

## Spatiotemporal dispersal of *Meriones shawi* estimated by radio-telemetry

Wissem Ghawar, Wajdi Zaätour, Sadok Chlif, Jihene Bettaieb, Bilel Chelghaf, Mohammed-Ali Snoussi, Afif Ben Salah

Department of Medical Epidemiology, Laboratory of Transmission, Control and Immunobiology of Infections (LR11IPT02),  
Pasteur Institute of Tunis, 13, Place Pasteur, BP, Tunis-Belvédère, Tunisia

### Abstract

A longitudinal study was designed to accurately measure the movements of *Meriones (M.) shawi* using geographic information systems and radio-telemetry tools. Radio collars were placed on the necks of 30 *M. shawi* on April 2012 and tracked by radio-telemetry until December 2012 in an endemic area of zoonotic cutaneous leishmaniasis in Tunisia. The mean home range, the mean of the maximum distance between the start and the final locations and the mean of the real traveled distance linking all detected positions for each rodent were calculated. Two coefficients of diffusion were estimated, corresponding to the pre-and post-harvest seasons, respectively. This study demonstrated and quantified, for the first time, the ecological niche and the migratory capacity of the *M. shawi*, and confirmed its crucial role in the geographical dispersal of *Leishmania* parasites and the emergence of epizootics and epidemics in new foci.

**Keywords:** Diffusion coefficient, Ecological niche, Geographical spread, *Meriones shawi*, Radio-telemetry, Zoonotic Cutaneous Leishmaniasis.

### 1. Introduction

*Meriones (M.) shawi* is recognized as a reservoir host of *Leishmania (L.) major* in some parts of Tunisia, Algeria, and Morocco [1-3]. This rodent inhabits clay and sandy deserts, arid steppes, grasslands, and mountain valleys. It is seen in fields in non-irrigated cereal crops, *Ziziphus* mounds, and *Opuntia* hedges, or in the bases of jujubes tufts [4]. It settles down easily in the crops fields and digs its housing under a hillock, in a bush between 10 and 40 cm. The diet of *M. shawi* is based on leaves and seeds of *Graminea* in spring and summer, and on vegetables and herbs belonging to the families *Composaceae* and *Malvacea* in autumn and winter [5]. This wild rodent is also known as an important species responsible for destruction of cereal and vegetable crops [6].

Another important reservoir host of *L. major* is *Psammomys (P.) obesus*. This rodent lives in sedentary, fragmented populations because of its restricted diet of chenopods [7-10]. In contrast, *M. shawi* has an important adaptation for extreme conditions—its resistance to prolonged dehydration [11] and consequently it readily moves to find food. It has been considered, without evidence, as a migrant rodent and more active than other rodent reservoir hosts of zoonotic cutaneous leishmaniasis. A recent study demonstrated that *M. shawi* plays an important role in the transmission of *L. major* cutaneous leishmaniasis in Tunisia [10]. It is intuitively expected that *M. shawi* is responsible for the geographical spread of this disease and its transmission between different populations of *P. obesus* because of its migratory ability, but this has never been accurately measured.

This longitudinal study was designed to accurately measure the spatial movements and the areas occupied by *M. shawi* using radio-telemetry. Radio-telemetry has proven to be an important tool for answering questions about habitat requirements and other important aspects of species' natural history [12]. The information from this study will permit characterization of its

ecological niche, to better understand its role in the dispersal of *L. major* and to illustrate its contribution in the emergence of new epidemic foci.

### 2. Materials and methods

#### 2.1. Study site

*M. shawi* rodents were captured at the village of AL MNARA (average altitude 80, 8483 m; Lat 35°12'36''N, Long 9°49'14''E) which is in Kairouan, Central Tunisia, and is an area where zoonotic cutaneous leishmaniasis is endemic (Fig. 1).

