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SHORT NOTE

Preferential use of one paw during feeding in the subterranean rodent *Ctenomys talarum*

Cristian E. Schleich

Laboratorio de Ecofisiología, Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata – CONICET - Argentina. Email: cschleic@mdp.edu.ar

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Initially believed to be a uniquely human characteristic, the preference to use one extremity for carrying out diverse activities, such as feeding or self-grooming, has been observed in several groups of vertebrates and even in some invertebrates (1,2,3). These behavioral asymmetries, which may reflect differences in the roles of the two brain hemispheres, are classified according to their occurrence in the individuals at the population level: no asymmetry, when all individuals prefer to use both the left and the right limb with equal probability; individual-level asymmetry, when some individuals of the population prefer to use one extremity while others prefer to use the other limb (no asymmetry at the population level); and population asymmetry, when most of the individuals prefer to use either the left or the right limb (3).

Among mammals, rodents constitute one of the most studied groups in the field of limb preferences. However, there are still controversies about how to classify this mammalian order basing on their paw lateralization. While some studies suggest that paw preferences in rodents show individual, but not population-level asymmetry (4,5,6), others indicate a population-level right handedness (7,8), although individual characteristics, such as sex, reproductive condition or strain, and even environmental factors or the kind of testing protocol used, appear to influence the degree and direction of lateralization in these species (3). At this point, it should be noted that most of the studies were carried out on "model organisms", such as *Rattus norvergicus* and *Mus musculus*, while investigations of paw preferences in wild species of rodents are comparatively scarce.

Ctenomys talarum (Thomas, 1898), commonly named as tuco-tuco, is a solitary species of subterranean rodent that inhabits sand dune belts in Buenos Aires Province, Argentina (9). This herbivorous rodent forages aboveground, when tuco-tucos emerge from burrow openings and travel short distances (less than one meter) to cut grasses and perennial forbs growing in the soil. However, the consumption of the collected food occurs inside their tunnels (10,11,12). Despite the difficulty of recording their feeding behavior in their natural habitat, laboratory observations suggested that individuals of this species prefer to use one paw when manipulating and consuming the leaves and stems. The feeding behavior of this subterranean rodent comprises several different steps that include catching food items with the mouth and one or both hands, cutting them into small pieces with the teeth, the removal of the superficial layers of the stems with the teeth while rotating the stems with the hands, and taking the leaves or stems to the mouth to ingest them after mastication.

The main aim of this study was to explore whether this species of wild subterranean rodent displays forepaw preferences while feeding, and if so, whether this lateralization occurs at the

individual and/or population level. The results of this study will add valuable information to our understanding of laterality in mammals in general and in rodents in particular, a group where a profound bias exists in terms of the number and diversity of species that have been studied.

Adult *C. talarum* individuals (n=14) were captured at Mar de Cobo (Buenos Aires Province, Argentina) using live traps set at fresh surface mounds. Then, individuals were carried to the biotherium and housed individually in plastic cages (42 × 34 × 26 cm) with wood shavings as bedding. A fresh supply of vegetables (carrots, sweet potatoes, lettuce and mixed grasses) was provided daily. The animal room was maintained at a thermoneutral temperature (23 ± 1 °C) and natural photoperiod. Relative ambient humidity ranged from 50 to 70%. Before recording the feeding behavior, animals were food-deprived for 24 hr to increase their motivation to eat. As a result, individuals devoted most of the recording time to eating or manipulating food items.

To record tuco-tucos´ feeding behavior, a Plexigas transparent chamber (45 × 30 × 30 cm) was used. Before starting the recordings, the individuals were left inside the testing chamber for 10 min to acclimate to it. Then, several items of *Panicum racemosum* (the most abundant plant species both in the habitat and diet of *C. talarum*) (11) were placed inside the chamber equidistant to the individual's sides, and the feeding behavior was recorded for a single 30 min period with a video camera. Later, videotapes were viewed and the following feeding parameters registered:

a) paw used by tuco-tucos to reach food to cut it.
b) paw used to rotate the plant stems while removing the superficial layers of them with the teeth.
c) paw used to take food to the mouth to eat.

