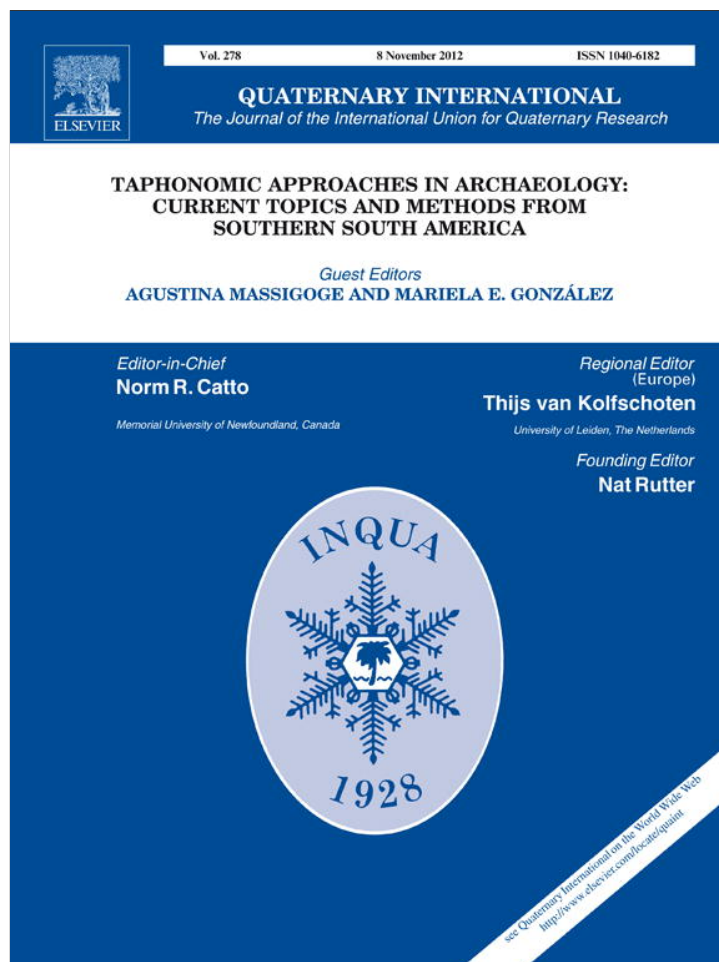


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## Owl pellet dispersal by wind: Observations and experimentations

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### ARTICLE INFO

#### Article history:

Available online 25 January 2012

### ABSTRACT

Pellets produced and accumulated by owls are subject to biological and atmospheric agents, and may be dispersed before their disaggregation. Observations on dispersion of *Athene cunicularia* and *Tyto alba* (Aves, Strigiformes) pellets were performed in a natural environment (Pampean region, Argentina) and in a wind tunnel. Ten burrows were visited, and the distances of pellets and isolated bones from the burrow entrance holes were registered. Intact pellets predominated between 0 and 1 m from the entrance holes. Partially disaggregated and disaggregated pellets showed similar distributions. In two burrows, the transport of new pellets and incorporated bones was observed during one month. Only in a few cases were the pellets mobilized and reoriented according to the predominant winds. Substrate features or the presence of vegetation favored fixing of their positions and prevented their mobility. Many of the pellets suffered total disaggregation or burial within the first 20 days to 1 month. Evaluated isolated bones showed a greater representation of mandibles and long bones, as well as skeletal elements with low susceptibility to wind transport. Pellets evaluated in the wind tunnel, at low wind speed (2.70 m/s), were mobilized very short distances. At high wind speed (4.70 m/s), transport distance was greater. The distances travelled could be related to their initial orientation at the beginning of the experiments, as those that were placed at 90° to the wind flow showed greater transport. The observations showed that there were some differences in mobility between pellets of *A. cunicularia* and *T. alba*, as *A. cunicularia* were more susceptible to transport at each wind speed, likely attributed to their smaller size. Wind increased bone dispersion from partially disaggregated pellets, causing the loss of some of them.

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### 1. Introduction

Zooarchaeological assemblages with abundant microvertebrate remains (<1 kg) are common in the Pampean region (Argentina). However, the study of small vertebrates is uncommon in zooarchaeological studies, and only recently has some research focused on taphonomic analysis (e.g., Pardiñas, 1999a, 1999b; Quintana et al., 2002; Santiago, 2004; Quintana, 2005; Gómez and Kaufmann, 2007; Fernández et al., 2009, 2011). Predation by nocturnal owls, diurnal birds of prey and carnivore mammals is recognized as an important mechanism leading to the concentration of microvertebrate remains (Mellett, 1974; Hoffman, 1988; Andrews, 1990; Kusmer, 1990; Fernández-Jalvo and Andrews, 1992). Some of the most common bird predators responsible for microvertebrate accumulations are owls. Pellets produced by these predators contain undigested components of their food, and in particular, owl

pellets preserve a high proportion of skeletal elements of their prey, with little damage, that can provide a sample of local microvertebrate faunas (Andrews, 1990; Lyman, 1994; Terry, 2004).

In archaeological sites, the predator's pellets or scats disaggregate over time and can become accumulated. Terry (2004) indicated that the taphonomic history of a pellet consists of multiple phases, each with particular biases. During the first phase, the author mentions the importance of the owls hunting behavior and the local environmental conditions. The second phase is regulated by digestive processes that produce breakage patterns and bone loss characteristics. Finally, the third phase is the history following regurgitation (weathering, transport, disaggregation, and burial). All the processes can modify the original features of the microvertebrate bone assemblages included in each pellet, leading to biases in the zooarchaeological record.

In open plains continental environments, such as the Pampean region (Argentina), owl pellets are located in areas associated with nests and regurgitation perches. The total disaggregation of pellets can be promoted and facilitated by the action of diverse atmospheric and biological agents (Lyman, 1994). Understanding the initial history of the pellets and how they could have been affected

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by different processes and agents before their burial is essential. Studies of post-regurgitation processes acting on pellets and pellets derived assemblages are scarce, limited to Andrews (1990) for cave deposits and Terry (2004) in temperate forest environments.