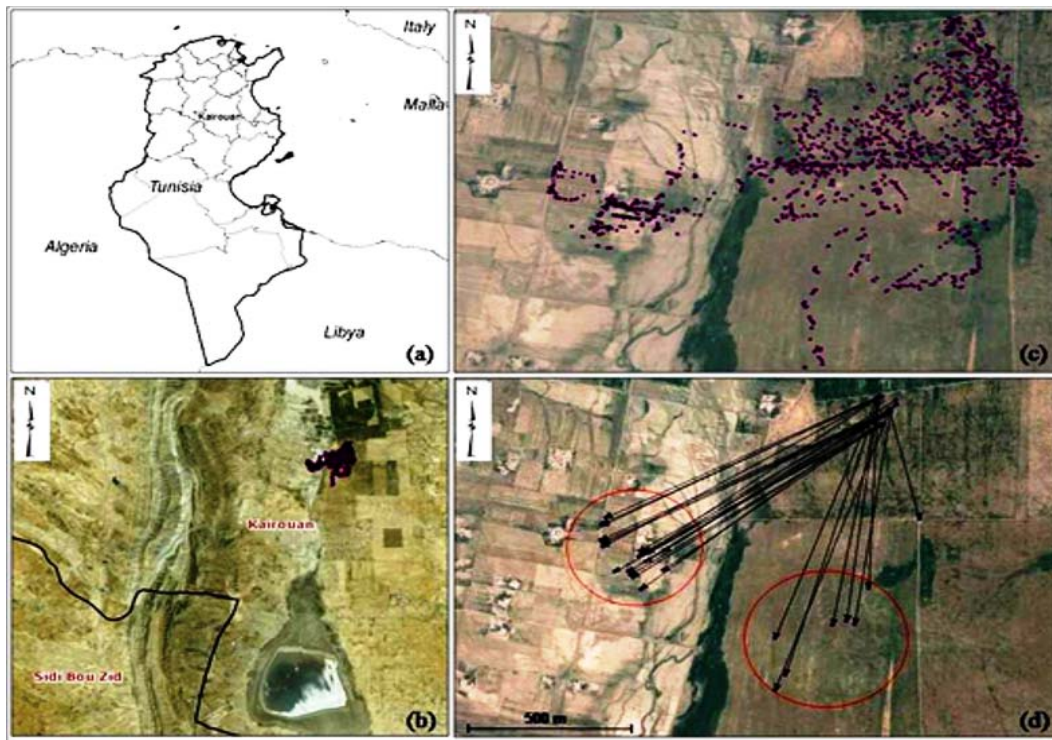
#### 2.2. Study population

In April 2012, *M. shawi* rodents were captured during 15 days. A wire mesh cage was used as a trap baited with fresh food and placed close to active burrow entrances. The cages were placed overnight and checked in the early morning. The rodents were identified according to a morphological key and evaluated for weight, sex, and presence of signs of *Leishmania* infection (cutaneous lesions in different parts of the skin, mainly at the tail and the ears, as previously described [10]).

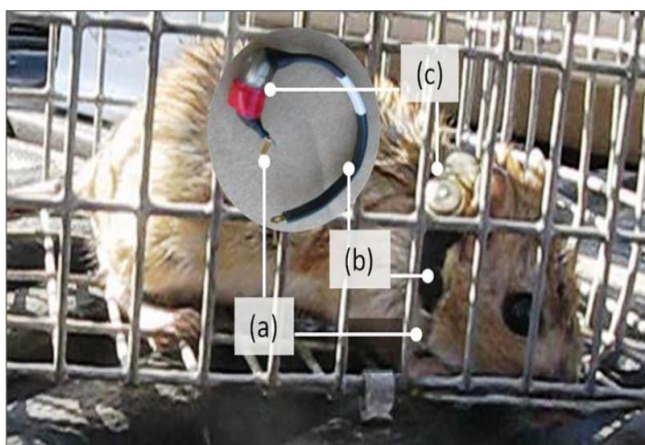
#### 2.3. Radio tracking

Each captured rodent was equipped with a radio transmitter placed around its neck with a brass collar (Biotrack Ltd, Wareham, Dorset BH20 5AX, United Kingdom), and then released at the same site where it was trapped (Fig. 2).

Collars were resistant to chewing, and each transmitter was set to a different frequency, allowing each rodent to be located individually. The equipment was less than 5% of the weight of the rodent, as recommended to avoid disturbing the natural behavior of mammals [13, 14]. Two types of collars were used according to the rodents' weight: blue collars weighing 3.6g and red collars weighing 4.8g.



**Fig 1:** Study site for the tracked *Meriones shawi* population and their spatial dispersal. (a) Location of the Kairouan governorate in Tunisia, in the Mediterranean region. (b) A land sat image of the study area (superposed GPS locations in purple) at Kairouan governorate. (c) A land sat image of the study area with all GPS locations of the tracked rodent population (each point in purple represents a detected location). (d) A land sat image of the study area showing the maximum distance for each tracked rodent (arrow between the starting and the ending locations) and the fragmentation of the rodent population into two subpopulations (circles in red) after the tracking period.