Only clear views of tuco-tucos´ behavior while feeding were used to calculate paw preference. When an animal took a food item with one paw and carried it to its mouth repeatedly without dropping it, this was calculated as a single bout. If the individual passed the same food item from one hand to the other recurrently while eating, the most frequent paw used to carry the food to the mouth was considered to classify the bout and for the analysis. The measure of paw preference was calculated as the number of times the animals used their left, right or both paws to manipulate food items in all recorded bouts. Based on the frequencies of use, paw preference was conferred to the individuals using one paw for at least 66% of times (13). Therefore, tuco-tucos displaying 66% or more left paw uses were classified as left-preferent, those with 33% or less left paw uses were classed as right-preferent, and those with scores between 34% and 65% were classed as ambidextrous (13). Also, handedness index values (HI) and z scores were calculated. The HI value is calculated by dividing the difference between the total number of left and right paw reaches by the sum of them (RP - LP)/(LP + RP). Positive values reflect right hand preferences and negative values indicate left hand preferences. Although there is some controversy about its utility in laterality studies (14), the z score is still one of the most used statistical tests for analyzing handedness. The forepaw preference in each type of feeding behavior for each animal was determined by calculating an individual z score on the basis of the total number of left and right forepaw responses using the binomial test. Z score values of ± 1.96 are the critical values. Based on z scores, individuals are categorized as right-handed ($z > 1.96$), left-handed ($z < -1.96$), or ambidextrous ($1.96 > z > -1.96$) (14).

RESULTS

Paw used by tuco-tucos to catch food to cut it

No individual displayed left-paw preference and only one displayed right-paw preference (Fig. 1). The majority of the individuals (n=9) more frequently used both paws to catch food items to cut them with their teeth, while the others used the right or left paw more often but always less than 66% of the times, clearly suggesting an absence of preference in paw use in this feeding behavior. Values of HI and z scores

are represented in Table 1. Since these methods are based only on right and left preferences, they are not very valuable for analyzing this feeding behavior when most of the individuals are using both paws. Even so, it can be seen that most of the tuco-tucos did not display right or left preferences after excluding both paw frequencies.

Paw used to rotate the plant stems while removing the superficial layers of them with the teeth

In all the events collected, the individuals used both paws to remove the superficial layers of the stems.

Paw used to take food to the mouth to eat

Ten out of the 14 studied individuals displayed a clear left-paw preference to take food items to the mouth to eat, although no single animal used the left paw 100% of the time (Fig. 2). The other 4 tuco-tucos did not use any paw more than 66% of the times, being therefore classified as ambidextrous. However, of these four individuals, three more frequently used the left paw, while the last one used both paws likewise. A similar trend was observed in the HI, with 10 individuals showing a strong left-paw preference (mean: -0.65, n = 10). On the basis of individual z scores, eleven tuco-tucos were classified as "left-handed" and the other three as ambiguously "handed". Based on this classification, statistical analysis indicated that the three categories (left-, right-paw preferent or ambidextrous) were not similarly represented (chi-square test, df = 2, $p < 0.01$). Also, when analyzing if proportions of left-pawed and non left-pawed individuals were equally represented, the analysis revealed statistical differences, indicating a left bias for this task (chi-square test, df = 1, p= 0.03).

The historical view that no other animal species display preferences in the use of one limb in a similar way to that observed in humans has been refuted in light of new evidence that has demonstrated the preferential use of one extremity in several species of vertebrates and even invertebrates (2). For example, population-level asymmetries were described in the dog (*Canis familiaris*) although sex differences in the expression of this preference were observed. While male dogs preferred their left paw to remove an adhesive strip from the snout,