Water transport is another process acting in vertebrate accumulations, and previous studies have focused on evaluating the effects of skeletal element rearrangement by the action of fluvial transport (Voorhies, 1969; Dodson, 1973; Behrensmeier, 1975; Korth, 1979). In particular, Dodson (1973) and Korth (1979) experimentally evaluated small vertebrate bone transport by water, while Korth (1979) and Fernández-Jalvo and Andrews (2003) described the durability of owl pellets in their experimental studies. Although the importance of wind as an agent of bone transport has been habitually noted (Andrews, 1990; Lyman, 1994; Terry, 2004; Arcos et al., 2010), in general, there are few studies that have fully evaluated this effect (Cheme Arriaga et al., 2011).

The working hypothesis of this paper is that in open plain environments, wind is able to transport and disperse pellets, and can produce new distribution patterns of skeletal elements included in these pellets. The results presented here will allow for the evaluation of biases in the distribution of faunal remains in archaeological sites from plains environments. The effect of wind in the dispersion of owl pellets and bones contained within them was evaluated by means of naturalistic observations and an experimental study using a wind tunnel.

## 2. Materials and methods

The naturalistic study in this paper evaluated pellets and small bones transport from 10 nesting burrows of Burrowing Owl, *Athene cucularia* (Aves, Strigiformes) situated on the outskirts of the city of Santa Rosa (36°37'10"S, 64°19'45"W), province of La Pampa, Argentina (Fig. 1). The study area is located within the Espinal phytogeographic province (Cabrería, 1976), and has undergone significant changes as a result of agricultural and urban activities.

The Burrowing Owl generally nests in burrows created and abandoned by other animals such as plain viscachas and armadillos. These burrows are usually located in open areas of short grasses and sparse vegetation (Smith et al., 2005). In the study area, the landscape is flat, with a shallow lake and small depressions with occasional water filling due to rainfall.

The observations were performed by making imaginary concentric circles from the center of the burrow entrance holes and up to 6 m away. Pellets and bones found on the surface within the circles were recovered and the distances to the burrow entrance holes was registered.

Two nests were visited three days-a-week for one month; and in these opportunities, scattering of pellets and bones, disaggregation of pellets, and new pellets and bones incorporated in the burrows area during the observation period were evaluated. An attempt was made to link the pellets and bones transport and the wind speed in this environment.

Pellets were subdivided into three categories: 1.- intact, 2.- partially disaggregated and 3.- disaggregated. Intact pellets were smooth, matted fur, and oblong. Partially disaggregated pellets were those which no longer had a smooth and matted surface, were partly broken, or some of the skeletal elements had fallen loose. Disaggregated pellets were identified by a spatially definable assemblage of bones and the absence of matted fur (Terry, 2004). Once the skeletal elements were exposed, dispersion, loss, and burial were monitored.

To evaluate the pellets (intact, partially disaggregated, and disaggregated) and isolated bones in function of the distance, and determine their distribution, a chi-square test ( $X^2$ ) was used. Skeletal elements proportion and degree of breakage of rodent

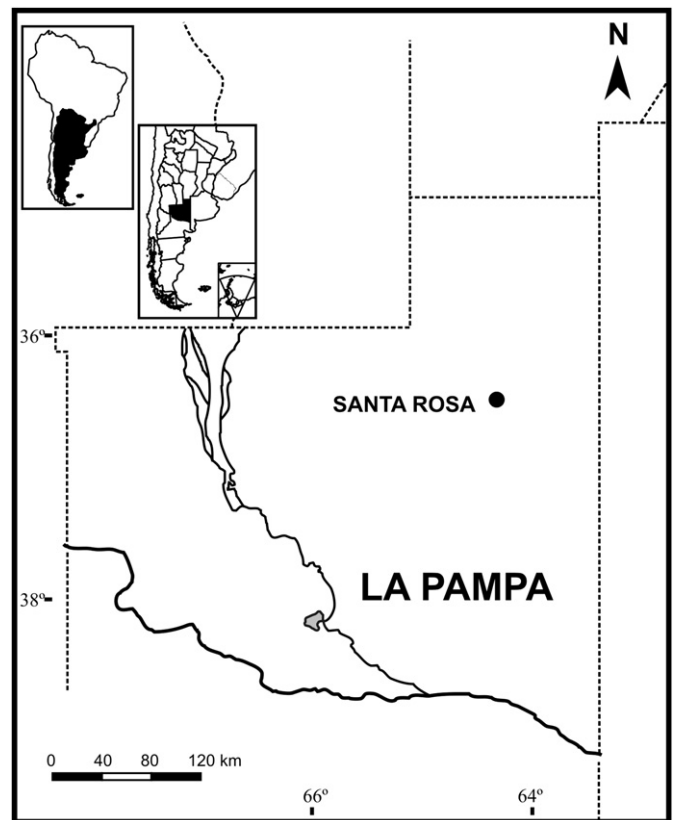


Fig. 1. Geographic location of Santa Rosa in La Pampa province, Argentina (area of naturalistic study).

bones included in 10 intact pellets and 10 disaggregated pellets were analyzed and compared among them.

Thirty intact pellets of local Barn Owl (*Tyto alba*, Aves, Strigiformes) were placed at six locations in a low depression containing no water or vegetation, but with a salt crust on the substrate surface. This area was visited daily for one month. Wind speed and direction for every day during the observation period was recorded using the local and National Weather Forecast Office "(Servicio Meteorológico Nacional)".

The experimental study on pellets transported by wind action was performed using an artificial wind tunnel belonging to the Agronomy College "(Facultad de Agronomía) at the Universidad Nacional de La Pampa, Santa Rosa, Argentina". This tunnel is 8 m long and powered by a Honda GX 670 24 HP engine that moves a one meter diameter fan with 8 blades. Air pushed by the fan is driven into the tunnel through a descending S-shaped section, made of galvanized sheet. Moving air then passes through a plate with 196 perforations, each 2.5 inches in diameter to reduce air flow turbulence. The tunnel has three sections built from galvanized sheet (total 6 m). The simulations were performed in the last two sections, which have no floor. Experiments were made using chipboard tables (wood) as a flat substrate. In addition, a plastic bag container (100  $\mu$ m thick) was placed at the end of the tunnel to collect materials that were expelled. Accordingly, each pellet was potentially able to travel a total distance of 5.7 m from designated line of origin to the end of the container bag.