**Fig 2:** *Meriones shawi* with radio-transmitter collar placed around its neck. (a): Self-locking nut, (b): brass collar and (c): Battery and PIP3 transmitter.

We tracked *M. shawi* using a telemetry Sika receiver and a 3-element Yagi antenna (Biotrack Ltd, Wareham, Dorset BH20 5AX, United Kingdom), which is able to detect frequencies between 173.000 and 174.999 MHz. The frequencies of all the collars were registered as channels in the receiver before tracking. Locations of rodents were determined by the homing method<sup>[15, 16]</sup>. This consists of following the strongest signal of the frequency and approaching the animal by walking to identify its burrow. Once the burrow was located, we recorded the rodent's coordinates using a Garmin global positioning system (GPS) unit with 2–3 m precision.

Every two weeks, during our trip to the study area, eight positions were recorded during three consecutive days (two positions on the first and third days, and four positions on the

second day, alternating midday and twilight). This program was continued for each radio-tracked rodent until the signal was lost (due to the animal's death or exhaustion of the collar's battery). A pilot phase preceded the project to fine tune all procedures, but positions tracked in the pilot phase were excluded from analysis.

#### 2.4. Home range and diffusion coefficient calculations

The home range (HR) sizes were calculated using the minimum convex polygon (MCP) method, which defines the HR by drawing a set of points around the external locations of a rodent's movements<sup>[17]</sup>. The maximum distance (MD), between the start and the final locations, and the real traveled distance (RTD) linking the all detected positions of each rodent were estimated using Hawth's Analysis Tools (version 3.27). The diffusion coefficient ( $D$ ) was considered the best parameter to reflect the variation of the occupied surface over time<sup>[18-21]</sup>. It was defined as the space variation over time and was estimated using the following formula:  $(D = (S(t_{i+1}) - S(t_i)) / (t_{i+1} - t_i))$ , with  $t$  representing time in the  $x$  axis and  $S$  the surface in the  $y$  axis. To account for the correlation between  $D$  and HR as well as the potential effect of other time-dependent factors (season, availability of food, and impacts of the environment) on the HR, we estimated the variation of the average HR overtime.

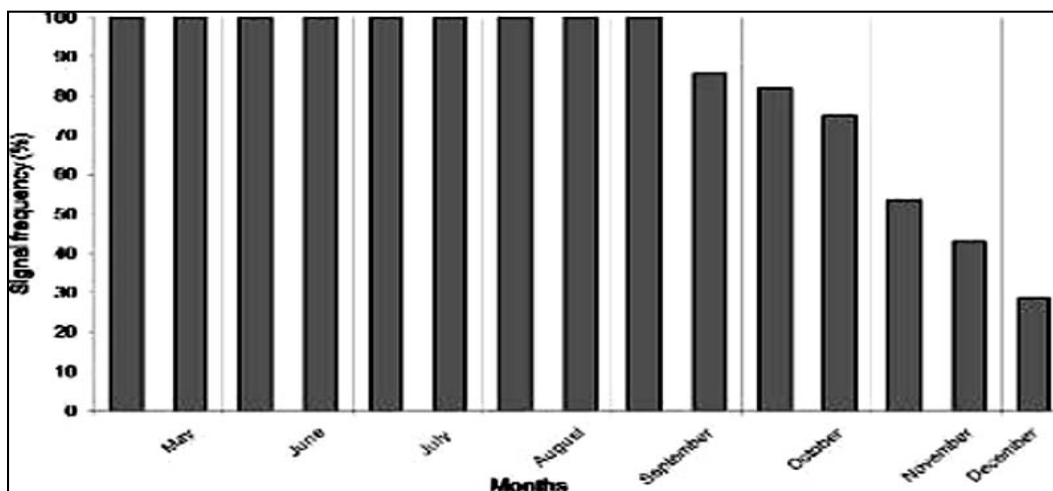
Geographic data were analyzed using ArcGis 9.3 software. Continuous variables and paired samples were respectively tested by Mann–Whitney and Wilcoxon signed-rank nonparametric tests. Fisher exact  $\chi^2$  tests were used to compare association of categorical variables. SPSS software version 17.0 for Windows<sup>[22]</sup> was used to perform these statistical analyses (Stata Corporation).