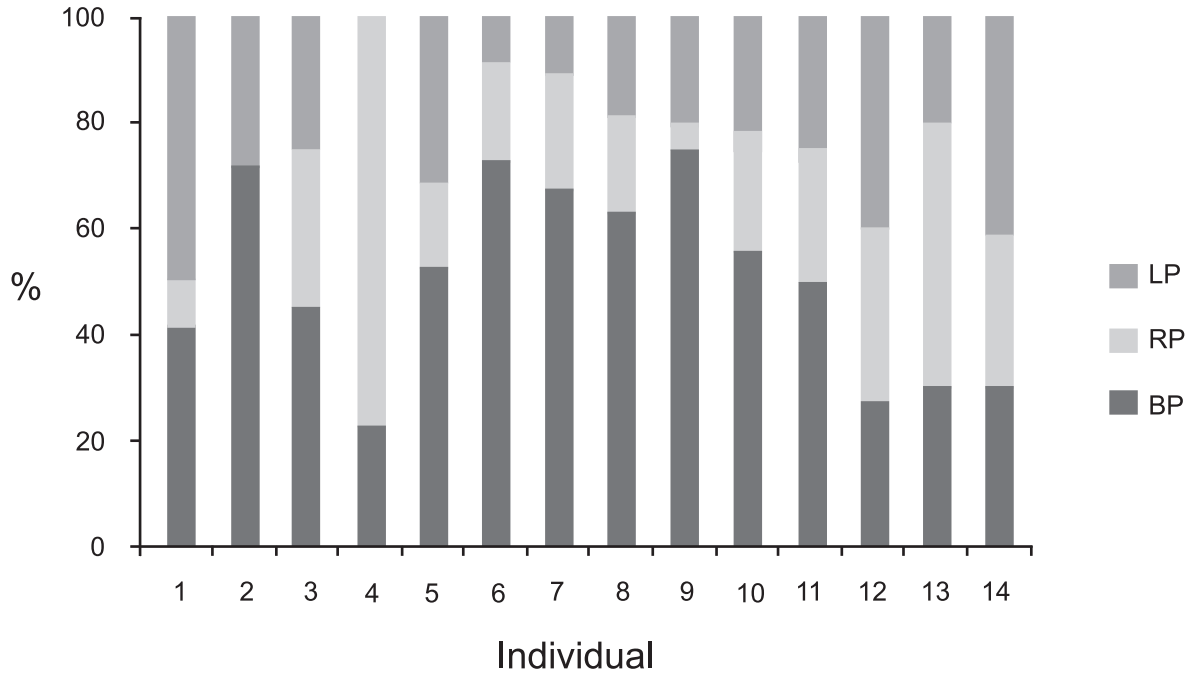

Fig.1. – Percentage of left paw (LP), right paw (RP) and both paws (BP) use by tuco-tucos to catch food to cut it.

TABLE 1

Table setting out the handedness index (HI) and z score for each individual for two of the three feeding behaviors recorded.

	Catch food items		Eat food items	
Individual	HI	Z score	HI	Z score
1	0,71	-2,67	-0,42	-2,59
2	1	-2	-0,48	-2,5
3	-0,09	0,3	-0,11	-0,57
4	-1	3,16	-0,55	-2,88
5	0,33	-1	-0,52	-2,18
6	-0,33	0,57	-0,21	-1,04
7	-0,33	0,57	0	0
8	0	0	-0,76	-3,8
9	0,6	-1,34	-0,8	-3,7
10	0	0	-0,5	-2,23
11	0	0	-0,88	-3,63
12	0,09	-0,42	-0,52	-2,6
13	-0,42	1,6	-0,89	-3,9
14	0,16	-1,23	-0,73	-2,84

