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ARTICLE

Effect of using different types of animal dung for feeding and nesting by the dung beetle *Onthophagus lecontei* (Coleoptera: Scarabaeinae)

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Abstract: *Onthophagus lecontei* Harold, 1871 is an American dung beetle that feeds on the dungs of a variety of species, perhaps owing to hitherto unknown differences in their effect on its development and survival. We tested whether using different types of dung (exotic and native) for feeding and nesting affects *O. lecontei*'s progeny. Adult beetles from the field were randomly paired and assigned to horse (*Equus ferus* Boddaert, 1785), goat (*Capra hircus aegagrus* Erxleben, 1777; domestic), or wild rabbit (*Sylvilagus cunicularius* (Waterhouse, 1848); native, endemic) dung under laboratory conditions. The number, mass, and volume of their brood masses, the number of emerged beetles, adult size, and duration of preimaginal stages (egg, larva, and pupa) were evaluated. There were differences for all variables: *O. lecontei* reared in wild rabbit dung produced more progeny, more brood masses, and larger adult beetles, and offspring remained in each preimaginal stage for a shorter period of time. *Onthophagus lecontei* is able to feed and nest using all three types of dung, but wild rabbit dung is the most favorable for its development. This suggests the existence of a long-standing association between *O. lecontei* and this native rabbit and the optional relationships with introduced herbivores; plasticity in reproductive behavior that may be useful when the optimal resource is not available.

Key words: exotic and native herbivore dungs, feeding and nesting resources, *Onthophagus lecontei*, *Sylvilagus cunicularius*, wild rabbit.

Résumé : *Onthophagus lecontei* Harold, 1871 est un bousier américain qui se nourrit des déjections de diverses espèces, possiblement en raison de variations jusqu'ici inconnues de l'effet de ces différentes déjections sur son développement et sa survie. Nous avons vérifié si l'utilisation de différents types d'excréments (exotiques ou indigènes) pour l'alimentation et la nidification avait une incidence sur la progéniture d'*O. lecontei*. Des bousiers adultes pris sur le terrain ont été jumelés de manière aléatoire et affectés à des excréments de cheval (*Equus ferus* Boddaert, 1785), de chèvre (*Capra hircus aegagrus* Erxleben, 1777; domestique) ou de lapin sauvage (*Sylvilagus cunicularius* (Waterhouse, 1848); indigène, endémique) dans des conditions de laboratoire. Le nombre, la masse et le volume de leurs couvains, le nombre de bousiers émergés, leur taille adulte et la durée des étapes préimaginales (œuf, larve et pupe) ont été évalués. Toutes les variables présentaient des variations, les *O. lecontei* élevés sur des excréments de lapin sauvage produisant une plus grande progéniture, plus de couvains et des adultes plus grands, et leur progéniture demeurant à chaque étape préimaginale pour une période plus courte. *Onthophagus lecontei* peut se nourrir et nidifier en se servant des trois types de déjections, mais les excréments de lapin sauvage sont les plus favorables à son développement. Cela indiquerait l'existence d'une association de longue date entre *O. lecontei* et ce lapin indigène et des relations facultatives avec les herbivores non indigènes, donc une plasticité du comportement reproducteur qui pourrait être utile quand la ressource optimale n'est pas disponible. [Traduit par la Rédaction]

Mots-clés : excréments d'herbivores exotiques et indigènes, ressources d'alimentation et de nidification, *Onthophagus lecontei*, *Sylvilagus cunicularius*, lapin sauvage.

Introduction

Spatial and temporal variations in the abundance of a resource, like food, can favor the evolution of phenotypic plasticity in animals as a way of tracking changing environments (for birds see Sofaer et al. 2012). Food availability has an important effect on the reproductive output of organisms (Tamburi and Martín 2011; Díaz et al. 2012). In insects, food availability affects body size (Hunt and Simmons 1998, 2000; Shafiei et al. 2001; Moczek and Nijhout 2002; Araújo et al. 2012; Berger et al. 2012; Jiménez-Cortés et al. 2012; Vargas et al. 2012; Barry 2013; Roark and Bjorndal 2014), longevity (Hunt and Simmons 1998, 2000; Wei 2012; Araújo et al. 2012; Barry 2013; Hopwood et al. 2013; Li et al. 2013; Roark and Bjorndal 2014), body mass (Hunt and Simmons 1998, 2000; Jiménez-Cortés et al. 2012; Saastamoinen et al. 2013), development time (Jiménez-Cortés et al. 2012; Saastamoinen et al. 2013), larval or nymph development (Shafiei et al. 2001; Moczek and Nijhout 2002; Barry 2013), reproductive output, reproductive success, fitness components (Dmitriew and Rowe 2011; Berger et al. 2012; Barry 2013; Hopwood et al. 2013; Segoli and Rosenheim 2013; Stahlschmidt et al. 2013), fecundity (Vargas et al. 2012; Barry 2013; Stahlschmidt et al. 2013; Saastamoinen et al. 2013; Roark and Bjorndal 2014), egg size (Vargas et al. 2012; Stahlschmidt et al. 2013), sexual selection (Miller and Svensson 2014),