### 3. Results

During April 2012, 17 female and 13 male *M. shawi* were captured in the study area. Cutaneous lesions indicating leishmaniasis infection were noted in 57% ( $n=17$ ) of this sample (Table 1) and were positively correlated with rodent weight ( $P<0.001$ ).

Two of the tracked rodents (MS06 and MS26) were regarded as dead because their locations remained the same during the tracking period, so they were excluded from the analysis.

During the 8 months follow-up, GPS locations representing the trajectories of the study population were recorded. Signals were detectable for all the tracked rodents until four months, and then signals were lost until only ~30% were detectable after eight months. Fig. 3 shows the proportion of rodents detected through time.



**Fig 3:** Proportions of tracking signals detected over time among the studied *M. shawi* population.

The rodents ( $n=28$ ) had a mean HR size of ( $48.94 \pm 20.72$  ha (range 20.67–97.73 ha)), mean MD of ( $1.24 \pm 0.28$  km (range 0.59–1.59 km)), and mean RTD of ( $5.93 \pm 2.41$  km (range 1.77–9.94 km)) (Table 1).

**Table 1:** Description of each captured *M. shawi* with their clinical manifestation (CM), home range (HR) sizes, maximum distance (MD), and real traveled distance (RTD) as revealed by radio-telemetry during the study period from April 2012 to December 2012.

Rodent code	Sexe	CM	Weight (g)	HR (ha)	MD (km)	RTD (km)
MS01	♀	-	80	40.03	1.16	2.49
MS02	♂	-	78	89.09	1.60	5.33
MS03	♂	+	79	25.83	1.09	2.36
MS04	♂	-	85	90.03	1.09	9.95
MS05	♂	-	87	23.78	1.18	3.41
MS06	♂	-	84	/	/	/
MS07	♀	+	115	53.40	1.50	6.75
MS08	♀	+	102	42.67	0.79	4.55
MS09	♀	+	100	29.52	1.31	4.63
MS10	♀	-	83	20.67	1.16	1.77
MS11	♀	+	97	97.73	1.42	8.78
MS12	♀	+	114	59.99	1.54	8.19
MS13	♂	+	111	35.27	0.71	8.17
MS14	♂	-	82	40.59	0.60	9.21
MS15	♀	-	76	65.45	1.54	6.48
MS16	♀	-	76	61.78	1.53	3.13
MS17	♂	-	78	27.68	0.74	5.04
MS18	♂	+	122	54.53	1.57	9.00
MS19	♀	+	82	45.61	1.53	7.27
MS20	♀	+	88	43.96	1.38	4.04
MS21	♀	+	80	36.10	1.23	5.56
MS22	♀	+	118	60.64	1.39	9.33
MS23	♀	-	80	44.71	1.27	8.74
MS24	♀	+	89	60.36	1.40	7.49
MS25	♂	+	158	29.05	0.94	3.62
MS26	♀	+	118	/	/	/
MS27	♀	+	100	50.76	1.31	5.26
MS28	♂	+	89	34.94	1.41	4.43
MS29	♀	-	87	30.58	1.39	3.98
MS30	♂	-	80	75.64	1.05	7.16

No significant difference was noticed between males and females for mean HR (47.67 ha versus 49.89 ha), MD (1.12 km versus 1.33 km), or RTD (6.24 km versus 5.69 km). The presence of clinical manifestations of leishmaniasis was not

associated with these three variables. We noticed a sharp increase of the population mean HR between the period  $t = 3$  and  $t = 3.5$  months, represented by a “jump” in the curve (Fig. 4).