Wind speed was calculated using Hellman's equation (taken from Kaltschmitt et al., 2007: 55):  $v_w(h) = v_{0.5} \cdot (h/h_{0.5})^\alpha$ , where  $v_w(h)$  is the speed at a given height  $h$  (the unknown quantity);  $v_{0.5}$  is the wind speed measured at a height of 50 cm (calibrated with a Testo 512 digital anemometer);  $h$  is the height at which wind speed is being calculated (1 cm);  $h_{0.5}$  is the height at which wind

speed was measured and  $\alpha$  corresponds to Hellman's exponent, which depends on terrain roughness and location (based on the 0.16 value given by that author for neutral air on a flat shore, a slightly higher one of 0.18 was used). Thus, the estimated wind speeds at the floor of the tunnel were defined as: low 2.70 m/s, medium 3.70 m/s and high 4.70 m/s. Low wind speed estimated for the experiments is the same as the average wind speed registered in the area where natural observations were performed.

The monitoring was carried out with a chronometer for three minutes. After this lapse (0–3'), the engine was switched off and the distance traveled by each pellet was recorded. Subsequently, when the engine was switched on again generating the desired speed from the beginning, an additional three minutes were measured (3–6'), with the materials in the positions reached at the end of the previous experiment. Materials that were driven out from the tunnel were excluded. Observations were repeated, the final timing and measurements were made after leaving the engine on for other four minutes (6–10'), totaling 10 min for each experiment.

A line traced at 53 cm from the start of the experimental substrate was considered the line of origin (point 0 for measurements); pellets were placed on that line at the beginning of each experiment. The experiments were performed using 9 intact pellets and 30 partially disaggregated pellets of *T. alba*, and 9 intact pellets of *A. cunicularia*. Several different trials were made in these experiments. For the analysis of intact pellets, they were placed in the line of origin in two groups: parallel and at 90° to the wind flow for each wind speed. When the experiments were performed using partially disaggregated pellets, more pellets were used because each was fully disaggregated in each experiment and the skeletal elements had fallen loose from the pellet.

Intact pellets were measured with a mechanical caliper. The average length and width were registered, and values obtained were: *T. alba* pellets, length 4.21 cm (maximum 5.70 cm; minimum 3.37 cm); width 2.65 cm (maximum 3.06 cm; minimum 2.32 cm); *A. cunicularia* pellets, length 3.56 cm (maximum 4.51 cm, minimum 2.60 cm); width 1.50 cm (maximum 1.95 cm, minimum 1.20 cm).

### 3. Results

#### 3.1. Natural environment

##### 3.1.1. Pellets around burrow entrance holes

Observations around the burrow entrance holes were measured for pellets recovered in 10 burrows of Burrowing Owl (*A.*

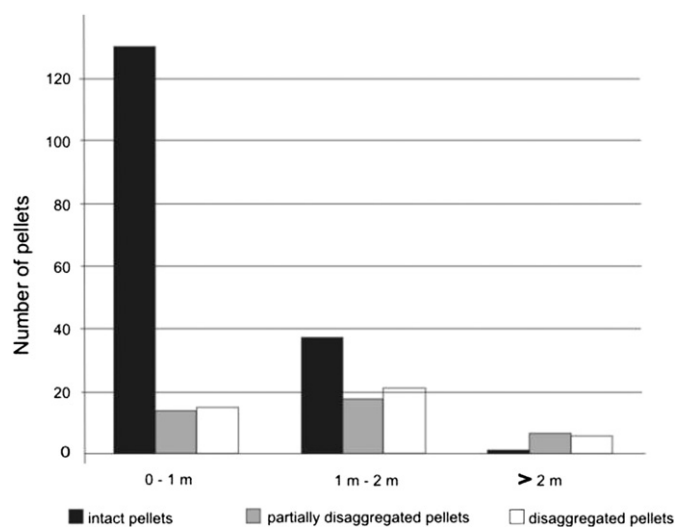


Fig. 3. Number of different type of pellets (intact, partially disaggregated and disaggregated) with distances from the burrow entrance holes.

*cunicularia*) (Fig. 2A). A total of 249 pellets were collected, and the average number of pellets in each nest was 25 (maximum 60, minimum 2); 67% were intact, 16% were partially disaggregated and 17% were disaggregated. Disaggregated pellets had an average number of 19 bones (maximum 63, minimum 3). Fig. 3 shows distribution of pellets in relation with the distance to the burrow entrance holes; 160 pellets were found between 0 and 1 m away, 76 between 1 and 2 m. Thirteen pellets were recovered at more than 2 m from the hole and only two pellets exceeded a distance of 5 m. In three of the burrows, ants were observed as a significant agent in pellet disaggregation.

The anatomical composition from 10 intact pellets and 10 disaggregated pellets, found in the range of 0–2 m away from the burrow entrance holes, were evaluated. Skeletal elements extracted from these pellets correspond to Cricetidae rodents. There were preserved 632 skeletal elements in the intact pellets sample (25% cranial bones, 75% postcranial bones), while a total of 79 elements were found in the disaggregated pellets sample (30% cranial bones, 70% postcranial bones).

From intact pellets, the average of anatomical representation was higher than 50%. Long bones were represented in both samples, but with different representation. In Table 1 there are

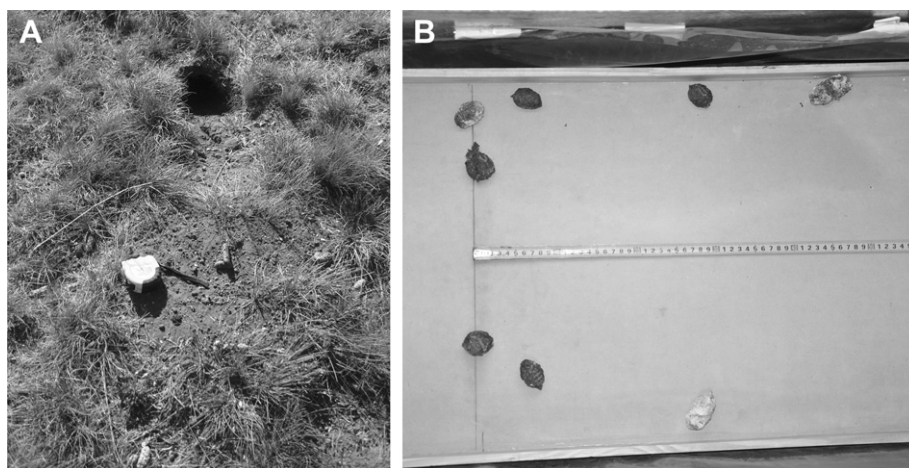


Fig. 2. A. View of the burrow entrance hole of one of the *Athene cunicularia* nests visited in natural environment with pellets and isolated bones. B. Dispersion of *Tyto alba* intact pellets in the wind tunnel experiments after 10 min at low wind speed.