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timing of pupation, time of eclosion and metamorphosis (Shafiei et al. 2001), etc.

Like other insects, dung beetles undergo complete metamorphosis and build brood masses that will house their offspring during development (Halffter and Edmonds 1982). The quality and quantity of a brood mass determines adult body size (Hunt and Simmons 1997, 1998, 2000; Moczek 1998, 2002) and subsequent fitness (Hunt and Simmons 2001; Hunt et al. 2002). Each brood mass usually contains a single individual (Halffter and Edmonds 1982; Halffter 1997), and the mass of the brood mass provides a reliable indicator of the quality of the offspring produced (Hunt and Simmons 1998). The larva is unable to move out of the nest for food and develops in an underground chamber that, under natural conditions, contains a finite amount of food provided by its parents (Halffter and Edmonds 1982; Halffter and Matthews 1966; Scholtz et al. 2009). The development and completion of each preimaginal stage (egg, larva, and pupa) requires that a sufficient quantity and quality of food be initially provided by the parents (Halffter and Edmonds 1982, Halffter and Matthews 1966). However, dung availability is limited in time and in space. Thus, a brood mass represents the entire amount of resource available to the larva.

Parent dung beetles adjust the amount of food that they provide for their offspring according to diet quality, which may help compensate for environmental variation induced by differential resource quality in the field (Moczek 1998; Kishi and Nishida 2006). The quantity (Lee and Peng 1981; Emlen 1996; Hunt and Simmons 1997) and quality of the food provided by the parents, such as its protein content, have been observed to influence the development and size of offspring (i.e., the greater the protein contents of the resource, the larger the offspring) (Lee and Peng 1981, 1982; Cook 1993; Hunt and Simmons 2000).

Dung beetles of the American genus *Onthophagus* Latreille, 1802 (Insecta: Coleoptera: Scarabaeinae) use a variety of types of herbivorous mammal dung from both domestic and native species for feeding and nesting (Halffter and Edmonds 1982). This extensive use of dung may be associated with formerly unknown differences in dung beetle development and survival, as food availability is a factor that determines their reproductive output (González-Megías and Sánchez-Piñero 2004). The quantity and quality of the resource used by *Onthophagus* for feeding and nesting influence both the development (Moczek 1998) and the survival of its larvae (Owen et al. 2006), as well as the morphology, size (Moczek and Emlen 1999; Emlen et al. 2007), and mass of the emerged adults (Emlen 1996; Moczek 1998). Variations in food availability for the final larval instar affect its growth and the timing of pupation (Shafiei et al. 2001) and may also result in smaller and (or) lighter adults. In contrast, in the presence of sufficient good-quality food resources, the emerged adults are larger and there is marked growth of the structures important to sexual selection, such as the males' horns (Emlen 1996). It is also known that a high-quality diet allows the adults to store compounds that are important to metabolism and development, such as lipids, carbohydrates, and proteins (Van der Horst and Ryan 2005).

The capacity to choose the type of dung for consumption is also related to the supply available in the type of habitat used (Barbero et al. 1999). *Onthophagus* species can live in a variety of habitats and feed on the wide range of organic material encountered depending on the temporal and spatial availabilities of these resources (Halffter et al. 1995). There have been many studies on the reproductive success and parental investment of sexually dimorphic species of *Onthophagus*, such as *Onthophagus taurus* (Schreber, 1759), *Onthophagus binodis* (Thunberg, 1818), *Onthophagus atripennis* Waterhouse, 1875, *Onthophagus vacca* (L., 1767), etc. (see, e.g., Simmons and Ridsdill-Smith 2011). Studies from Mexico include descriptions of the behavior and nesting patterns (see Halffter and Edmonds 1982), a study describing the ecological and reproductive traits of *Onthophagus incensus* Say, 1835 as they relate to their phenology (Martínez et al. 1998), one describing their preimaginal stages (Huerta et al. 2010), and another that describes the nesting behavior of this species (Huerta and García-Hernández 2013). There is no information about the preferences of *Onthophagus* for the dung of exotic or native mammal species and its effects on nesting behavior and reproductive success.

