se encuentra en productos almacenados. Su período de desarrollo es de 21 a 30 días a 15.5 °C y 90% de humedad; todos los estados de desarrollo se encuentran en el invierno (Atyeo, 1960).

### Cheyletidae

#### *Cheyletus eruditus* (Schrank)

COLECTA: MEXICO: Mpio. Temamatla, Temamatla, *Hirundo rustica* (Passeriformes: Hirundinidae), 11/8/85. MORELOS: Cuernavaca, Colonia Buenavista, *Hirundo rustica* (Passeriformes: Hirundinidae), 22/10/85.

Esta especie se colectó en nidos abandonados. Se encontró asociada con una población abundante de psócidos. Coombs y Woodroffe (1968) señalan que en granos almacenados son capaces de alimentarse de estados juveniles de palomillas, escarabajos y psócidos. *C. eruditus* es un habitante regular de nidos de pájaros carroñeros y mamíferos (Woodroffe, 1953). También se ha encontrado en el polvo de casa y en los colchones (Hughes, 1979). En granos almacenados se considera como una especie depredadora que controla las poblaciones de otras especies de ácaros. Su distribución es mundial.

#### *Cheyletus sp.*

COLECTA: DISTRITO FEDERAL: Cd. Universitaria, *Passer domesticus* (Passeriformes: Passeridae), 28/4/86.

Por las características que presenta, parece tratarse de una especie inédita.

#### *Hemicheyletia bakeri* (Ehara)

COLECTA: OAXACA: Mpio. Miltepec, 2 km. al N de las Palmas, Zona de la Laguna Dolores, *Campylorhynchus rufinucha* (Passeriformes: Troglodytidae), 6/9/88.

Se reporta por vez primera para México en nidos de *C. rufinucha*. Se ha colectado principalmente en pastos y en hojas con hongos (Summers & Price, 1970).

## Cunaxidae

### *Cunaxoides biscutum* (Nesbitt)

COLECTA: MORELOS: Mpio. Huitzilac, 1 km. NE Fierro del Toro, *Turdus migratorius* (Passeriformes: Muscicapidae), 3/6/88.

Se encontró asociada con ácaros de la familia Tarsonemidae. Es frecuente en suelo, musgo y plantas. Algunos la reportan en alimento almacenado y trigo (Hughes, 1979). Su población fue mínima.

## Ereynetidae

### *Ereynetes* sp.

COLECTA: MICHOACAN: 10 km. dev. Uruapan-Anganocas camino Pancutus, *Catharus aurantiirostris* (Passeriformes: Muscicapidae), 27/6/88. Mpio. Tingambato, 3 km. NO Tingambato, *Pipilo fuscus* (Passeriformes: Emberizidae), 10/7/88.

Las especies de *Ereynetes* son fitófagas. Los miembros de la subfamilia Speleognathinae habitan en la mucosa nasal de una amplia variedad de pájaros y mamíferos (Krantz, 1978). La población colectada fué reducida.

## Penthaleidae

### *Penthaleus* sp.

COLECTA: MORELOS: Mpio. Huitzilac, 1 km. NE Fierro del Toro, *Pipilo erythrophthalmus* (Passeriformes: Emberizidae), 3/6/88. MICHOACAN: Mpio. Zinapécuaro, km. 116.5 Carretera 126 tramo Maravatio-Queréndaro (zona de pinos), *Catharus occidentalis* (Passeriformes: Muscicapidae), 21/6/88.

Las especies de la familia Penthaleidae tienen una distribución tropical y se alimentan de una variedad de plantas de importancia económica como chícharo, algodón y varias plantas ornamentales (Krantz, 1978). Los nidos posiblemente son utilizados como reservorio, ya que pudieron haber sido transportados a ellos accidentalmente durante su construcción.

## Raphignathidae

### *Raphignatus* sp.

COLECTA: MICHOACAN: Mpio. Zinapécuaro, km. 116.5 Carretera 126 tramo Maravatio-Queréndaro, *Campylorhynchus gularis* (Passeriformes: Troglodytidae), 21/6/88. 1 km. W Pueblo Viejo (zona de cultivos), *Pipilo fuscus* (Passeriformes: Emberizidae), 22/6/88.

Las especies del género *Raphignatus* se encuentran a menudo en granos almacenados. Son ácaros de color blanco hialino de movimientos rápidos.

### **Tarsonemidae**

*Tarsonemus sp.*

COLECTA: MORELOS: Mpio. Huitzilac, 1 km. NE Fierro del Toro (bosque mixto), *Turdus migratorius* (Passeriformes: Muscicapidae), 28/5/88. MICHOACAN: Mpio. Zinapécuaro, km. 116.5 Carretera 126 tramo Maravatío-Queréndaro (zona de pinos), *Catharus occidentalis* (Passeriformes: Muscicapidae), 21/6/88.

Este género se encuentra asociado con especies de la familia Acaridae. Son ácaros pequeños, de color blanco opalino, de movimientos rápidos.

### **Tydeidae**

*Tydeus sp.*

COLECTA: MICHOACAN: Mpio. Zinapécuaro, km. 116.5 Carretera 126 tramo Maravatio-Queréndaro (zona de pinos), *Catharus occidentalis* (Passeriformes: Muscicapidae), 21/6/88.

Se encuentran libres en las hojas de las plantas y en granos almacenados. Sus hábitos alimentarios son fitófagos, micófagos y depredadores; su función en los nidos parece ser depredadora y micófaga.

### **Tetranychidae**

*Bryobia praetiosa* Koch

COLECTA: MORELOS: Mpio. Jojutla, Las Huertas, *Leptotila verreauxi* (Columbiformes: Columbidae), 6/4/86.

Esta especie es fitófaga, frecuente en los tréboles; son ácaros de color rojizo de movimientos rápidos. A principios de marzo puede invadir las casas cercanas a prados o jardines, se han colectado en esta forma en sitios como la Ciudad Universitaria y en los viveros de Coyoacán, D.F. Posiblemente por este motivo se encuentran invadiendo los nidos.

*Tetranychus (Tetranychus) urticae* Koch

COLECTA: MORELOS: Cuernavaca, Buenavista, *Hirundo rustica* (Passeriformes: Hirundinidae), 22/10/85.