**Table 1**  
Comparison of proportion of broken long bones from two pellets samples (intact and disaggregated) from the Burrowing Owl nest site.

	Intact pellets	Disaggregated pellets
% femur breakage	18.52	66.66
% humerus breakage	17.39	75.00
% tibia breakage	33.33	40.00
% ulna breakage	0	50.00

compared percentages of broken long bones in intact and disaggregated pellets; the number of complete elements is higher in the first sample.

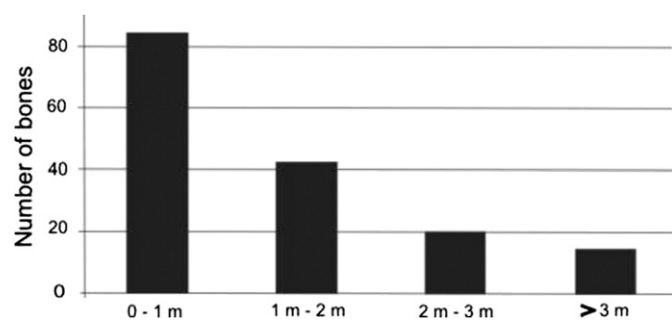
In intact pellets sample the ribs represent 12% of the total skeletal elements; scapula, even though scarce, are broken, having 2.20% representation; metapodials and vertebrae with 20% and 15.5% respectively; maxilla and mandibles reach 4%; isolated teeth are scarce. In disaggregated pellets samples, no ribs and only one broken scapula were found; metapodials and vertebrae represent 8.8% and 14% respectively. The mandibles represent 14% and only one isolated incisor was recovered.

### 3.1.2. Isolated bones around burrow entrance holes

In the 10 evaluated burrows, 160 isolated bones were collected. Fig. 4 shows distribution of bones in relation to the distance to the burrow entrance holes. From the total number of bones 29 specimens (18%) were identified as mandibles, one skull fragment was recovered without the occipital region, 14 (9%) specimens were identified as vertebrae, and four as maxillae. The remaining specimens were identified as indeterminate long bone fragments.

### 3.1.3. Pellets and bones dispersed around burrow entrance holes

New pellets and isolated bones that the Burrowing Owls incorporated in two burrows were evaluated over one month. In burrow 1, 8 intact pellets were found. Three were recovered between 0 and 1 m from the entrance hole. One was lost; the second was dispersed 20 cm, and then was recovered partially buried; the last pellet was mobilized only 4 cm and in this final position was disaggregated. The other five pellets were found between 1 and 2 m away. They were not mobilized, but three became completely disaggregated during the observation period. Nine isolated microvertebrate bones were also monitored. Between 0 and 1 m from the burrow entrance hole, three bones were found, one was lost and the others had moved 1 and 22 cm respectively, but finally both were lost. Two bones were found between 1 and 3 m; one of them had moved 1 cm and the other 21 cm during the observation period. Four were recovered at more than 5 m. One was transported 4 cm during the observation period, two were observed in the same location in this period, and the last was lost.



**Fig. 4.** Number of isolated bones recovered with distances around the burrow entrance holes.

During the observations, many specimens were fixed in place by some ground vegetation.

In burrow 2, two intact pellets and one pellet fragment were found between 0 and 1 m away from the hole. During the second day of observations, one of the intact pellets had moved 53 cm and the other 26 cm. No more transport was observed, and after 30 days of the experiment all pellets and isolated bones were lost. The third pellet was lost after the second day of observations. In addition, 12 microvertebrate bones were recovered. Six of these bones were fixed for some time during the observation period, one had dispersed only 1 cm, two 14 cm and the others 22 and 69 cm respectively. Finally, 5 of them were lost.

### 3.1.4. Experiments in natural environment

In natural conditions, an experiment was carried out by placing intact *T. alba* pellets in an open clean depression, without water or vegetation, but with a salt crust on the substrate surface. Six locations were chosen for the experiment, and five pellets were placed at each location (Table 2). During the observation period, in two opportunities rainfall filled the depression and the experiment had to be stopped.

In two locations, all pellets were transported and the average mobility exceeded 1 m during the observation period. In three locations, there were pellets that did not move, but others moved up to 10 cm. Finally, in one location no pellets were mobilized.

During the time of experimentation, in some cases, pellets were dispersed and reoriented in relation with the predominant wind (N–NE; S–SW, Cano et al., 1980), while those which were located at 90° to the wind were transported further.

## 3.2. Wind tunnel experiments

### 3.2.1. Experiments with *T. alba* and *A. cunicularia* intact pellets

When *T. alba* intact pellets were placed parallel to the flow at low wind speed, only one of them had moved (Fig. 2B). At intermediate speed, most had been transported during the first 3 min, registering only a small transport during the other times. At high wind speed, mobility was frequent at the beginning of experiments; two pellets were expelled out of the tunnel during the initial 3 min and other two during the second period of time (Table 3).

When *T. alba* intact pellets were placed at 90° to the flow on the origin line, at low wind speed only four of them had moved during the first 3 min and then maintained their position during the rest of the experiment. At intermediate speed, one was completely expelled before the first 3 min and the rest of the pellets showed some transport during this initial time but no more during the rest of the trials. At high wind speed, the pellets were mobilized but none had been expelled out of the tunnel (Table 4).