Onthophagus lecontei Harold, 1871 has been recorded in temperate forests (Morón 1996; Navarrete-Heredia and Galindo Miranda 1997; Arellano and Halffter 2003; Anduaga 2000; Arriaga et al. 2012), xerophyllous and submontane scrubland and tropical low deciduous forest (Morón et al. 2000), and surrounding open areas, where the species feeds on different types of dung. This species has been collected in the dung of domestic animals such as cows, dogs, horses, and sheep (Morón et al. 2000; Arellano and Halffter 2003; Anduaga 2000; Arriaga et al. 2012), as well as in that of the wild rabbit (Arellano et al. 2009). These types of dung have contrasting physical and chemical characteristics. It is not known whether *O. lecontei* is capable of nesting in all of these types of dung (native and exotic), or whether the development of the offspring or adults would differ as a result of feeding on them. Currently, there are no published studies that provide information on aspects of feeding, nesting, or development or that describe the life cycle of *O. lecontei.* There is only one on the ovarioles of female *O. lecontei* (Pluot 1979) and one on the taxonomy of the species (Howden and Génier 2004).

The aim of our study was to determine whether the type of dung used for feeding and nesting produces differences in the progeny of *O. lecontei*. If brood-mass size and adult-body size differ in this species as a function of dung type, the results would be valuable in the context of parental investment. We addressed the extent to which the use of dung from domestic or native mammal species affects (*i*) nesting behavior; (*ii*) the number, mass, and size of brood masses; and (*iii*) the number and development time of larvae, pupae, and emerged adults. Due to the recent ecological association of introduced herbivores with *O. lecontei* in contrast to their long-time association with native herbivores, we predicted that beetle offspring reared in the dung of introduced herbivores would pay a cost in terms of their reproductive success, as might their descendants. That is, we expect fewer, lighter, and smaller brood masses; fewer larvae, pupae, and emerged adults; and a longer development time for each preimaginal stage for offspring reared in the dung of introduced herbivores relative to those raised on the dung of a native herbivore.

Materials and methods

Sampling of dung beetle adults

Adult *O. lecontei* were collected from Cantona, state of Puebla, Mexico (19°28′22.51″N, 97°23′3.29″W), in July 2012 using pitfall traps baited with goat dung and also directly from the soil (at a depth of 3–10 cm) below the semifresh goat dung. The beetles were identified using the taxonomic keys of Howden and Génier (2004). This species is not sexually dimorphic; gender was therefore determined based on the number of carinas on the clypeus (the male has only one clypeal carina, whereas the female has two) and on the characteristics of the abdominal sternum.

Experimental protocol

Mating pairs were formed using a random-numbers table and each pair was kept in a terrarium. Each terrarium consisted of a semitransparent plastic box (13 cm × 9 cm × 4 cm) with a 10 cm layer of finely sieved sterile soil (see Huerta et al. 2010). The beetles were kept under greenhouse conditions with a 12 h light : 12 h dark photoperiod, at an environmental temperature of 15.3 °C and a relative humidity of 77%.

Collection and characteristics of the three types of dung used

We used the dung of two introduced domestic herbivores, *Equus ferus* Boddaert, 1785 (horse) and *Capra hircus aegagrus* Erxleben, 1777 (goat), and of the native herbivore *Sylvilagus cunicularius* (Waterhouse, 1848) (wild rabbit). These species occur in Cantona, Puebla, and feed mostly on grasses. Neither the horses nor the goats were provided with supplementary feed. However, we noted that a fraction of the wild rabbit pellets of dung contained the partially digested remains of juniper cones (*Juniperus deppeana* Steud.).

Table 1 lists the concentrations of macroelements present in the different types of dung used in the treatments. To obtain this information, samples were collected directly from the animal's habitat. Ten pads of horse dung and goat dung were checked in the field and a small portion was taken from each of them to obtain 500 g fresh mass for each type of dung. For wild rabbit dung, a 500 g sample was obtained from bed sites and latrines.

In the laboratory, using 60 g of each type of dry dung, nitrogen content was determined by the Kjeldahl method (Greenfield and Southgate 1992), phosphorus by the Spinreact method (Farrell and Kaplan 1984), potassium by flame photometry (Eaten et al. 1992), soluble carbohydrates by the technique of furfural formation with phenol (D'Ocon et al. 1998), and trace elements were determined by acetate extraction and the Bray-solution technique (Bray and Kurtz 1945).