Los ácaros de la familia Tetranychidae son fitófagos. Los nidos parecen ser utilizados como lugar de hibernación por la época en que fue colectado.

## ORDEN ASTIGMATA.

### **Acaridae**

#### *Tyrophagus neiswanderi* Johnston & Bruce

COLECTA: MORELOS: Coajomulco, *Psaltriparus minimus* (Passeriformes: Aegithalidae), 11/6/86. MICHOACAN: 10 km. desv. Uruapan-Anganocas camino Pancutus, *Catharus aurentiistrostris* (Passeriformes: Muscicapidae), 27/6/88. Mpio. Tingambato (matorral de 1.20m, área de huertas), *Pipilo fuscus* (Passeriformes: Emberizidae), 1/7/88.

Esta especie es numerosa en los nidos de aves. Se colectó por vez primera en plantas de calabaza alimentándose del follaje (Johnston & Bruce, 1965). En el nido es posiblemente saprófaga.

### **Glycyphagidae**

#### *Glycyphagus ornatus* Kramer

COLECTA: MORELOS: Cuernavaca, Colonia Buenavista, *Hirundo rustica* (Passeriformes: Hirundinidae), 22/10/85. DISTRITO FEDERAL: Delegación Iztapalapa, Santa Martha, *Passer domesticus* (Passeriformes: Passeridae), 21/6/86.

Se registra por vez primera para México en nidos de aves. Se colectó en nidos activos de *Passer domesticus* donde la población era abundante; en nidos abandonados de *Hirundo rustica*, la población fue menor. Se ha encontrado en nidos de diferentes especies de animales, es abundante en nidos de topos, musarañas (Zachvatkin, 1941) y roedores (Vysotzkapa, 1961).

### **Pyroglyphidae**

#### *Dermatophagoides pteronyssinus* (Trouessart)

COLECTA: DISTRITO FEDERAL: Cd. Universitaria, *Passer domesticus* (Passeriformes: Passeridae), 28/4/86. Delegación Iztapalapa, Santa Martha, *Passer domesticus* (Passeriformes: Passeridae), 21/6/86. MEXICO: Mpio. Temamatla, Temamatla, *Hirundo rustica* (Passeriformes: Hirundinidae), 11/8/85. MORELOS: Cuernavaca, *Hirundo rustica* (Passeriformes: Hirundinidae), 3/8/85. OAXACA: Mpio. Miltepec, 2 km. N Las Palmas, Zona Laguna Dolores *Campylorhynchus rufinucha* (Passeriformes: Troglodytidae), 6/9/88.

Es una especie abundante en los nidos de estas aves y de acuerdo con las observaciones de Mausell *et al.* (1967), posiblemente se alimenta del tejido escamoso de la piel lo que indica una labor de limpieza del nido.

Es un grupo de vida libre con representantes nidícolas, contaminantes de granos almacenados y como uno de los agentes responsables de la alergia al polvo de casa (Voorhoorst *et al.*, 1964).

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RELACION NIDO DE AVE - ACARO

NIDO	GENERO Y ESPECIE	FAMILIA	HABITO
<b>Columbidae</b>			
<i>Leptotila verreauxi</i>	<i>Bryobia praetiosa</i>	Tetranychidae	fitófago
Ave residente	<i>Pellonyssus nidicolus</i>	Macronyssidae	parásito
Paloma perdiz común			
<i>Columbina inca</i>	<i>Pellonyssus nidicolus</i>	Macronyssidae	parásito
Ave residente			
Tórtola colilarga			
<i>Columbina passerina</i>	<i>Pellonyssus nidicolus</i>	Macronyssidae	parásito
Ave residente			
Tortolita pechipunteada			
<b>Hirundinidae</b>			
<i>Hirundo rustica</i>	<i>Cheyletus eruditus</i>	Cheyletidae	depredador
Ave migratoria.	<i>Ornithonyssus sylviarum</i>	Macronyssidae	parásito
Golondrina tijereta	<i>Pellonyssus nidicolus</i>	Macronyssidae	parásito
	<i>Dermayssus gallinae</i>	Dermanyssidae	parásito
	<i>Dermatophagoides pteronyssinus</i>	Pyroglyphidae	detritófago
	<i>Glycyphagus ornatus</i>	Glycyphagidae	desconocido
	<i>Tetranychus (T.) urticae</i>	Tetranychidae	fitófago
<b>Aegithalidae</b>			
<i>Psaltriparus minimus</i>	<i>Tyrophagus neiswanderi</i>	Acaridae	saprófago
Ave residente			
Sastrecito			
<b>Troglodytidae</b>			
<i>Campylorhynchus rufinucha</i>	<i>Dermatophagoides pteronyssinus</i>	Pyroglyphidae	detritófago
Ave residente	<i>Hemicheyletia bakeri</i>	Cheyletidae	depredador
Matraquita nuquirrufa	<i>Cheyletus eruditus</i>	Cheyletidae	depredador
<i>Campylorhynchus gularis</i>	<i>Pellonyssus nidicolus</i>	Macronyssidae	parásito
Ave residente	<i>Raphignathus sp.</i>	Raphignathidae	saprófago
Matraca encinera			
<b>Muscicapidae</b>			
<i>Catharus aurentiiostris</i>	<i>Lasioseius penicilliger</i>	Ascidae	depredador
Ave residente	<i>Lasioseius sp.</i>	Ascidae	depredador
Zorzalito piquinaranja	<i>Tyrophagus neiswanderi</i>	Acaridae	saprófago
	<i>Ereynetes sp.</i>	Ereynetidae	fitófago
<i>Catharus occidentalis</i>	<i>Tarsonemus sp.</i>	Tarsonemidae	micófago
Ave residente	<i>Ornithonyssus sylviarum</i>	Macronyssidae	parásito
Zorzalito piquioscuro	<i>Penthaleus sp.</i>	Penthaleidae	fitófago
	<i>Tydeus sp.</i>	Tydeidae	micófago