In the first experiment with *A. cunicularia*, intact pellets were placed parallel to the flow at the line of origin. At low wind speed, two were expelled from the tunnel before the initial 3 min and other three pellets remained in position without transport. The rest of the pellets had moved very differently, ranging from only a few to more than 270 cm. Most of the pellets had been only slightly transported during the rest of the trials. At intermediate speed, all pellets had mobilized only during the initial 3 min and three were expelled in this time lapse. At high wind speed, four pellets were expelled from the tunnel during the first 3 min and the rest were transported, but remained in that position through the rest of the experiment (Table 5).

When the *A. cunicularia* intact pellets were placed at 90° to the wind flow, at low wind speed, some failed to become mobilized, while others showed little movement and four of them had moved up to 80 cm. Except for one pellet that was transported very little

**Table 2**

Distance of wind transport of *Tyto alba*'s pellets placed intentionally in six sites near Santa Rosa city. It is pointed out the number of days in which relevant data could be taken in each site.

	Pellet	Distance from origin (cm)	Average		Pellet	Distance from origin (cm)	Average		Pellet	Distance from origin (cm)	Average
Location 1 (21 days)	I	191	156.6	Location 2 (7 days)	I	21	109.6	Location 3 (6 days)	I	28	9.6
	II	175			II	373			II	20	
	III	180			III	17			III	0	
	IV	79			IV	110			IV	0	
	V	158			V	27			V	0	
Location 4 (6 days)	I	10	17.8	Location 5 (7 days)	I	75	15	Location 6 (7 days)	I	0	0
	II	43			II	0			II	0	
	III	36			III	0			III	0	
	IV	0			IV	0			IV	0	
	V	0			V	0			V	0	

during the next 3 min, the rest did not move. At intermediate speed, two were expelled from the tunnel in the initial 3 min while the rest did not move more than 1 m. Only one pellet had mobilized in the next 3 min. At high speed, 8 pellets were transported over more than 350 cm, while the other two showed less transport and remained in their position through the rest of the experiment (Table 6).

During these experiments, some bones were separated from the pellets. At low and intermediate wind speeds, long bones and mandibles stayed close to the line of origin. Vertebrae, ribs and skulls were the first skeletal elements expelled from the tunnel. At high wind speed, skeletal elements showed similar reactions, but long bones were expelled out of the tunnel in a range of 3–6 min.

**3.2.2. Experiments with *T. alba* partially disaggregated pellets**

At low wind speed, two partially disaggregated pellets of *T. alba* had moved without changes or loss of inner materials, while the other 8 showed some bone loss through the rest of the experiment. At intermediate speed, three pellets showed no changes, while the other 7 had dispersed during the trials. At high wind speed, two remained without changes while the rest showed an increasing grade of dispersion. Table 7 shows the transport for those pellets, considering when necessary clusters that still showed some consistence.

**4. Discussion**

**4.1. Natural environment observations**

Observations in 10 *A. cunicularia* burrows area showed that once pellets are regurgitated, they become exposed to different

processes, such as physical and chemical weathering, but also trampling by the owls themselves. Ants and other insects attacked the pellet matrix and promoted disaggregation.

In a temperate forest, Terry (2004) observed that intact pellets were more abundant between 1 and 2 m away from the base of the tree where they were accumulated and did not persist at greater distances, whereas partially disaggregated and disaggregated pellets were abundant at further distances. In the 10 burrows surveyed here, the total number of pellets decreased with distance from the burrow entrance holes. Partially disaggregated and disaggregated pellets were scarce in all the categories evaluated, but they were more abundant in the 1–2 m range. More than 2 m away from the burrow entrance holes, pellets were very scarce. Partially disaggregated pellets were distributed similarly at all distances evaluated ( $p > 0.09$ ).

Intact and disaggregated pellets showed a dispersal pattern with respect to the burrow entrance holes (see Fig. 3). Both types of pellets were recovered near the holes, but intact pellets were abundant between 0 and 1 m ( $X^2 = 50.81$ ;  $p < 0.05$ ), and disaggregated pellets were abundant between 0 and 2 m ( $X^2 = 8.14$ ;  $p < 0.05$ ). The distribution of semidisaggregated pellets was similar to all distance ( $X^2 = 4.77$ ;  $p > 0.09$ ). This could be linked to either the particular behavior of *A. cunicularia* that can contribute to pellet dispersion as they move throughout the burrow area, or the regurgitation of the pellets far away from the burrow entrance hole. However other meteorological agents, such as rainfall and wind, could have contributed to pellet dispersion.

Analysis of rodent bones included in intact and disaggregated pellets showed some difference in anatomical representation. From intact pellets, the anatomical representation was similar to those registered previously for an *A. cunicularia* sample (Montalvo and

**Table 3**

Transport of *Tyto alba*'s intact pellets in the experiments recorded at three speeds. At the start of the experiment pellets were placed parallel to the wind flow. Wind speed in meter/second (m/s). Distances are expressed in cm.

Pellets	2.70 m/s			3.70 m/s			4.70 m/s		
	0–3'	3–6'	6–10'	0–3'	3–6'	6–10'	0–3'	3–6'	6–10'
I	0	0	0	5.7	33.8	0	25.5	371.5	–
II	0	0	0	0	0	4.5	142	0	0
III	0	0	0	85.5	0	0	528	–	–
IV	0	0	0	101.5	0.5	0	461	–	–
V	0	0	0	3.8	32	0	60	0	0
VI	0	0	0	5.5	6.5	69.5	30	3.4	4
VII	0	0	0	148	0	0	224.7	0.3	0
VIII	0	0	0	0	0	0	96	1	1.2
IX	4.5	0	0	68.5	0	0	222.7	0.3	0

**Table 4**

Transport of *Tyto alba*'s intact pellets in the experiments recorded at three speeds. At the start of the experiment pellets were placed at 90° to the wind flow. Wind speed in meter/second (m/s). Distances are expressed in cm.