The following experimental protocol began on 27 July 2012: 17 pairs of *O. lecontei* were provided with horse dung, 22 pairs with goat dung, and 17 pairs with wild rabbit dung. Ten grams of semi-fresh dung were provided to each pair twice per week. The variables evaluated were the number, mass, and volume of the brood masses; the number of larvae, pupae, and adults; the size of emerged adults (pronotum width and body length); and the duration in days of each preimaginal stage. The preimaginal stage refers to the immature stages (egg, larva, and pupa). The duration of each preimaginal stage, as well as the feeding and nesting behaviors, were recorded by direct observation. With great care, a small opening was made in the brood mass, without causing any damage, to observe whether the egg had hatched and so on for each stage.

Brood masses were weighed using an analytical balance (Chio balance J-L 180). Pronotum width and body length (from the carina to the pygidium) were recorded with an electronic caliper (Mitutoyo® CD-6″CX) in the emerged adults. The parents were kept in separate terraria with goat dung until their natural death.

Feeding and nesting behaviors

The description of nesting pattern consists of a diagnosis, based upon traits defined by Halffter and Edmonds (1982): the way in which the larvae are provisioned, nest location, complexity, placement of brood masses, manipulation of larval provision, provisioning of subterranean nests, location of the egg chamber, male–female cooperation, and brood care. To describe the feeding and nesting behaviors of all mating pairs, we observed whether beetles were eating and using the dung. During the first 12 days, the pairs of beetles were observed four times daily until they finished the feeding phase. During nesting, beetles were observed twice a week until the emergence of the adults, 41 days later.

Statistical analysis

Variation among the three types of dung used, in terms of the number of brood masses, the number of emerged beetles, and development time for each preimaginal stage (larva and pupa) and to newly emerged adults was analyzed using the nonparametric Kruskal–Wallis test. Bonferroni and Dunn post hoc tests were used to determine the origin of any differences detected among the dung types in these response variables (Zar 1999).

For each of the dung-type treatments, the mass and size of the brood masses (width, length, and volume) and the pronotum width and body length of the emerged adults were analyzed using one-way ANOVAs (Zar 1999). Tukey's post hoc tests were used to determine the origin of any significant differences detected among dung types (Zar 1999). The volume (V) in cubic millimetres (mm^3) of the brood masses was estimated using the following formula: $V = (\pi/6)\cdot L\cdot W^2$, where L is length and W is width.

Table 1. Moisture content, macroelement concentration, and protein content of the three types of dung (horse, *Equus ferus*; goat, *Capra hircus aegagrus*; wild rabbit, *Sylvilagus cunicularius*) used by the dung beetle *Onthophagus lecontei* during the resource-use experiment.

	Type of dung		
Parameter	Horse	Goat	Wild rabbit
Humidity (%)	70.90	63.80	58.80
Total nitrogen (g/kg)	8.58	15.40	10.10
Phosphorus (g/kg)	8.05	2.27	1.92
Potassium (g/kg)	5.43	4.52	1.26
Ash (g/kg)	34.9	85.80	72.00
Soluble carbohydrate (g/kg)	8.93	6.35	7.70
Crude protein (%)	5.40	9.60	6.30

Note: Ash consists of manganese, iron, nickel, copper, magnesium, zinc, and molybdenum.

To identify any association between the brood-mass variables, pairwise Spearman's correlations were run between mass and width, length and volume, width and length, width and volume, and length and volume (Zar 1999). Similarly, we tested for correlations between the mass of the brood mass and the width of the pronotum and the body length of the emerged adults, as well as between the latter two variables.

Results

Feeding and nesting behaviors

Onthophagus lecontei used all three types of dung during the experiment. The same feeding and nesting behaviors were observed in all three treatments and the latter corresponded to pattern I (sensu Halffter and Edmonds 1982): (*i*) construction of brood masses, (*ii*) oviposition of a single egg per brood mass, (*iii*) development of three larval stages and a pupal stage, and (*iv*) emergence of adults.