NIDO	GENERO Y ESPECIE	FAMILIA	HABITO
<i>Catharus guttatus</i>	<i>Bdella muscorum</i>	Bdellidae	depredador
Ave migratoria	<i>Trichouropoda sp.</i>	Uropodidae	saprófago
Zorzalito colirrufo		Erythraeidae	depredador
<i>Turdus migratorius</i>	<i>Ornithonyssus sylviarum</i>	Macronyssidae	parásito
Zorzal pechirrojo	<i>utrechtensis</i>		
Ave residente	<i>Cunaxoides biscutum</i>	Cunaxidae	depredador
	<i>Tarsonemus sp.</i>	Tarsonemidae	micófago
	<i>Tyrophagus neiswanderi</i>	Acaridae	saprófago
<b>Emberizzidae</b>			
<i>Pheucticus melanocephalus</i>	<i>Ornithonyssus sylviarum</i>	Macronyssidae	parásito
Ave residente			
Picogrueso pechicafé			
<i>Atlapetes pileatus</i>	<i>Lasioseius penicilliger</i>	Ascidae	depredador
Ave residente			
Atlapetes gorrirrufo			
<i>Pipilo erythrophthalmus</i>	<i>Lasioseius penicilliger</i>	Ascidae	depredador
Ave residente	<i>Penthaleus sp.</i>	Penthaleidae	fitófago
Rascador pinto			
<i>Pipilo fuscus</i>	<i>Lasioseius penicilliger</i>	Ascidae	depredador
Ave residente	<i>Tyrophagus neiswanderi</i>	Acaridae	saprófago
Rascador pardo	<i>Raphignathus sp.</i>	Raphignathidae	saprófago
	<i>Ereynetes sp.</i>	Ereynetidae	fitófago
<i>Junco phaeonotus</i>	<i>Lasioseius sp.</i>	Ascidae	depredador
Ave residente	<i>Bdella muscorum</i>	Bdellidae	depredador
Junco ojilumbre	<i>Tur lativentralis</i>	Laelapidae	parásito
<b>Fringillidae</b>			
<i>Carpodacus mexicanus</i>	<i>Proctolaelaps sp.</i>	Ascidae	depredador
Ave residente			
Carpodaco doméstico			
<b>Passeridae</b>			
<i>Passer domesticus</i>	<i>Cheyletus sp.</i>	Cheyletidae	depredador
Ave urbana	<i>Glycyphagus ornatus</i>	Glycyphagidae	desconocido
Gorrión doméstico	<i>Pellonyssus nidicolus</i>	Macronyssidae	parásito
	<i>Dermatophagoides pteronyssinus</i>	Pyroglyphidae	detritófago
	<i>Androlaelaps (H.) farhenholzi</i>	Laelapidae	parásito

**SPATIAL MICRODISTRIBUTION OF TWO INTRODUCED DUNG  
BEETLE SPECIES *DIGITONTHOPHAGUS GAZELLA* (F.) AND  
*EUONITICELLUS INTERMEDIUS* (REICHE) (COLEOPTERA  
SCARABAEIDAE) IN AN ARID REGION OF NORTHERN MEXICO  
(DURANGO, MEXICO)**

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**RESUMEN**

*Digitonthophagus gazella* (F.) y *Euoniticellus intermedius* (Reiche) son dos especies de escarabajos coprófagos que fueron introducidos en el continente americano y, que en la actualidad, constituyen las especies dominantes dentro del gremio en Mapimí (Durango, México). Se analizaron las distribuciones de ambas especies en un ambiente aparentemente homogéneo mostrado a lo largo de transectos constituidos por boñigas de vaca depositadas artificialmente y por trampas pitfall. Ambas especies mostraron distribuciones agregadas, las cuales se presentan a densidades bajas, medias y altas, así como cuando hay o no hay emigración. La agregación intraespecífica observada probablemente se deba a una cierta preferencia de los procesos de inmigración hacia las boñigas (y trampas) seleccionadas repetidamente así como por aquellas boñigas o trampas con mayor número inicial de individuos. A esta escala espacial la correlación negativa mostrada entre *D. gazella* and *E. intermedius* se debe probablemente a tasas de emigración diferenciales. Esta tasa de emigración para cada especie depende del número de individuos de la misma especie que llegan al excremento y no del número de individuos de la otra especie. Concluimos que las interacciones competitivas entre individuos intraespecíficamente agregados son muy probablemente las causas de la emigración diferencial y de la segregación microespacial observada de estas dos especies en esta región.

**Palabras Clave:** Distribución espacial, agregación, covariación, escarabajos del estiércol, especies introducidas, región árida.

**ABSTRACT**

The introduced dung beetle species *Digitonthophagus gazella* (F.) and *Euoniticellus intermedius* (Reiche) have become the dominant species into the Scarabaeinae guild of the Mapimí region (Durango, México). The distributions of these two species in an apparently homogeneous environment was analyzed through transects of artificially placed dung pats and pitfall traps baited with cow dung. Both species showed aggregated distributions. Aggregation occurred at high, moderate and low densities and was not affected by emigration. The observed intraspecific aggregation was probably due to immigration processes: repeated dung beetle selection for the same dung pats and selection of dung pats with larger initial populations. The spatial negative association between *D. gazella* and *E. intermedius* observed at this spatial scale was probably due to differential emigration rates. The rate of emigration of both species depended on the number of the conspecifics into a dung pat, but not on

the number of beetles from the other species. We conclude that the competitive interactions among individuals intraspecifically aggregated likely led to differential emigration rates and caused the observed microspatial segregation.

**Key Words:** Spatial distribution, aggregation, covariation, dung beetles, introduced species, arid region.

## INTRODUCTION

The composition of the dung beetle community in the Mapimí arid region is very simple in comparison with those in tropical and temperate areas and even with those occurring at the edges of the Chihuahuan desert (Lobo, 1996). In fact, it was simpler 20 years ago when it was composed by a very few species. At the present time, at least 3 of the 6 species found in the Mapimí region arrived in the last 13 years, while another 2 were probably introduced very recently (Lobo, *op. cit.*). In this new formed and poor dung beetle assemblage, two species *Digitonthophagus gazella* (F.) and *Euoniticellus intermedius* (Reiche) are dominant both in abundance and biomass.