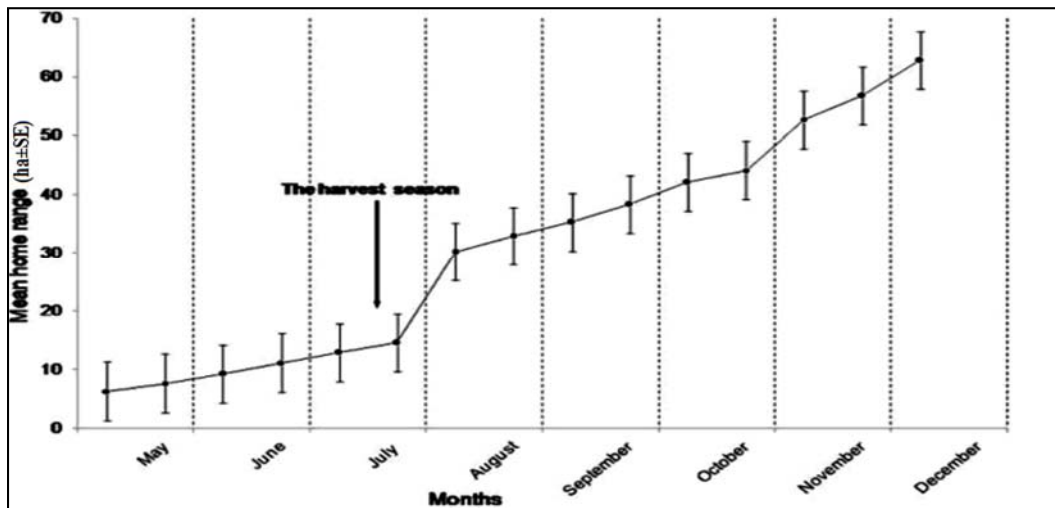


Fig 4: Average home range of the *M. shawi* population during the study period. SE: standard error.

This period followed the harvest season (the end of July) when most of the rodents left their territories at the cereal field, as confirmed by new active burrows in a new area where mallow plants and some pistachio plants were available. Before the harvest season, the mean HR and the mean RTD of the rodent population were calculated ( $14.52 \pm 7.76$  ha and  $2.57 \pm 1.35$  km, respectively). After the harvest season, the mean HR increased significantly ( $34.41 \pm 20.59$  ha ( $P < 0.001$ )) and the RTD reached the maximum ( $3.36 \pm 1.99$  km ( $P = 0.095$ )). Thus, we estimated two functions:  $S1(t) = 3.37t + 4.34$  and  $S2(t) = 8.11t - 0.77$  with significantly different slopes corresponding to coefficients of diffusion ( $D1 = 3.37$  ha/month (95% CI=3.15–3.59) and  $D2 = 8.11$  ha/month (95% CI=6.72–9.51) for the pre- and post-harvest seasons, respectively).

After the harvest season, rodents left the high density zone in the direction of a low density one. This was indicated by the number, position, and density of new burrows in the newly colonized area. In addition, the tracked rodent population was fragmented into two subpopulations at the extremes of the spatial (Fig. 1d).

#### 4. Discussion

To our knowledge, this is the first longitudinal study in North Africa investigating the ecological niche and spatiotemporal dynamics of *M. shawi* using radio-telemetry. The main factors that influence the frequency and extent of movement, and the size and type of areas occupied by these species of rodents were identified for the first time. Indeed, after a tracking period of eight months of 28 *M. shawi*, we estimated the diffusion coefficient, and we confirmed the strong relationship between the spatial patterns and availability of food.

Previous studies of the spatial behavior of some rodents showed a broad range of HRs, from a few square meters to 9 ha depending on the species of rodents, the biotope nature, and the method used [23–30]. This high variability might be explained by the cross-sectional designs of most studies, which could not take into account the variation of HR through time or the high sampling fluctuations due to small sample sizes, as well as by

the low reliability of estimation techniques such as field observation and capture–mark–recapture.

Our estimates of the mean HR ( $48.94 \pm 20.72$  ha), the mean MD ( $1.24 \pm 0.28$  km), and the RTD ( $5.93 \pm 2.41$  km) of the *M. shawi* population are the highest described so far. In fact, for *M. shawi*, the only study in which the spatial distribution was determined (using the capture–mark–recapture method) was conducted over 25 years ago in Morocco, and the mean traveled distance of this species was estimated as around 19 m and varied according to the season and the sex [31]. It has been assumed that the HR size increases with the body mass [28, 32–34]. This was not supported by our results; we found no significant differences according to sex, weight, or clinical manifestations of leishmaniasis. This difference might be explained by the ecological behavior of this species, such as reproduction and search for food, environmental factors, and the high impact of the human intervention. Indeed, *M. shawi* moved at the slowest speed ( $D1 = 3.37$  ha/month) and occupied a smaller area (14.52 ha) when they found food near their original biotope, and emerged more vigorously ( $D2 = 8.11$  ha/month) when they moved to another biotope and occupied a larger area (34.41 ha). This pattern of occupation might be partly explained by an exploratory phase to search for food and an appropriate biotope where they can settle. Habitat type was important in determining the rate of movement for *M. shawi*. The animals moved at slower rates through cereal crops than in mallow and pistachio crop fields, presumably because food was more distant in mallow and pistachio crop fields which increase their exposure to predators. Likewise, the growth of tracked *M. shawi* through time might be explained the requirement for higher amounts of energy and, consequently, stronger rodents were able to move greater distances to find enough food [35].