Number, mass, and size of brood masses

The number of brood masses produced per mating pair of beetles varied from one to seven and differed significantly among the three dung types used (Kruskal–Wallis, $\chi^2_{[2]} = 19.97$, $P = 0.00005$) (Fig. 1). There were fewer brood masses produced using the dung of domesticated animals (goat: Bonferroni and Dunn post hoc tests, $P = 0.006$; horse: Bonferroni and Dunn post hoc tests, $P = 0.04$) (exotic dung) than using wild rabbit dung (native species). There were significant differences in the mass of brood masses produced using the three different dung types ($F_{[2,78]} = 51.83$, $P < 0.0001$) (Table 2). The brood masses produced in goat dung were the heaviest, while those produced in wild rabbit dung were the lightest (Fig. 2A). Likewise, there was significant variation among dung types in terms of brood mass width ($F_{[2,78]} = 4.78$, $P = 0.01$), length ($F_{[2,78]} = 18.07$, $P < 0.0001$), and volume ($F_{[2,78]} = 26.81$, $P < 0.0001$) (Fig. 2B). In general, those produced with wild rabbit dung tended to be narrower and shorter and lower in volume than those produced with the other dung types.

Number of larvae, pupae, and adults

The number of individuals produced (larvae, pupae, and adults) from each type of dung differed significantly (Kruskal–Wallis, $H_{[2]} = 12.82$, $P = 0.001$): the most larvae, pupae, and adults were produced with wild rabbit dung (Table 3). No mortality was recorded between developmental stages in any of the treatments.

Duration of each developmental stage

There were significant differences among types of dung in terms of larval (Kruskal–Wallis, $H_{[2]} = 12.08$, $P = 0.002$) and pupal (Kruskal–Wallis, $H_{[2]} = 6.34$, $P = 0.04$) development times, and for the time to the emergence of imagos (Kruskal–Wallis, $H_{[2]} = 7.12$, $P = 0.03$) (Table 3). The larval and pupal stages were shorter in

Fig. 1. Median number of brood masses prepared by the dung beetle *Onthophagus lecontei* by dung type (horse, *Equus ferus*; goat, *Capra hircus aegagrus*; wild rabbit, *Sylvilagus cunicularius*). Different letters above the bars indicate statistically significant differences ($P < 0.05$). The whiskers extend from the minimum to the maximum and the lines within the rectangles of the boxplot indicate the first quartile, median, and third quartile. The median of the goat dung overlays the third quartile.

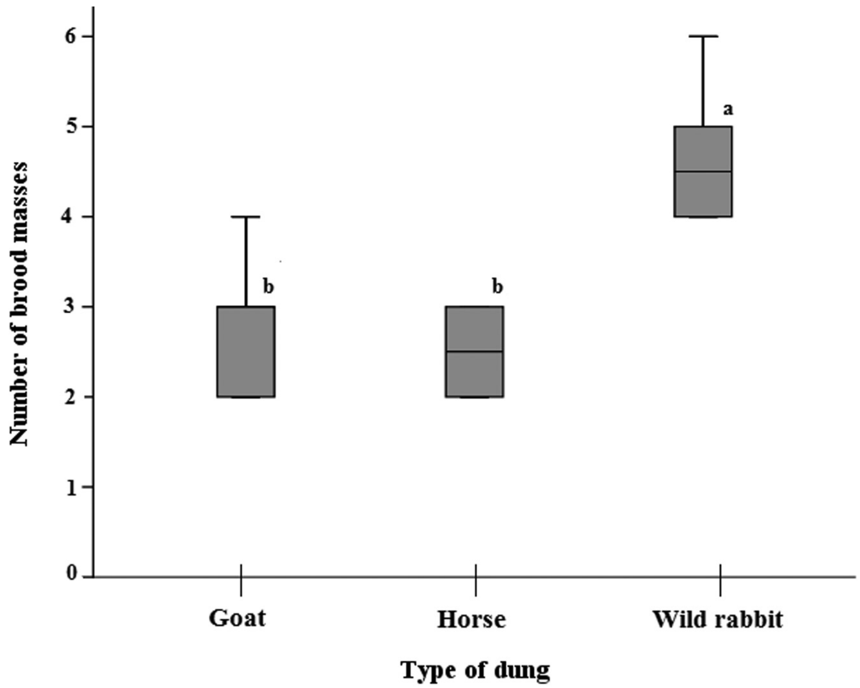

Table 2. Mean (±SE) measurements for the brood masses of the dung beetle *Onthophagus lecontei* obtained from three types of dung (horse, *Equus ferus*; goat, *Capra hircus aegagrus*; wild rabbit, *Sylvilagus cunicularius*).