*Digitonthophagus gazella* and *E. intermedius* are two Indoafrican dung beetle species which coexist in many African regions (Cambefort, 1991; Doube, 1991; Rougon & Rougon, 1991). These species have been used successfully in the introduction programs carried out in Australia and United States for controlling dung accumulation and dung-breeding flies (Blume, 1984; Blume & Aga, 1978; Doube *et al.*, 1991). *D. gazella* was first collected in Mapimí in 1984 (Zunino & Halffter, 1988), 12 years after its first releases in continental United States. *E. intermedius* was released in 1979-1980 (Blume, 1984) and its presence in La Michilfa and Mapimí Biosphere Reserves was recorded in 1992 (Montes de Oca *et al.*, 1994). Accordingly the time elapsed between the release and record dates, the dispersal capability of both species toward Mapimí has been similar.

The spontaneous arrival of these exotic species to Mapimí provide the opportunity to follow the development of a simple dung beetle community in a distant and biogeographically different region from the species original home (Africa). The purpose of this paper is to describe the spatial distribution of these two introduced species at the level that Hanski & Cambefort (1991) considered the most interesting to analyze, i.e. among nearly dung pats located in an apparently homogeneous habitat. Such a study of the spatial distribution of beetles at this scale in Mapimí can permit to know the processes involved in microhabitat selection level in the formation of the community. With this information we can at a later date observe and analyze the evolution of possible interactions between these species and their role in determining spatial distribution and coexistence.

At the small spatial scale, aggregated distribution seems to be a general trend showed by dung beetles (Holter, 1982; Hanski, 1980; Hanski & Cambefort, 1991)

and other insects (i.e. Diptera) exploiting patchy and ephemeral resources (Hanski & Kuusela, 1977; Shorrocks *et al.*, 1979; Atkinson & Shorrocks, 1981; Kneidel, 1985; Ives 1988, 1991). Some patches have large numbers of individuals while others have only few individuals. One can observe a high spatial variance in the density patch-occupation of one species (intraspecific aggregation) and a covariation in the numbers of two species across a set of patches (interspecific aggregation). The existence of an intraspecific aggregation does not necessarily lead to an interspecific aggregation. Also, two species can be positively or negatively associated with or without the action of the interspecific competition (Hanski, 1986; Hanski & Cambefort, 1991). Hanski (1991) argues that intraspecific spatial aggregation is often much greater than interspecific aggregation facilitating the species coexistence. Such a type spatial distribution between two species promote an increase of intraspecific competition and a decrease of interspecific competition (Shorrocks *et al.*, 1979; Hanski, 1981, 1991; Hanski & Cambefort, 1991; Kouki & Hanski, 1995).

The dynamics and structure of a dung pat beetle community can be considered as the result of the interplay between immigration and emigration processes (Hanski, 1980). Main causes of intraspecific aggregation are related with the immigration process (Hanski & Cambefort, 1991): i) organisms always choose patches with similar suitable conditions (Hanski, 1980); ii) organisms repeatedly choose for colonizing patches containing more individuals, facilitating sexual encounters (Holter, 1982), or iii) due to some other reasons. The first process leads to aggregation as a consequence of environmental heterogeneity undetected by us, which could be a particular case of typical resource partitioning (Ives, 1988). The second highlights the idea of male-female encounters or congregative behavior among individuals. Communication mechanisms like pheromones, whose action has been supposed or proved in the case of some dung beetle species (Tribe, 1975; Bellés & Favila, 1983; Houston, 1986; Pluot-Sigwalt, 1988), perhaps causes attraction to particular dung pats.

On the contrary to the immigration process, the role played by the emigration process in spatial microdistribution is not obvious. Since a high density per patch could increase the degree of intraspecific interactions, an increase of emigration from dung pats must decrease the degree of intraspecific aggregation. Certainly, several studies indicate that the emigration from droppings is often density-dependent at sufficiently high densities (Landin, 1961; Yasuda, 1987; Hanski & Cambefort, 1991). However, a well established property of aggregated distributions is the increasing of spatial variance (aggregation) with the increasing mean abundance (The Taylor Power Law) (Taylor, 1961; Taylor, 1981; Perry, 1988). At all events, the differential emigration processes between two species

also can be responsible of the interspecific spatial covariation among dung-pats, with or without the action of the interspecific competition.

This paper aims to answer the following questions: i) Have *D. gazella* and *E. intermedius* aggregated distributions among apparently homogeneous set of dung-pats?; ii) are the two species negatively or positively associated at this spatial scale?; and iii) are both intraspecific and interspecific aggregations due to immigration or emigration processes?

## MATERIAL AND METHODS

### Description of the study area

The Mapimí Biosphere Reserve lies within the Bolsón de Mapimí, located in the northern Mexican Plateau, and is part of the Chihuahuan Desert. It includes some portions of the states of Coahuila, Chihuahua and Durango. The climate is dry, midwarm, with a chilly winter, a summer rainy season and annual mean temperatures ranging from 18° to 22 °C. There are two major seasons, a dry season from October to May and a hot and more humid season from June to September. In the Reserve, rains are torrential, of short duration and very localized. The result is a great variability in the spatial distribution of rain in the zone. The meteorological station in this Reserve recorded from 1978-1988 an annual precipitation of 283.8 mm. The flora includes a great variety of life forms dominated by shrub species with small leaves, which give the appearance of xerophitic underbrush.

### Sampling

The data were obtained during two field studies carried out in the same season of two consecutive years: from 21 to 24 August 1992 and from 21 to 25 September 1993. In 1992, seven transects were set near the Laboratory of the Mapimí Biosphere Reserve (transects numbered from 1 to 7). Each transect consisted of ten 1-kg cow dung pats placed 12 m apart. Fresh cow dung was previously collected from the pasture of Rancho La Flor. Amounts of this material were homogenized and pats were artificially deposited in the afternoon, at 18.00 p.m. The dung pats of four transects were inspected at 6.00 a.m. next morning, whereas the pats of the remaining transects were inspected 24 hours after placement. The difference in the exposure time allowed to determine the activity schedules of the species in the study zone: *Euoniticellus intermedius* is active at noon and *D. gazella* at dawn and dusk (Montes de Oca *et al.*, 1994).

In 1993, six independent transects were studied in the same zone in a west-east direction. Three of them consisted of eight 1-kg dung pats each too, but placed six meters apart (transects numbered 8, 9 and 10). The other three transects

consisted of 20 dung baited pitfall-traps of standard design (CSR type) (Lobo *et al.*, 1988; Veiga *et al.*, 1989) placed also six meters apart (transects numbered 11, 12 and 13). The pitfall traps consisted of a plastic basin of 210 mm in diameter buried to its rim in the soil, containing a water soap mixture. Fresh cattle dung was supported on a wire grid on the top of the bucket. The dung used to form the pats as well as the bait for the pitfall traps was fresh and previously collected and homogeneized. So, the attractiveness variation effect within and between transects was intended to minimize.