The organization within colonies of *Meriones* spp. does not appear to be as rigid as for other rodent species [36]. Some species live in permanent groups, others live in temporary groups, and some live in individual burrows and are socially intolerant [37]. Our results suggest that *M. shawi* can be classified in the second category, as they live in non-stable

groups. Furthermore, changes in the use of space by *M. shawi* were correlated with density variations in the population. The population size of these sub-desert rodents depends on food availability, climate factors, and biotic factors such as reproduction [38, 39]. These factors could explain the fragmentation of the tracked rodent population. Moreover, the harvest season of cereals and the season of mallow and pistachio growth might explain the preferred direction of these rodents, confirming the influence of the food availability and the specificity of the rodent diet in its HR size and movements [5]. Our findings confirm the results of other studies showing a negative correlation between food availability and rodents' HR sizes [40-42].

The diffusion coefficient we estimated for the *M. shawi* population was high compared with the desert species of *Meriones* (*M. crassus* and *M. libycus*). This difference can be explained by the low ability for spatial memory among the desert species [43]. The diffusion coefficient can be very useful in the design of control interventions, targeting this species of wild rodent, by providing leishmaniasis risk zones.

Several studies have tried to quantify the HR and movement patterns of rodent species, but most applied traditional techniques such as field observations, powder-tracking, and capture-mark-recapture using live traps placed in grids characterized by low precision [23, 25, 27, 29, 44, 45]. These classic techniques require permanent tracking, which needs continuous presence of researchers in the field, and carries a risk of losing contact with the animal. These shortcomings can be resolved by using GPS collars, which remain permanently active and can continuously supply data for the whole day without the need of a human's presence [46]. This technique of radio-telemetry combined with GPS and a geographical information system is reproducible [47]. It is not limited by trap numbers, the area covered by traps, or the capture rate. Consequently, it is expected to provide less biased estimates for important ecological parameters such as HR and movement patterns. Unfortunately, this technique is not available yet for tracking rodents because the GPS collars are heavy and usually exceed 5% of the rodent's weight, which is the maximum weight acceptable without disturbance of the natural behavior of mammals [13, 14]. Therefore, in this study, we used radio-telemetry combined with geographical information system tools, which constitutes the best available tradeoff between performance and feasibility. The proportion of rodents detected over time by radio-telemetry provides valuable information for the design of future studies for these species.

## 5. Conclusion

This study helped to characterize the ecological niche and demonstrated the migratory capacity of *M. shawi*. We have demonstrated, using valid and reproducible techniques and study design, that these rodents have high prevalence of leishmaniasis and have migratory behavior that could contribute to the spatial dispersal of leishmaniasis by establishing the disease in naïve stable geographically fragmented colonies of *P. obesus*, the classic sedentary reservoir, as well as contributing to the emergence of epidemics among naïve human populations.

## 6. Acknowledgments

Sincere thanks are extended to Mr. Jomâa Chemkhi (Pasteur Institute of Tunis) for his contribution to biotope localization. We are grateful to Mr. Adel Slema (Pasteur Institute of Tunis)

who facilitated access to the field. This work is part of a research project supported by US-NIAID-NIH, Grant number 1P50AI074178-01, and approved by the Institutional Review Board of Pasteur Institute of Tunis; and the Tunisian Ministry of Higher Education and Scientific Research (Laboratory of Transmission, Control and Immunobiology of Infections, LR11IPT02). Permissions were obtained from the parcel owners to conduct the study on their lands. The study and rodents handling protocols were approved by the Institutional Review Board and the ethics committee at Pasteur Institute of Tunis, and according to the guidelines of International Guiding Principles for Biomedical Research Involving Animals. The use of the radio-telemetry tools at the study site was approved by the Tunisian Ministry of Higher Education, Scientific Research and Information and Communication Technologies.