	Type of dung		
Variable	Horse (n = 10)	Goat (n = 31)	Wild rabbit (n = 40)
Mass (g)	0.63 ± 0.03 b	0.88 ± 0.03 a	0.55 ± 0.01 c
Width (mm)	23.13 ± 0.01 a	23.18 ± 0.02 a	23.11 ± 0.00 b
Length (mm)	23.59 ± 0.03 a	23.54 ± 0.02 a	23.38 ± 0.01 b
Volume (mm³)	28 578.16 ± 0.05 a	28 573.79 ± 0.03 a	28 305.33 ± 0.02 b

Note: Different letters across the same row indicate significant differences ($P < 0.05$). Sample size is given in parentheses for each type of dung.

offspring reared in wild rabbit dung and the emergence of imagos was quicker.

Adult morphometric measurements

Mean values for the morphometric measurements of the emerged adult *O. lecontei* are given in Table 4. There were statistically significant differences in pronotum width ($F_{[2,72]} = 5.46$, $P = 0.006$) depending on the type of dung consumed during larval development. Offspring that consumed wild rabbit dung (3.45 ± 0.03 (mean ± SE), $n = 44$) had a wider pronotum than those that consumed goat (3.34 ± 0.03, $n = 8$) or horse (3.26 ± 0.10, $n = 23$) dung. Likewise, the length of the emerged adults differed significantly among the three treatments ($F_{[2.72]} = 4.69$, $P = 0.01$); the offspring reared in wild rabbit dung were longer (5.45 ± 0.05, $n = 44$) than those reared in goat (4.90 ± 0.07, $n = 8$) or horse (4.82 ± 0.16, $n = 23$) dung. Beetles reared in horse dung had the shortest width and length.

Correlations between brood-mass size and adult morphometric measurements

Correlation analysis indicated that the heaviest brood masses did not produce larger beetles; however, the most voluminous brood masses did produce larger beetles for all three dung types (Tables 4, 5).

Fig. 2. Mass (A) and volume (B) of the brood mass prepared by the dung beetle *Onthophagus lecontei* by dung type (horse, *Equus ferus*; goat, *Capra hircus aegagrus*; wild rabbit, *Sylvilagus cunicularius*). Different letters above the bars indicate statistically significant differences ($P < 0.05$). Bars are means ± SE.

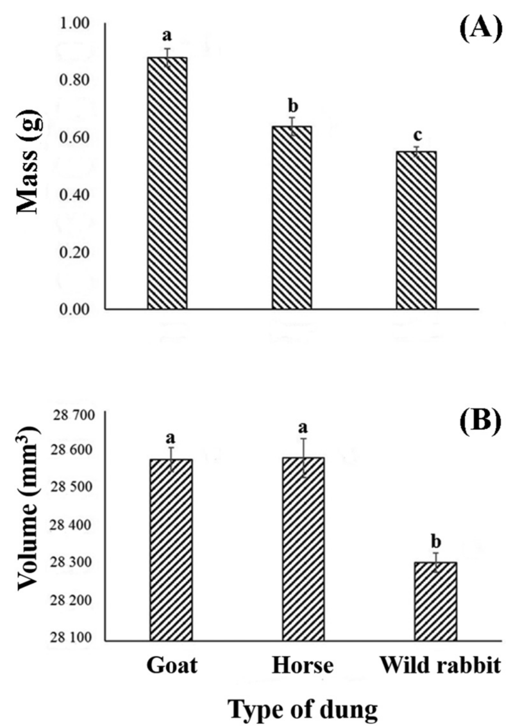

Table 3. Median number of emerged individuals and duration in days of each developmental stage (larva, pupa, and adult) of the dung beetle *Onthophagus lecontei* breeding and feeding on three types of dung (horse, *Equus ferus*; goat, *Capra hircus aegagrus*; wild rabbit, *Sylvilagus cunicularius*).

	Type of dung		
Variable	Horse (*n* = 4)	Goat (*n* = 12)	Wild rabbit (*n* = 10)
Number of emerged individuals	2 b	2 b	4.5 a
Duration of the larval stage	22.5 a	23 a	21 b
Duration of the pupal stage	10.5 b	11 a	11 ab
Time to emergence	3.5 b	4.5 a	3 b

Note: Different letters across the same row indicate significant differences ($P < 0.05$). Sample size for each type of dung is given in parentheses.

Table 4. Correlations between mass of the brood mass (MBM) and morphometric measurements (pronotum width (PW) and body length (BL)) of emerged adult dung beetle *Onthophagus lecontei* that developed in brood masses made from three types of dung (horse, *Equus ferus*; goat, *Capra hircus aegagrus*; wild rabbit, *Sylvilagus cunicularius*).