Pellets	2.70 m/s			3.70 m/s			4.70 m/s		
	0–3'	3–6'	6–10'	0–3'	3–6'	6–10'	0–3'	3–6'	6–10'
I	9	0	0.3	131.5	0	0	24.5	7	9.5
II	0	0	0	11	16.5	11.5	27.5	6.7	9.8
III	0	0	0	183.5	0	0	135.5	34.5	0
IV	39.2	0	0	510.5	–	–	94.5	0	0
V	0	0	0	90.5	0	0	57.5	0.5	1
VI	0	0	0	187.5	6	5.5	98.1	7.4	6.7
VII	1.2	0	0	25	0	0	10	0	49
VIII	0	0	0	147.2	0	0	15.2	2.9	1.9
IX	86	0	0	42.6	0	0	35.5	0.2	0

**Table 5**

Transport of *Athene cucicularia*'s intact pellets in the experiments recorded at three speeds. At the start of the experiment pellets were placed parallel to the wind flow. Wind speed in meter/second (m/s). Distances are expressed in cm.

Pellets	2.70 m/s			3.70 m/s			4.70 m/s		
	0–3'	3–6'	6–10'	0–3'	3–6'	6–10'	0–3'	3–6'	6–10'
I	0	0	0	150	0	0	28.1	0	0
II	1	0	0	53.5	0	0	189.6	0.4	0
III	9.6	5.2	12.2	158	0	0	358	0	0
IV	85	0	0	528	–	–	543	–	–
V	279.5	0	0	519.5	–	–	552	–	–
VI	0.6	0.4	92	530	–	–	577	–	–
VII	0	0	0	88	0	0	111	0	0
VIII	0	0	0	34	0	0	100.7	0	0
IX	0	132.5	0	340	0	0	131	0	0

Tejerina, 2009), with an average higher than 50%. Evaluations of degree of breakage show similar results, with a high percentage of whole long bones (more than 80%). When bones included in disaggregated pellets were evaluated, it was noticed that there were high percentage of bone fragments. Only 40% of total long bones were preserved whole. Comparing both samples, the loss of some skeletal elements, such as ribs, vertebrae, metapodials and isolated teeth, is evident. The preserved bones show a degree of breakage higher than the one found in intact pellets, possibly related with breakage caused by owl trampling. In this sense, Andrews (1990) found differences in the completeness of samples from caves for bones extracted from intact and disaggregated pellets. The number of mandibles was high in both samples, but the relative proportion of maxillae is less in disaggregated sample. In this case, a higher proportion of isolated teeth was present in the disaggregated sample. Its absence and the absence of other smaller elements in the disaggregated pellet sample of *A. cucicularia* can be attributed to burial or dispersion which causes their loss at the time of sampling. Accordingly with Andrews (1990) evaluation, the sample of disaggregated pellets does not have skulls. These are skeletal elements that are easily lost by breakage.

Analysis showed that isolated bones recovered around the burrow entrance holes were abundant within the first concentric circle (0–1 m). The number of isolated bones decreased at higher distances to the hole, but their presence was more persistent than the pellets at distances greater than 3 m away. The distribution of isolated bones (see Fig. 4) followed a similar pattern to the ones found in pellets; near the hole is where a higher probability of finding remains existed ( $X^2 = 16.90$ ;  $p < 0.05$ ). Terry (2004) however, found in her observations that bones were distributed at more than 4 m away from the tree. The abundance of bones in the first circle may respond to *A. cucicularia* behavioral aspects previously mentioned, so that the owl trampling promotes pellet

**Table 6**

Transport of *Athene cucicularia*'s intact pellets in the experiments recorded at three speeds. At the start of the experiment pellets were placed at 90° to the wind flow. Wind speed in meter/second (m/s). Distances are expressed in cm.

Pellets	2.70 m/s			3.70 m/s			4.70 m/s		
	0–3'	3–6'	6–10'	0–3'	3–6'	6–10'	0–3'	3–6'	6–10'
I	51	0	0	125	0	0	478.5	–	–
II	0.5	0	0	104	0	0	358.5	–	–
III	131	0	0	188	20	0	558.5	–	–
IV	270.5	0	0	555.5	–	–	574.5	–	–
V	80	0	0	116.5	0	0	550	–	–
VI	106.5	0	0	562	–	–	542	–	–
VII	0	0	0	276	0	0	77.5	0	0
VIII	4	0.5	0	201	0	0	530	–	–
IX	107.5	0	0	31	0	0	55	0	0

disaggregation in those areas near the hole and facilitates the dispersion of bones. In longer distances from the burrow entrance holes, the number of isolated bones decreased. Without ruling out other possible factors of destruction or quick burial (Behrensmeier et al., 2003), the presence of isolated bones at greater distances from the burrow entrance holes could be attributed to wind dispersal.

Mandibles and broken long bones were the most frequent isolated skeletal elements recovered. In a wind tunnel experiment carried out with different rodent long bones, femora, humerii, tibiae, and radii showed intermediate susceptibility to wind transport (Cheme Arriaga et al., 2011). Vertebrae, skulls and scapulae moved faster in the same experiments (Cheme Arriaga et al., 2011). These skeletal elements were low or absent in the evaluated disaggregated pellet and isolated bones samples, which could be linked to wind dispersion. Finally, rodent mandibles predominated both in disaggregated pellets and in the isolated bones samples. Mandibles showed less transportability by wind in the wind tunnel experiment (Cheme Arriaga et al., 2011). On the other hand, this predominance could result in the loss of other types of skeletal elements whose susceptibility to wind transport is greater.

In the two burrows where bone transport was evaluated during one month, it was observed that when pellets or bones were fixed to vegetation, they did not move any more during the observation period. Only in a few cases did the pellets move in connection with the prevailing winds. The substrate characteristics and the presence of vegetation favored fixed positions and prevented mobility. For these reasons, in these cases it is difficult to distinguish if the pellets mobility or stability is linked with the prevailing wind direction or other factors such as substrate or other meteorological variables. Observations found that some pellets had totally disaggregated or had been buried during the observation period in this environment.

As for the 21 monitored isolated bones that are surely material from the pellets, 10 showed some transport, 8 were fixed in position during the entire observation period and three were rapidly lost. In the course of the observations, 5 more bones were lost (24% of the assessed total) and subsequently could not be located. Armour-Chelu and Andrews (1994) described burial and lateral transport of rodent small skeletal elements due to earthworm bioturbation. Although it is possible that the bones were destroyed, or dispersed by bioturbation, the alternatives proposed to explain this loss are that the wind moved them beyond the observation area and therefore they were not recorded, or that the bones were buried, and therefore were not visible.