## 7. Reference

1. World Health Organization. Control of the leishmaniasis: Report of WHO Expert Committee. Geneva, Switzerland, 1990, 159.
2. Wasserberg G, Abramsky Z, Anders G, El-Fari M, Schoenian G, Schnur L *et al.* The ecology of cutaneous leishmaniasis in Nizzana, Israel: infection patterns in the reservoir host, and epidemiological implications. *Int. J Parasitol*, 2002; 32(2):133-143.
3. Salah AB, Kamarianakis Y, Chlif S, Alaya NB, Prastacos P. Zoonotic cutaneous leishmaniasis in central Tunisia: spatio-temporal dynamics. *Int. J Epidemiol.* 2007; 36(5):991-1000.
4. World Health Organization. Report of the WHO meeting on rodent ecology, population dynamics and surveillance technology in Mediterranean countries. Geneva, Switzerland, 1992.
5. Adamou-Djerbaoui M, Denys C, Chaba H, Seid MM, Djelaila Y, Labdelli F. Étude du régime alimentaire d'un rongeur nuisible (*Meriones shawii* Duvernoy, 1842, Mammalia, Rodentia) en Algérie. *Lebanese Science Journal*. 2013; 14(1):15-32.
6. Stenseth NC, Leirs H, Skonhøft A, Davis SA, Pech RP, Andreassen HP *et al.* Mice, rats, and people: the bio-economics of agricultural rodents pests. *Front Ecol Environ* 2003; 1(7):367-375.
7. Petter F. Répartition géographique et écologie des Rongeurs désertiques (du Sahara occidental à l'Iran oriental). *Mammalia* 1961; 25:1-222.
8. Daly M, Daly S. Behavior of *Psammomys obesus* (Rodentia: Gerbillinae) in the Algerian Sahara. *Z Tierpsychol*, 1975; 37(3):298-321.
9. Fichet-Calvet E, Jomaa C, Giraudoux P, Ashford RW. Estimation of fat sand rat *Psammomys obesus* abundance by using surface indices. *Acta Theriol* 1999; 44(4):353-362.
10. Ghawar W, Toumi A, Snoussi MA, Chlif S, Zâatour A, Boukthir A *et al.* *Leishmania major* infection among *Psammomys obesus* and *Meriones shawi*: reservoirs of zoonotic cutaneous leishmaniasis in Sidi Bouzid (central Tunisia). *Vector-Borne and Zoonotic Dis* 2011; 11(12):1561-1568.
11. Bouyatas M, Gamrani H. Etude immuno-histochimique de l'effet d'une intoxication aigue et chronique sur le cerveau de la Mérione shawi. *Semlalia, Marrakech: Laboratoire de*