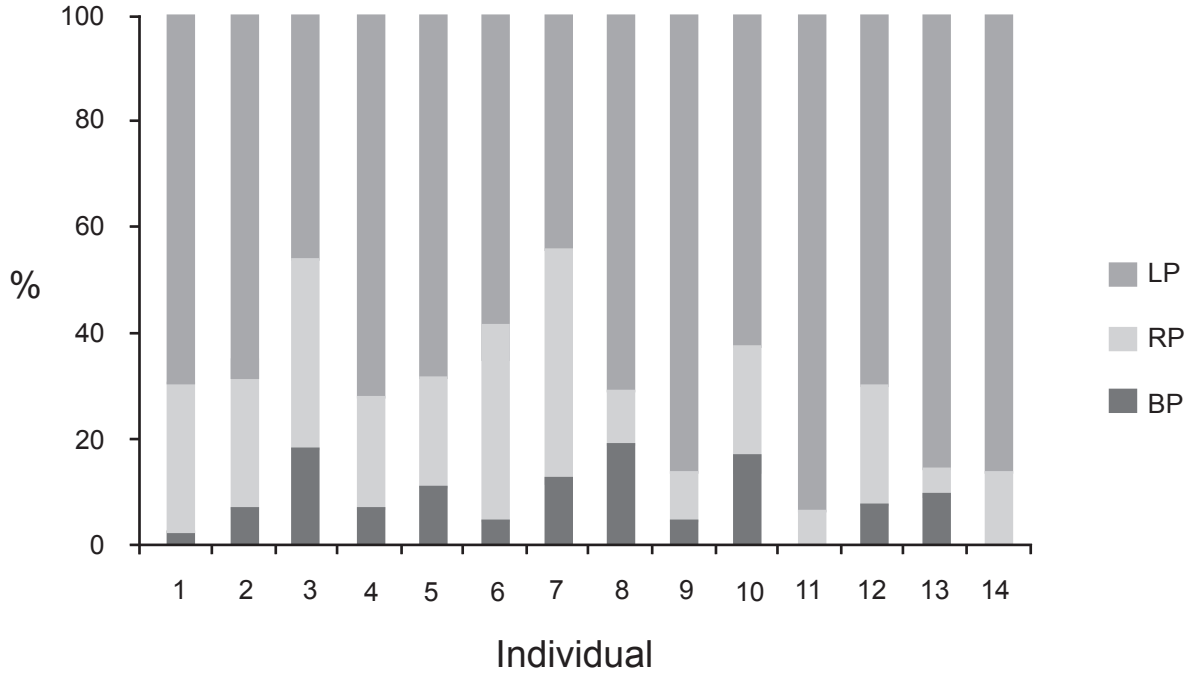

Fig.2. – Percentage of left paw (LP), right paw (RP) and both paws (BP) use by tuco-tucos to take food to the mouth to eat.

females preferred to use the right paw (15). Paw preferences were also observed in the domestic cat (*Felis silvestris catus*) although no population-level asymmetry was recorded, but instead an individual-level asymmetry was observed (13). Using a food handling test, authors observed that 46% of the cats were right-preferent, 44% were left-preferent and 10% were ambilateral, with no differences between male and female cats in the proportions of left and right paw-preferent individuals.

While several studies have addressed the question of paw preference in rodents (see 3), none has previously examined paw preference in a wild species of subterranean rodent. The majority of tuco-tucos analyzed in this study showed a significant left-paw preference for carrying the food items to the mouth, a situation that contrasts with most of the studies in rodents, which provide evidence for a lateralization in paw preference, but in the opposite direction (3,16,17,18). However, and as explained before, testing protocol used and kind of task studied could result in the appearance of different or contrasting results. Therefore, a comparison of different studies of paw preferences in diverse rodent species should be undertaken cautiously.

Regarding the other feeding parameters analyzed, none revealed any preference in paw usage. When rotating plant stems to remove the superficial layers with the teeth, tuco-tucos always utilized both paws, a situation that may reflect the complexity of the task, which requires the use of both paws simultaneously, rather than the absence of paw preferences.

As reviewed by Ströckens et al. (3), the majority of studies suggest that paw preferences in rodents show individual-level asymmetry, but not population level asymmetry. In the case of *C. talarum*, the results of this work provide support for a leftward population-level asymmetry. Nevertheless, as only 14 individuals from one population of *C. talarum* were studied, additional animals should be studied before firm conclusions are drawn regarding this species' paw preference.

In conclusion, this study presents the first evidence for a lateralization in paw use during feeding in a wild species of subterranean rodent. Further research is necessary in order to investigate if this lateralization occurs in various manual tasks and if it is manifest in other populations of this and other species of tuco-tucos.

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