Each day, only one dung pat transect and one pitfall trap transect were simultaneously conducted two meters apart, so that the spots of the first eight dung pats were front of the position of the last eight western pitfall traps. Both the dung pats and the pitfall traps were always set up in the same place.

In the transects 8, 9, 11 and 12, the dung pats and the pitfall traps were set up in the afternoon at 18.00 p.m. In the transects 10 and 13, the dung pats and the pitfall traps were set up in the morning at 8.00 a.m. The distinct periods of the placement of bait in the transects facilitated the distinct colonization of dung by the two species.

Both the length (108 and 114 m) and the exposure time of dung pats of the 1992 and the 1993 transects, were similar and comparable. Almost all the transects were inspected 24 hours after placement. Beetles trapped in the pitfall traps of the 11 and 13 transects were collected every two hours on 22-23 September and 24-25 September periods, respectively.

### **Spatial distribution analysis**

Aggregation as a concept is difficult to define. Typically its measurement raises several objections (see Hurlbert, 1990). We used the Morisita Index (MI) as the most appropriate aggregation index (Hurlbert, *op. cit.*) as well as the Aggregation Model proposed by Ives (1988). This model provides an intraspecific aggregation measure ( $J$ ) and a interspecific aggregation measure ( $C$ ). Both the Morisita Index and the Aggregation Model are simple and less dependent on variance. They have a higher biological sense than, for example, the variance to mean ratio, commonly used as a dispersion index. The statistical signification of intraspecific aggregation was measured by testing the deviation of the variance to mean ratio from 1.0 using the Chi-Square test statistic. The Spearman rank correlation coefficient was computed to test the interspecific covariation according to Ives (1988).

To know if the immigration rate of beetles was higher in some dung pats than in others, the Pearson correlation coefficients were calculated among the pitfall trap pair abundances for the same site but among the different transects. Beetles collected every two hours from the pitfall traps of transects 11 and 13 allowed to find out the immigration rate was higher in the spots already colonized than in



previously little colonized or uncolonized spots. As traps were efficient at a stretch, and as the two species had different daily activity periods, one can calculate the correlations between the abundance observed when each species was active and the abundance obtained at the end. On the other hand, in order to estimate the importance of emigration processes, the number of beetles found in the pitfall traps and in the dung pats at the same place were compared. The emigration of beetles from the pitfall traps is almost impossible. As from the pitfall traps the emigration was prevented but as it was allowed from the dung pats, the difference between was considered as an estimation of the level of emigration.

## RESULTS

### Intraspecific aggregation

The higher was the mean abundance of both species, the higher was is the variance (Fig. 1). For mean densities above than five individuals per dung pat, the Morisita index (MI) and the intraspecific aggregation measure ( $J$ ) values indicated aggregated patterns. Nevertheless, several MI and  $J$  values indicated aggregation even when population densities were less than five ind./pat (Table 1 and Fig. 1).

For both species, the mean abundances were significantly higher from pitfall traps than from dung pats (*D. gazella*: dung pats  $10.71 \pm 8.69$  (mean  $\pm$  SD), pitfall traps  $15.90 \pm 14.27$ ;  $t=2.035$ ;  $P<0.05$ ; *E. intermedius*: dung pats  $3.17 \pm 2.60$ ; pitfall traps  $9.22 \pm 8.11$ ;  $t=5.153$ ;  $P<0.001$ ). As the mean densities were higher for pitfall-traps, all the variance to mean ratios as well as the MI and  $J$  values indicated a significant aggregation for *D. gazella* (Table 1). However, the magnitude of the MI and  $J$  indices did not differ with regard to their values from the dung pats (Kolmogorov-Smirnov two-sample test;  $DN=0.40$ ;  $P=0.85$ ). The intraspecific aggregation indices for *E. intermedius* were also significant in the two pitfall trap transects with higher densities (transects 12 and 13, Table 1), but their magnitude did not differ with regard to those from dung pats (Kolmogorov-Smirnov two-sample test;  $DN=0.50$ ;  $P=0.70$ ).

The number of individuals of *E. intermedius* captured in the pitfall traps located in the same place was significantly correlated once (Fig. 2). Presumably, when the *E. intermedius* numbers increased (transects 12 and 13), the beetles tended to colonize the western pitfall traps. In the case of *D. gazella*, the spatial arrangements were variable and there were even significant negative correlations between the abundances in transects 11 and 13, and in transects 11 and 12 (Fig. 2). For *D. gazella*, there were no significant correlations at  $P=0.05$  between the abundance observed during the period when the species was active and the abundance finally obtained (transect 11:  $r=0.420$ ,  $df=18$ ; transect 13:  $r=0.121$ ,  $df=18$ ). However, in transect 11 the correlation was nearly significant

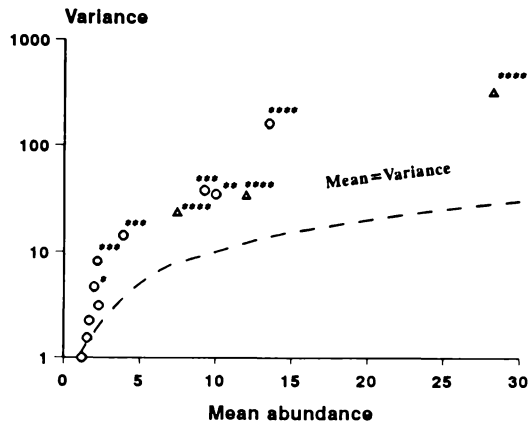
( $0.05 < P < 0.1$ ). For *E. intermedius*, the correlation was negative but not statistically significant in transect 11 ( $r = -0.345$ ,  $df = 18$ ), and positive and significant in transect 13 ( $r = 0.546$ ,  $df = 18$ ,  $0.01 < P < 0.02$ ).