Finally, as a result of experiments with *T. alba* pellets in a natural environment, dispersal at 6 locations was dissimilar. Some pellets were mobilized more than 1 m, but others did not move. Meteorological factors (rainfall during the observations period) and substrate characteristics (drying and crusting salt) favored fixing to locations and pellet loss when the depression flooded. However, in times where conditions during the observation period were favorable, there was significant transport.

#### 4.2. Wind tunnel experiments

When *A. cucicularia* and *T. alba* intact pellets were evaluated in the wind tunnel, at low wind speed they became mobilized at short distance, but *A. cucicularia* pellets showed slightly more transport. Considering the parallel position of pellets in relation with the wind flow, *A. cucicularia* pellets suffered more transport than the *T. alba* pellets at intermediate speed.

When pellets were placed in the wind tunnel at 90° orientation to the wind flow, most of the *A. cucicularia* pellets had moved at low wind speed and also were expelled out of the tunnel during the first minutes at high wind speed. However, *T. alba* pellets were also

**Table 7**Transport of partially disaggregated *Tyto alba*'s pellets in the experiment recorded at three wind speeds. Wind speed in meter/second (m/s). Distances are expressed in cm.

Pellets	2.70 m/s			Pellets	3.70 m/s			Pellets	4.70 m/s		
	0–3'	3–6'	6–10'		0–3'	3–6'	6–10'		0–3'	3–6'	6–10'
I	1.5	33	0.5	XI	201	3	2	XXI	163	0	0
II	4	1.5	4.5	XII	68	0	0	XXII	524.5	–	–
III	0	1	42	XIII	294.5	0.5	121.5	XXIII	155	0	0
IV	37.5	0	5.5	XIV	40.5	0	0	XXIV	201	0	0
V	236	0	0	XV	127	0	0	XXV	58	2	5.5
VI	567	–	–	XVI	45.5	18.5	3.5	XXVI	73.5	14.2	6.3
VII	0.5	0.5	1	XVII	56.5	0	0	XXVII	544	–	–
VIII	31.5	261.5	0	XVIII	67	0	0.6	XXVIII	188.6	0.9	2.5
IX	99.5	83	0	XIX	29	5	4.5	XXIX	84	23.5	0.5
X	0	0	0	XX	155.5	143.5	3	XXX	540.5	–	–

mobilized at intermediate and high wind speed, but in comparison their transport was minor.

These different behaviors registered in pellets produced for different owl species could be related to their size and shape. *A. cucularia* pellets are smaller than *T. alba*, and because of that they would be more easily transported.

At high wind speed, for *T. alba* intact pellets a high tendency of mobilization was observed for those that were placed parallel to the wind flow at the beginning of the experiments. In several cases it was observed that pellets expelled from the tunnel were found at the end of the container bag with some evidence of disaggregation, probably aided by the wind action.

Several experiments were performed to verify the effects of water flow on the pellets, showing that in those conditions pellets become disaggregated very quickly. Korth (1979) observed that at 20 m away from the point of origin, pellets subjected to water transport begin to lose some of their bones. Fernández-Jalvo and Andrews (2003) performed experiments with pellets in water containers, observing that those which had been previously submerged in water did not experience significant changes after an hour of rotation (15 cm/s). After 4 h, they begin to lose their external texture and to disaggregate, after 16 h bones contained in the pellets were exposed, and after 32 h they were disaggregated.

When *T. alba* partially disaggregated pellets were subjected to wind action, they experienced greater breakage and bones contained within had expelled. This data suggests that when the disaggregation process begins (which in natural environments can be facilitated by many effects, such as arthropods action, trampling, rainfall action or even wind), if pellets are not quickly buried, bones contained within are released in the environment. In natural observations, that disaggregation can be produced between 20 or 30 days. Those bones liberated from the pellets had a very similar behavior to transport experimented in the wind tunnel when they were evaluated individually, Vertebrae, skulls and scapulas are the most susceptible rodent skeletal elements to wind transport, while the mandibles are the least affected (Cheme Arriaga et al., 2011).

## 5. Conclusions

The observations and experiments presented in this paper show that the wind action can transport pellets and promote their disaggregation. This action can facilitate the posterior dispersion of pellet bones.

The open natural environment observations verified that pellets and bones are dispersed. Although other potential factors cannot be discarded, such as the action that the same predator can produce, wind participates in this displacement. It is emphasized here that in the cases where bones and pellets are fixed with vegetation located around burrows, this process reduces the chances of wind transport.

The evaluation of isolated bones found near the burrow entrance holes showed a predominance of those which are less susceptible to wind transport, for example mandibles and long bones, which suggests that those bones found in low percentages or absent could have been transported great distances by wind action.

When dispersion was evaluated in the wind tunnel, the position of pellets in relation to the wind flow is very important in the effect that this can provoke. On the other hand, the low wind speed used in the wind tunnel experiments represents very well the annual average wind speeds calculated for the study area where the observations were carried out, and the displacements verified at that speed were not excessive. Some different behaviors registered in pellets produced for different owl species could be related to their size and shape. However, for the other wind speeds used in the experiments, it was observed that a significant amount of pellets were transported. Those speeds could represent normal wind bursts in natural environments. When partially disaggregated pellets were evaluated, it was verified that wind is a good dispersion agent of pellets and also of skeletal elements contained in them.

To sum up, evaluations show that wind is an important factor acting in pellet dispersion in open continental environments, because it can help to provoke pellet disaggregation, and may affect the anatomical representation of microvertebrate bones contained within them. The possible action of wind, as one of the factors which affects pellets after their regurgitation, should be considered when evaluating microvertebrate associations which could result from predator deposition.

## Acknowledgements

This work was funded by the "Facultad de Ciencias Exactas y Naturales (Universidad Nacional de La Pampa)". We wish to thank R. Melchor and M. Zárate for critical reading of earlier versions. D. Rafuse and E. Braun helped us with the translation. We thank two anonymous reviewers for their useful comments that improved the manuscript.