	Horse (*n* = 8)			Goat (*n* = 23)			Wild rabbit (*n* = 40)		
Variable	*r*	*z*	*P*	*r*	*z*	*P*	*r*	*z*	*P*
MBM–PW	−0.32	−0.74	0.46	−0.16	−0.73	0.47	0.14	0.90	0.37
MBM–BL	−0.03	−0.07	0.94	−0.03	−0.01	0.86	0.10	0.66	0.51
PW–BL	0.80	2.50	**0.01**	−0.87	6.09	**<0.00**	0.89	8.70	**<0.00**

Note: Sample size for each type of dung is given in parentheses and significant values are set in boldface type.

Table 5. Correlation between dimensions of the brood mass of the dung beetle *Onthophagus lecontei* nesting on three types of dung (horse, *Equus ferus*; goat, *Capra hircus aegagrus*; wild rabbit, *Sylvilagus cunicularius*).

	Horse (*n* = 10)			Goat (*n* = 31)			Wild rabbit (*n* = 40)		
Dimensions of brood mass	*r*	*z*	*P*	*r*	*z*	*P*	*r*	*z*	*P*
Mass–width	0.53	1.56	1.11	0.24	1.32	0.18	0.67	4.92	**<0.00**
Mass–length	0.24	0.64	0.51	0.07	0.37	0.70	0.38	2.46	**0.01**
Mass–volume	0.39	1.09	0.27	0.28	1.56	0.11	0.58	3.84	**<0.00**
Width–length	0.47	1.37	0.17	−0.53	−3.12	**0.00**	0.42	2.77	**0.00**
Width–volume	0.75	2.62	**0.00**	−0.23	1.28	0.19	0.74	5.86	**<0.00**
Length–volume	0.93	4.47	**<0.00**	0.69	4.56	**<0.00**	0.92	9.69	**<0.00**

Note: Sample size for each type of dung is given in parentheses and significant values are set in boldface type.

Discussion

Onthophagus lecontei was able to feed and nest with all three dung types evaluated and thus behaved like a generalist species. The same feeding and nesting behaviors corresponding to pattern I (sensu Halffter and Edmonds 1982) were observed in all three treatments; however, there were significant differences in brood-mass characteristics, the number of brood masses, and in the preimaginal stages (number of larvae and pupae and the duration of each developmental stage). As we predicted, these differences were related to the type of dung.

Onthophagus lecontei beetles reared in wild rabbit dung produced more progeny and more brood masses, but lighter and larger adult offspring, than those reared in exotic dung (goat and horse). These results concur with the findings of Kishi and Nishida (2006) who tested parental ability to adjust the amount of investment per offspring by providing *O. atripennis* dung beetle parents with one of three dung types: Japanese macaque (*Macaca fuscata* (Blyth, 1875)) dung (native), cow dung (exotic), and a mixture of monkey and cow dungs. These authors found that parents produced more but smaller brood masses with monkey dung than with cow dung or the mixture. When exotic resources are offered, the results are reported to vary in the southwest of Western Australia where *O. taurus* readily colonized both horse dung and cattle dung but produced larger numbers of lighter brood masses and larger adults with horse dung than with cattle dung (Hunt and Simmons 1998, 2004). Relatively small amounts of horse dung were sufficient to support the development of adult body sizes >5 mm in length. In contrast, with cow dung, it was necessary to increase brood ball mass by roughly 50%–75% to yield comparable adult body sizes (Moczek 1998). Thus, in the three previously mentioned species of *Onthophagus*, parent beetles adjust the amount of food that they provision for their offspring according to dung type, which may compensate for the environmental variation induced by differential resource quality in the field. In species of *Onthophagus*, the observed plasticity in brood-mass size may represent an optimal strategy for maximizing parental fitness and thus reflect differences in the costs and (or) benefits associated with provisioning offspring under different conditions.

The larvae of various insect groups have developed biological mechanisms through evolution that allow them to respond to the quality of their nutrition (Nijhout 1999). The quality of these resources is a key factor in the regulation of their development (Moczek 1998). For some authors quality is synonymous with different types of dung (Moczek 1998), but for other authors quality is related to the diet of the animal that provides the food (Favila 1993; Hunt and Simmons 2004), as we found, because exotic mammals feed only on grasses, but rabbits feed on grasses and also on juniper cones. Seed consumption could increase the fat content of this type of dung.