Table 1

Values of mean ( $\mu$ ), variance ( $\sigma^2$ ), variance-mean ratio ( $\sigma^2/\mu$ ), Morisita index (MI), intra-specific aggregation ( $J$ ) and interspecific aggregation ( $C$ ) from dung pat (1-10) and pitfall trap (11-13) transects, carried out in a physiognomically homogeneous area of the Mapimi Biosphere Reserve. T = transect number. n = number of sampling units. Dg = *Digitonthophagus gazella* and Ei = *Euoniticellus intermedius*. P = statistical significance of  $\chi^2$  values: NS- no significant, \* -  $P < 0.05$ ; \*\* -  $P < 0.01$ ; \*\*\* -  $P < 0.001$ .

T	n	Species	$\mu$	$\sigma^2$	$\sigma^2/\mu$	$\chi^2$	P	MI	J	C
1	10	Dg	2.2	8.18	3.72	33.46	***	2.165		
2	10	Dg	1.7	2.23	1.31	11.82	NS	1.176		
3	9	Dg	1.56	1.53	0.98	7.86	NS	0.989		
4	10	Dg	3.9	14.32	3.67	33.05	***	1.633		
		Dg	1.22	0.94	0.77	6.18	NS	0.818	-0.138	
5	9	Ei	2.67	26.75	10.03	80.25	***	4.14	8.314	-0.718 NS
		Dg	2.3	3.12	1.36	12.22	NS	1.146	0.25	
6	10	Ei	1.6	2.71	1.69	15.25	0.08	1.417	0.522	-0.014 NS
		Dg	2	4.67	2.33	21	*	1.632	0.633	
7	10	Ei	2.2	2.4	1.09	9.82	NS	1.04	0.046	0.222 NS
		Dg	10	34.57	3.46	24.20	**	1.218	0.260	
8	8	Ei	1.63	1.41	0.868	6.08	NS	0.923	-0.085	-0.339 *
		Dg	13.50	160.86	11.92	83.41	***	1.714	0.479	
9	8	Ei	3.13	8.98	2.87	20.12	**	1.55	0.588	-0.289 *
		Dg	9.25	37.64	4.07	28.49	***	1.294	0.750	
10	8	Ei	4.75	6.21	1.31	9.16	NS	1.058	0.084	0.258 NS
		Dg	7.45	23.84	3.20	60.80	***	1.282	0.343	
11	20	Ei	4.35	4.24	0.975	18.52	0.5	0.994	0.000	-0.057 NS
		Dg	28.25	322.83	11.43	217.12	***	1.351	0.438	
12	20	Ei	6.05	18.47	3.05	58.01	***	1.325	0.360	-0.042 NS
		Dg	12.00	34.10	2.84	54.00	***	1.146	0.171	
13	20	Ei	17.25	78.20	4.53	86.13	***	1.195	0.216	-0.012 NS

*D. gazella*



*E. intermedius*

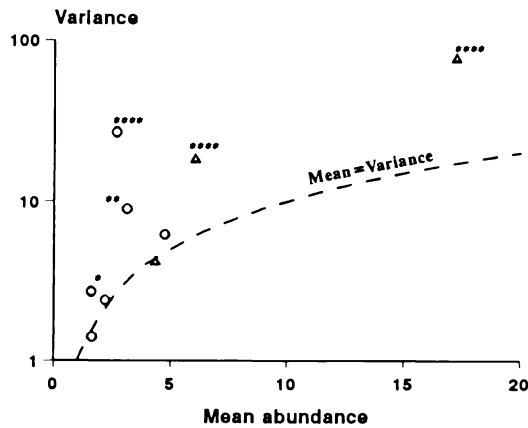
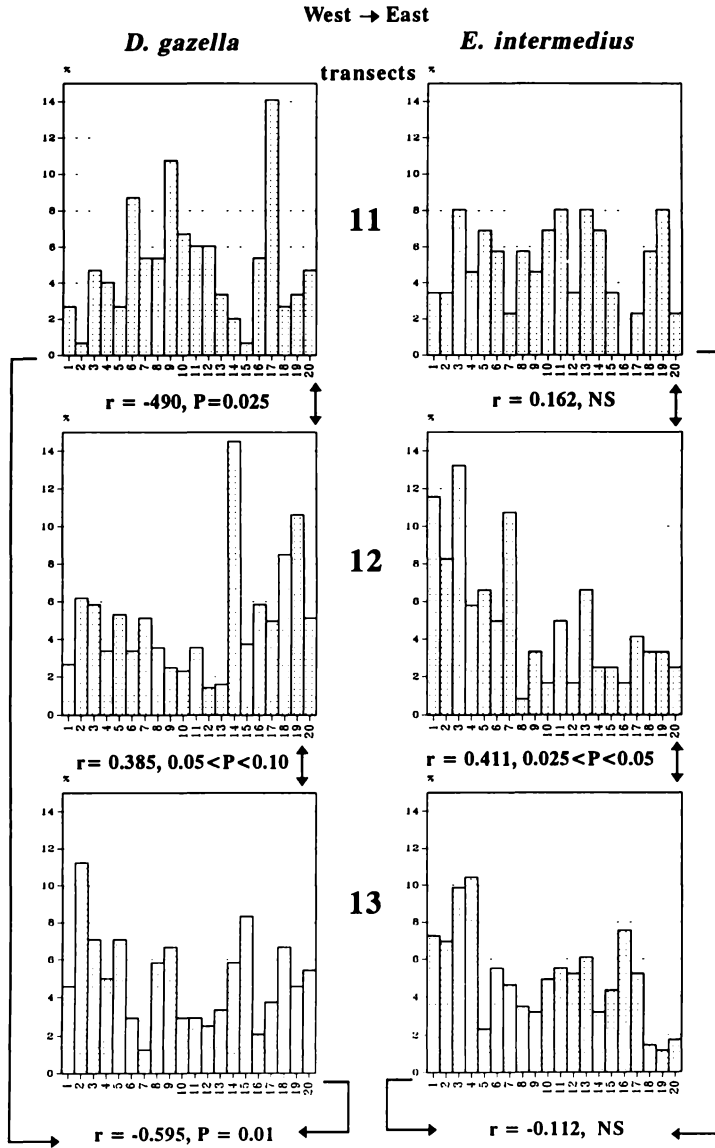


Figure 1

Relationship between the mean abundance and the variance for *Digitonthophagus gazella* and *Euoniticellus intermedius* from dung pat (circles) and dung baited pitfall-trap (triangles) transects.  $\chi^2$  values were calculated for the variance-to-mean ratio, where \*  $P < 0.05$ , \*\*  $< 0.01$ , \*\*\*  $P < 0.001$ , \*\*\*\*  $P < 0.0001$ .