## References

- Andrews, P., 1990. Owl, Caves and Fossils. The University of Chicago Press, pp. 231.
- Arcos, S., Sevilla, P., Fernández-Jalvo, Y., 2010. Preliminary small mammal taphonomy of FLK NW level 20 (Olduvai Gorge, Tanzania). Quaternary Research 74, 405–410.
- Armour-Chelu, M., Andrews, P., 1994. Some effects of bioturbation by earthworms (*Oligochaeta*) on archaeological sites. Journal of Archaeological Science 21, 433–443.
- Behrensmeyer, A.K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. Bulletin of the Museum of Comparative Zoology 146, 473–578.
- Behrensmeyer, A.K., Stayton, C., Chapman, R., 2003. Taphonomy and ecology of modern avifaunal remains from Amboseli Park, Kenya. Paleobiology 29, 52–70.



- Cabrera, A.L., 1976. Regiones fitogeográficas argentinas, Enciclopedia Argentina De Agricultura y Jardinería. In: Fascículo 1, Tomo II. ACME S. A. C. I., Buenos Aires.
- Cano, E., Casagrande, G., Conti, H., Salazar Lea Plaza, J., Peña Zubiato, C., Maldonado Pinedo, D., Martínez, H., Hevia, R., Scoppa, C., Fernández, B., Montes, M., Musto, J., Pittaluga, A., 1980. Inventario Integrado de los Recursos Naturales de la Provincia de La Pampa. Instituto Nacional de Tecnología Agropecuaria. Ministerio de Economía y Asuntos Agrarios de la provincia de La Pampa. Facultad de Agronomía de la Universidad Nacional de La Pampa, Buenos Aires, pp. 493.
- Cheme Arriaga, L., Montalvo, C.I., Sosa, R.A., 2011. Experiments on wind dispersal of rodent bones. *Museologia Scientifica e Naturalistica. Volume Speciale 2011: Taphos 2011. 6th International Meeting on Taphonomy and Fossilization*, 25.
- Dodson, P., 1973. The Significance of Small Bones in Paleocological Interpretation. In: *Contributions to Geology*, vol. 12. University of Wyoming, 15–19.
- Fernández, F.J., Moreira, G.J., Neme, G.A., De Santis, L.J.M., 2009. Microvertebrados exhumados del sitio arqueológico "Cueva Arroyo Colorado" (Mendoza, Argentina): aspectos tafonómicos y significación paleoambiental. *Archaeofauna* 18, 99–118.
- Fernández, F.J., Del Papa, L., Moreira, G., Prates, L., De Santis, L.J., 2011. Small mammal remains recovered from two archaeological sites in the middle and lower Negro River valley (Late Holocene, Argentina): taphonomic issues and paleoenvironmental implications. *Quaternary International* 245, 136–147.
- Fernández-Jalvo, Y., Andrews, P., 1992. Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. *Journal of Archaeological Science* 19, 407–428.
- Fernández-Jalvo, Y., Andrews, P., 2003. Experimental effects of water abrasion on bone fragments. *Journal of Taphonomy* 1, 147–163.
- Gómez, G.N., Kaufmann, C.A., 2007. Taphonomic analysis of *Pseudalopex griseus* (Gray, 1837) Scat assemblages and their archaeological implications. *Journal of Taphonomy* 5, 59–70.
- Hoffman, R., 1988. The contribution of raptorial birds to patterning in small mammal assemblages. *Paleobiology* 14, 81–90.
- Kaltschmitt, M., Streicher, W., Wiese, A., 2007. *Renewable Energy: Technology, Economics, and Environment*. Springer, pp. 538.
- Korth, W.W., 1979. Taphonomy of microvertebrate fossil assemblages. *Annals of Carnegie Museum* 48, 235–285.
- Kusmer, K.D., 1990. Taphonomy of owl pellet deposition. *Journal of Paleontology* 64, 629–637.
- Lyman, R.L., 1994. *Vertebrate Taphonomy*. Cambridge Manuals in Archaeology. Cambridge University Press, pp. 524.
- Mellet, J.S., 1974. Scatological origin of microvertebrate fossil accumulations. *Science* 185, 349–350.
- Montalvo, C.I., Tejerina, P., 2009. Análisis tafonómico de los huesos de anfibios y roedores depredados por *Athene cunicularia* (Strigiformes, Strigidae) en La Pampa, Argentina. In: Berón, M., Luna, L., Bonomo, M., Montalvo, C., Aranda, C., Carrera Aizpitarte, M. (Eds.), 2009. Mamül Mapu: pasado y presente desde la arqueología pampeana, vol. 1, pp. 323–334.
- Pardiñas, U.F.J., 1999a. Tafonomía de microvertebrados en yacimientos arqueológicos de Patagonia. *Arqueología* 9, 265–308.
- Pardiñas, U.F.J., 1999b. Los roedores muroideos del Pleistoceno Tardío-Holoceno en la Región Pampeana (sector este) y Patagonia (República Argentina): aspectos taxonómicos, importancia bioestratigráfica y significación paleoambiental. Ph.D. thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina.
- Quintana, C.A., 2005. Despiece de microroedores en el Holoceno Tardío de las Sierras de Tandilia (Argentina). *Archaeofauna* 14, 227–241.
- Quintana, C.A., Valverde, F., Mazzanti, D.L., 2002. Roedores y lagartos como emergentes de la diversificación de la subsistencia durante el Holoceno tardío en sierras de la región Pampeana Argentina. *Latin American Antiquity* 4, 455–473.
- Santiago, F.C., 2004. Roedores en el "menú" de los habitantes de Cerro Aguará (provincia de Santa Fe): su análisis arqueofaunístico. *Intersecciones en Antropología* 5, 3–18.
- Smith, M.D., Conway, C.J., Ellis, L.A., 2005. Burrowing owl nesting productivity: a comparison between artificial and natural burrows on and off golf courses. *Wildlife Society Bulletin* 33, 454–462.
- Terry, R.C., 2004. Owl pellet taphonomy: a preliminary study of the post-regurgitation taphonomic history of pellets in a temperate forest. *Palaos* 19, 497–506.
- Voorhies, M.R., 1969. Taphonomy and Population Dynamics of an Early Pliocene Vertebrate Fauna, Knox County, Nebraska. *Contrib. to Geol. Univ. of Wyoming. Spec. Pap. No. 2*. Univ. Wyoming Press, Laramie, Wyoming, pp. 1–69.