Our results do not concur with those reported by other authors who assert that the quality (or type) of food resource provided by the parents influences the development and size of their young, i.e., the greater the quantity and higher the protein content of the resource, the larger the size of the individual offspring produced (Lee and Peng 1981, 1982; Cook 1993; Hunt and Simmons 2000). Contrary to expectation, the brood masses produced using the wild rabbit dung were smaller in volume but produced larger individuals. In contrast, those in the goat- and horse-dung treatments (greater volume) produced smaller beetles. This suggests that, for this species, the type of dung rather than the quantity of dung is the determining factor in the size of new individuals. Protein content may not be important either because wild rabbit dung and horse dung contain less protein than goat dung (see Table 1).

Onthophagus lecontei has been collected abundantly from dung with a high moisture content, like cow dung (Arriaga et al. 2012). This concurs with the results of studies done in Africa, where most adult coprophagous beetles feed on the fresh dung of mammalian herbivores and preferred moist African elephant (*Loxodonta africana* (Blumenbach, 1797)) and African buffalo (*Syncerus caffer* (Sparrman, 1779)) dungs (76%–89% water) over drier impala (*Aepyceros melampus* (Lichtenstein, 1812)) or giraffe (*Giraffa camelopardalis* (L., 1758)) pellets (Holter and Scholtz 2007). However, in our study, *O. lecontei* preferred wild rabbit dung over moister goat and horse dungs (wild rabbit dung is the driest of the three). This preference was evaluated based on the reproductive success of the beetles but was not evaluated this way in the studies mentioned. In contrast, other studies on dung beetles nesting in wild rabbit dung have suggested that some dung beetle species have a preference for wild rabbit dung, in spite of its low moisture content and low nutritional value (see Verdú and Galante 2004).

Dung is mostly made up of water, carbohydrates, proteins, fats, inorganic substances, and cellular detritus. Wild rabbit dung appeared to have the necessary characteristics for the offspring feeding from the brood mass to grow larger than those reared in the other two types of dung. In wild rabbit dung, beetles spent less time in each developmental stage and the adults took less time to emerge. This could be an advantage in the field because more beetles emerge in less time and will have first access to available resources. Other authors, however, suggest that larvae respond to food deprivation by decreasing instar duration and pupating prematurely, leading to the early emergence of a small adult (Shafiei et al. 2001). As we expected, *O. lecontei* beetles reared in exotic dung (horse) spent more time in each developmental stage and those reared in goat dung spent more time as larvae than those reared in wild rabbit dung, although for the other preimaginal stages, values were similar to those obtained with wild rabbit dung.

We observed no impediment to the use of any of the three types of dung by *O. lecontei* for feeding or nesting; rather, their versatility appears to favor them. We measured the concentration of some of the macroelements in each type of dung and concentration differed among dung types. This may be an indicator of the quality of the beetles' diet, but further analysis (fats, carbon, diameter of particles, etc.) and more samples are needed to better understand how these traits relate to the quality of the different types of dung.

Introduced domestic versus native herbivores

The origin of the dung used for feeding and nesting seems to influence the reproductive success of *O. lecontei*. Our results show that using the dung of introduced herbivores (goats and horses) exacts a cost with respect to reproductive success (fewer brood masses, fewer offspring, longer duration of each developmental stage) and results in smaller descendants. In contrast, those who reared their offspring in dung of wild rabbits (*S. cunicularius*), a species endemic to Mexico, had greater reproductive success (more brood masses, more offspring, shorter duration of each developmental stage) and their descendants were physically larger.

We believe that the relationship between the beetle and the wild rabbit not only represents a certain degree of trophic opportunism on the part of *O. lecontei* in response to the abundance of food available in the latrines of wild rabbits, but also that there is a close relationship between these two species. *Onthophagus lecontei* uses wild rabbit droppings to nest and has also been associated with rodent dung (Sonoran Desert Packrat, *Neotoma phenax* (Merriam, 1903)) for the last 12 000 – 13 500 years (Elias 1992; Elias and Van Devender 1992; Elias et al. 1995). *Sylvilagus cunicularius* (wild rabbit) and *O. lecontei*, both endemic to Mexico, are amply distributed on the Central Plateau of Mexico and across the Trans-Mexican Volcanic Belt (Cervantes et al. 1992; Morón et al. 2000) and their current distributions partially overlap. Perhaps *O. lecontei* has adapted to feed on other types of dung, but it preferentially constructs nests using wild rabbit dung (Arellano et al. 2009) or rodent dung when the latter is available. Future studies on the biology and distribution of these species will further deepen our understanding of the extent of their association in Mexico.

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