**Figure 2**  
 Percentage of individuals attracted per trap in each 1993 transect. The Pearson correlation coefficients ( $r$ ) of abundance per trap in the same site among the pairs of transects are indicated.

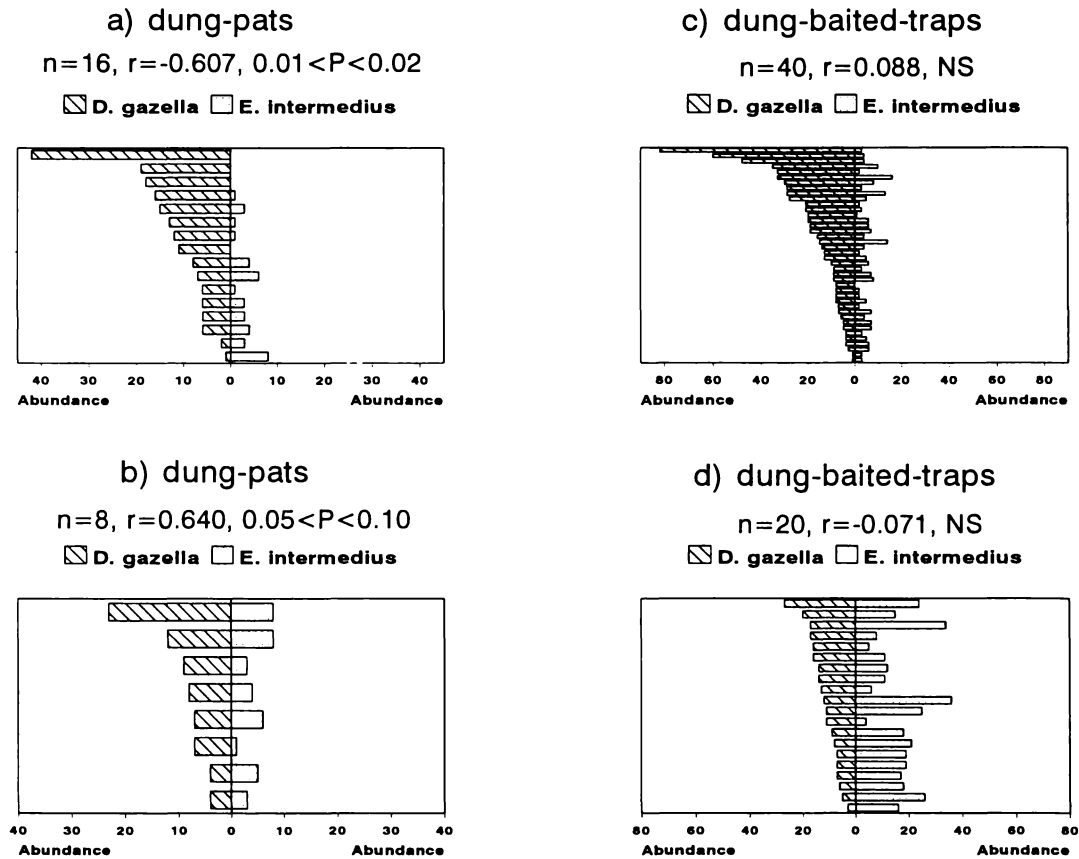


Figure 3

Abundance of *D. gazella* and *E. intermedius* i) per dung pat, in transects 8 and 9 (a) and in transect 10 (b); ii) per dung baited pitfall-trap, in transects 11 and 12 (c) and in transect 13 (d). The Pearson correlation coefficients ( $r$ ) between the abundances of the two species are indicated.

### Interspecific aggregation

When pitfall traps were used, the interspecific aggregation indices were not statistically significant (see C in Table 1). The only significant values of interspecific aggregation between *D. gazella* and *E. intermedius* were obtained for data from the two dung pat transects number 8 and 9 (Table 1). The values were negative, indicating a segregation between the two species. In these transects the mean densities of *D. gazella* per dung pat were high. The abundances of the two species in dung pats was negatively correlated in transects 8 and 9 when take them together ( $n = 16$ ;  $r = -0.607$ ;  $0.01 < P < 0.02$ ) (Fig. 3a). In the transect 10, the correlation between the abundances of two species was almost significant (Fig. 3b). On the contrary, when the pitfall traps were considered the correlations between the abundances of the two species were distant from a statistically significant level (Fig. 3c and d).

The emigration rate (difference between pitfall trap and dung pat abundances) increased for the two species as the immigration rate (abundance in pitfall traps) increased (Fig. 4a). The emigration rates of the two species were not correlated (Fig. 4b). The high *D. gazella* immigration rates were not correlated with the high *E. intermedius* emigration rates (Fig. 4c), as well as the high *E. intermedius* immigration rates were not correlated with the high *D. gazella* high emigration rates (Fig. 4d).

## DISCUSSION

In Mapimí, *D. gazella* and *E. intermedius* showed aggregated distribution at a small spatial scale (an area of 200 m<sup>2</sup>) in which environmental heterogeneity was difficult to detect. At this microspatial scale, the intraspecific aggregation seemed to be a general trend for the two species as it occurred for other dung beetles (Hanski & Cambefort, 1991). Aggregated distribution appeared when population densities were high and when emigration was prevented (pitfall traps), but also existed when population densities were low and when emigration occurred (dung pats). Therefore, intraspecific aggregation usually occurred at high population densities, but it was also frequent and of similar intensity at moderate or low densities (less than five individuals per dung pat).

The aggregated distribution observed in the two species seemed to be a consequence of differential immigration rates but their cause was still not clear. Was the immigration rate higher in some patches than in others? Was the immigration rate higher in those pitfall traps that had an initial abundance higher than those with a low abundance?. Presumably, when the mean population of *E. intermedius* increased, the individuals tended to colonize the pitfall traps of the western part of the site.