- neurosciences, Faculté des sciences Semlalia, Marrakech, 2004.
12. Kenward RE. A manual of wildlife radio tagging. San Diego, California, USA, Academic Press, 2001.
  13. Cochran WW. Wildlife management techniques manual. Wildlife Society, Washington, 1969.
  14. Moraes JrEA, Chiarello AG. A radio tracking study of home range and movements of the marsupial *Micoureus demerarae* (Thomas) (Mammalia, Didelphidae) in the Atlantic forest of south-eastern Brazil. *Rev Bras Zool* 2005; 22(1):85-91.
  15. Mech LD. A handbook of animal radiotracking. Minneapolis, Minnesota, USA, University of Minnesota Press, 1983.
  16. White GC, Garrott RA. Analysis of wildlife radio-tracking data. New York: Academic Press, 1990.
  17. Mohr CO. Table of equivalent populations of North American small mammals. *Am Midl Nat*, 1947; 37:223-249.
  18. Dwyer G, Elkinton JS. Host dispersal and the spatial spread of insect pathogens. *Ecology* 1995; 76:1261-1275.
  19. Holmes EE, Lewis MA, Banks JE, Veit RR. Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology* 1994; 75:17-29.
  20. Kallen A, Arcuri P, Murray JD. A simple model for the spatial spread and control of rabies. *J Theor Biol.* 1985; 116(3):377-393.
  21. Murray JD, Stanley EA, Brown DL. On the spatial spread of rabies among foxes. *Proc R Soc Lond B Biol Sci* 1986; 229(1255):111-150.
  22. SPSS-INC. SPSS Statistics for Windows, Version 17.0. Chicago, SPSS Inc, 2008.
  23. Fitzwater WD, Prakash I. Observations on the burrows, behavior and home range of the Indian desert gerbil, *Meriones hurrianae* Jerdon. *Mammalia*, 1969; 33(4):598-605.
  24. Agren G. Field observations of social behavior in a Saharan gerbil: *Meriones libycus*. *Mammalia*, 1979; 43(2):135-145.
  25. Wolff JO. The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*. *Can J Zool.* 1985; 63(11):2657-2662.
  26. Gromov VS. Spatial relationships and social structure of gerbils in the genus *Meriones* (Gerbillinae, Rodentia). *Zh Obshch Biol*, 1997; 58:35-54.
  27. Lindsey GD, Mosher SM, Fancy SG, Smucker TD. Population structure and movements of introduced rats in a Hawaiian rainforest. *Pacific Conservation Biology* 1999; 5(2):94-102.
  28. Tchabovsky A, Merrit JF, Aleksandrov DY. Ranging patterns of two syntopic gerbillid rodents: a radiotelemetry and trapping study in semi-desert habitat of Kalmykia, Russia. *Acta Theriol*, 2004; 49(1):17-31.
  29. Wang Y, Liu W, Wang G, Wan X, Zhong W. Home-range sizes of social groups of Mongolian gerbils *Meriones unguiculatus*. *J Arid Environ*, 2011; 75(2):132-137.
  30. Low WB, Mills H, Algar D, Hamilton N. Home ranges of introduced rats on Christmas Island: A pilot study. *Ecological Management & Restoration* 2013; 14(1):41-46.
  31. Zaime AK, Pascal M. Etude de la répartition spatiale des micromammifères d'une zone pastorale en milieu saharien (Guelmîle, Maroc). *Mammalia*, 1988; 53(1):67-75.
  32. Harestad AS, Bunnell FL. Home range and body weight—a reevaluation. *Ecology* 1979; 60:389-402.
  33. Mace GM, Harvey PH. Energetic constraints on home-range size. *Am Nat* 1983; 121:120-132.
  34. Kelt DA, Van Vuren DH. The ecology and macroecology of mammalian home range area. *Am Nat* 2001; 157(6):637-645.
  35. McNab BK. Bioenergetics and the determination of home range size. *Am Nat* 1963; 97:133-140.
  36. Sales GD. Ultrasound and aggressive behaviour in rats and other small mammals. *Anim Behav* 1972; 20(1):88-100.
  37. Randall JA. Convergences and divergences in communication and social organisation of desert rodents. *Aust J Zool.* 1994; 42(4):405-433.
  38. Bernard J. Les mammifères de Tunisie et des régions voisines. *Bull. Fac. Agr. Tunis* 1969; 24.
  39. Zaime A, Gautier JY. Analyse des fluctuations densitaires et de l'occupation de l'espace chez la Merione de Shaw (*Meriones shawii*) en milieu semi-aride au Maroc. *Sci Tech Anim Lab* 1988; 13(1):59-63.
  40. Tufto J, Andersen R, Linnell J. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *J Anim Ecol.* 1996; 65:715-724.
  41. Lurz PWW, Garson PJ, Wauters LA. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris* L.). *J Zool.* 2000; 251(02):167-178.
  42. Saïd S, Gaillard JM, Duncan P, Guillon N, Servanty S, Pellerin M *et al.* Ecological correlates of home range size in spring summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *J Zool.* 2005; 267(3):301-308.
  43. Komerovsky I, Petter F. La mémoire spatiale et le retour au gîte chez cinq espèces de Mériones (rongeurs, gerbillidés). Université Paris Diderot - Paris 7, 1991.
  44. Mikesic DG, Drickamer LC. Factors affecting home-range size in house mice *Mus musculus domesticus* living in outdoor enclosures. *Am Midl Nat*, 1992; 127:31-40.
  45. Ebensperger LA, Sobrero R, Campos V, Giannoni SM. Activity, range areas, and nesting patterns in the viscacha rat, *Octomys mimax*. *J Arid Environ.* 2008; 72(7):1174-1183.
  46. Walzer C, Kaczensky P. Choisir un émetteur ou une balise: revue des possibilités et limites. Actes du Vème Congrès International Vétérinaire sur les Animaux Sauvages et Exotiques. Muséum National d'histoire Naturelle, Paris, France, 2008, 174-178.
  47. Brøseth H, Pedersen HC. Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS and GIS. *J Appl Ecol.* 2000; 37(1):82-190.