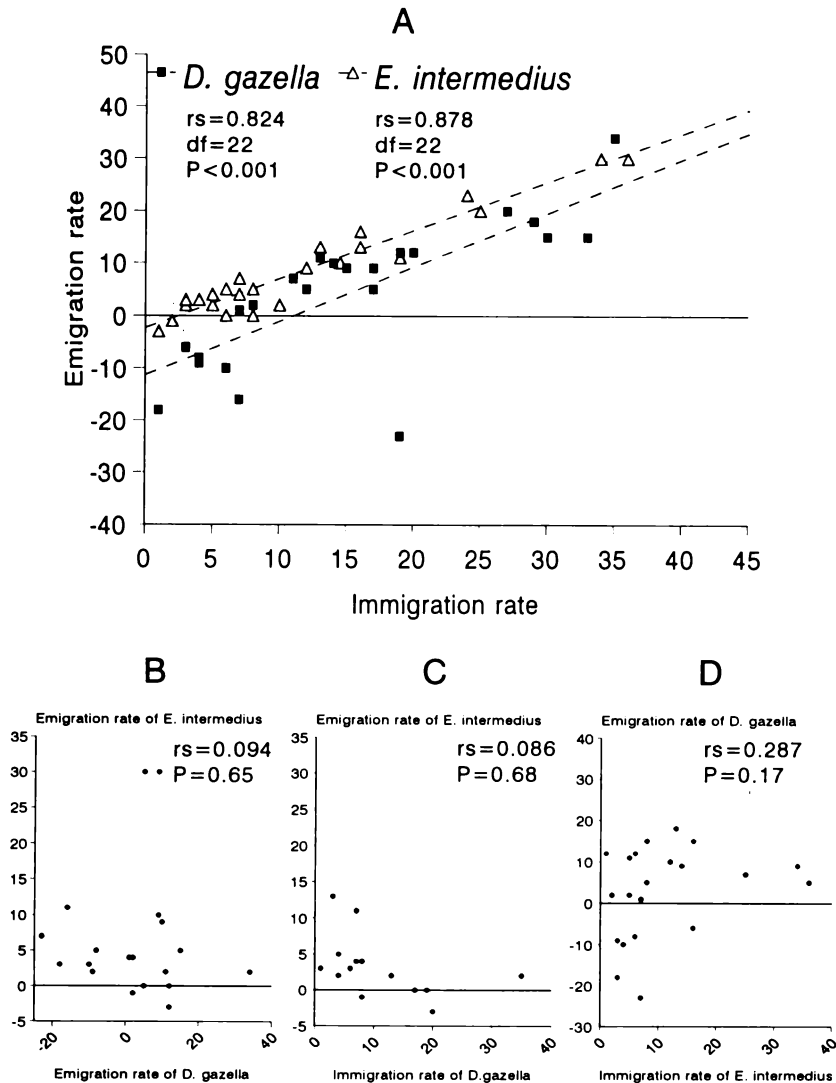


Figure 4

(A) Relationship between immigration rate (pitfall trap abundance) and emigration rate for each dung beetle species (1993 data). The emigration rate was calculated as the difference between the abundance in pitfall-traps and dung pats. (B) Relationship between emigration rate of the two species. (C) Relationship between the immigration rate of *Digitonthophagus gazella* and the emigration rate of *Euoniticellus intermedius*. (D) Relationship between the immigration rate of *E. intermedius* and the emigration rate of *D. gazella*.  $r_s$  is the Spearman rank correlation coefficient.

On the contrary, *D. gazella* did not show any preference for particular dung pats. On the other hand, sometimes the individuals of the two species tended to colonize patches with a larger initial number of beetles. Our results are not conclusive. The spatial microlocalization of dung pats can influence dung beetle colonization degree on some occasions (Hanski, 1987). There is always a certain degree of environmental heterogeneity that cannot be observed. A suitable microenvironment and its perception by individuals may lead to the spatial distribution observed on this scale, but several other experiments would be necessary to confirm this hypothesis. Other factors, such as wind direction, the location of the main source (pool) of beetles, or inclusive, differences on the attraction capability of dung used for dung pats and pitfall traps, also may influence the results. It could be possible that the previously treatment of homogeneization of the fresh dung collected was not as effective to reduce the attractiveness variation effect. But it is also possible that without heterogeneity, repeated choice of more densely populated patches could give rise to a pattern of intraspecific aggregation.

The present data suggest that the two species show a covariation in the number of the two species when emigration was not prevented. This interspecific aggregation was negative, indicated by a negative correlation between the distributions of species at this spatial scale. Yasuda (1987) found that the emigration of the dung beetle species *Liatongus phanaeoides* depended on the numbers of another species, *Aphodius haroldianus*. Is it possible that one of the two species was dominant and prevented the immigration of the other species or induced its emigration from the patches?. Are interspecific interactions the main responsible factors for the differential emigration of species from the pats?. The more individuals was attracted and arrived to the pitfall traps (immigration rate), the higher was the emigration from the dung pats. Others experiments also demonstrated that emigration from droppings was density dependent at sufficiently high densities (Landin, 1961; Yasuda, 1987). However, the immigration rate of *D. gazella* did not influence the emigration rate of *E. intermedius*, nor did the immigration rate of *E. intermedius* influenced the emigration rate of *D. gazella*. The emigration rate of both species was not spatially correlated and, perhaps, the responsible factors of emigration were not the same for both species. This suggests that neither of the two species induces the emigration by the other. In fact, *E. intermedius* was the first species attracted by the traps of transect 13 set up in the morning and, for that reason, its mean abundance was higher than that obtained with traps set up in the afternoon (transects 11 and 12) ( $17.25 \pm 8.84$  vs  $5.20 \pm 3.44$ ;  $t=14.57$ ,  $P<0.001$ ). *Digitonthophagus gazella* arrived later, at dusk and again at dawn. The probability of emigration due to competitive interactions between the two species is low,



unless the arrival of *D. gazella* led *E. intermedius* to emigrate from pats between dusk and dawn, when its normal activity period fell out. The intraspecific competition exerts a great influence on the emigration process, but the interspecific competition (or other factors such as microenvironmental dung pat changes, for example) cannot be disregarded. The competitive interactions among individuals intraspecifically aggregated could lead to the generation of differential emigration rates and microspatial segregation. At this scale, it is not necessary to suppose that extant environmental heterogeneity gives rise to spatial partitioning. Immigration as well as emigration can generate aggregated distributions in the absence of environmental heterogeneity.

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