

# Sociobiology

An international journal on social insects

## **RESEARCH ARTICLE - ANTS**

## Diversity, Richness and Composition of Ant Communities (Hymenoptera: Formicidae) in the Pre-Saharan Steppe of Algeria

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#### Article History

#### Edited by

Jacques Delabie, UESC, Brazil				
Received	16 February 2018			
Initial acceptance	28 April 2018			
Final acceptance	16 December 2019			
Publication date	18 April 2020			

#### Keywords

Steppe, myrmecofauna, diversity, trophic availability, seasonal variation, Algeria.

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## Abstract

This paper describes the structure and composition of ant communities in the pre-Saharan steppe of Algeria. The study focused on three stations located in two regions with different climates: semi-arid (Aflou) and arid (Laghouat). Ants were collected between March 2013 and February 2014, using pitfall trap sampling over a four-season period and quadrat counting techniques. A total of 20 ant species have been identified, which belong to 8 genera in three subfamilies: Dolichoderinae, Myrmicinae and Formicinae. Moreover, it was noticed that the study areas, which can be characterized by their floristic nature, physiognomic and even edaphic aspects, directly influence the ant community ecology and distribution. We classified them in both *eurytopic* and *stenotopic* species. It was also observed, using a Correspondence Factorial Analysis (CFA), that the ants' activity is seasonal and often correlated with temperature fluctuation and trophic availability.

Introduction

Algerian steppe is considered ecologically a buffer zone between coastal and Saharan Algeria (Nedjraoui & Bedrani, 2008). It is limited to the north by the Tellian Atlas and to the south by the Saharan Atlas and extends over a length of about 1,000 km from the Tunisian border to the Moroccan border. It covers an area of 20 million hectares out of a total of 42 million hectares of steppe for the entire Maghreb region. This wide area makes the Algerian steppe an ecosystem characterized by a diversity of landscapes submitted to a great variability of ecological factors (Bencherif, 2011).

Despite this diversity, there is a lack of information on the fauna living in this ecosystem, particularly arthropods, including ants. With more than 12,500 species, ants are considered to be the most diverse and abundant group of social insects (Dieng et al., 2016; Passera & Aron, 2005). They can be found everywhere, in forests as well as in open areas, near water or in dry places (Cagniant, 1973). Ants are widely applied in several biodiversity assessment programs (Agosti et al., 2000), as indicators of ecological change and environmental control (Andersen & Majer, 2004), which is undoubtedly related to their importance in terms of biomass (Hölldobler & Wilson, 1990).

In Algeria, ants have been the subject of previous studies, particularly in the northern regions with a humid and sub-humid bioclimatic stage. These include studies by Cagniant (1966, 1968, 1969, 1970 and 1973) and Djioua et al. (2014) on ant communities in Algerian forests. Belkadi (1990) and Oudjiane et al. (2007) studied the ants in Kabylia region, while Barech (2014) and Dehina et al. (2007) investigated the ants in the Algiers Sahel.



However, the myrmecofauna of the steppe and southern Algeria was unknown until Bernard's (1958) comparative study of ant communities of France and northern Africa, including some of the Algerian steppes, as well as the recent study of Souttou et al. (2011) and Barech et al. (2016). Therefore, this study aims to provide an updated inventory of ants in Algeria, to assess the diversity and distribution of ant species represented in the northern Algerian Sahara (steppe zone) and to determine their temporal succession in relation to seasonal variations.

#### **Materials and Methods**

### Study area and sample sites

This study was carried out in the Algerian steppe. It is characterized by an arid to semi-arid Mediterranean climate, with low irregular rainfall (100 to 450 mm/year), high temperature ranges (over 40°C in summer and below 0°C in winter) and an altitude of 700 to 1,500 m a.s.l. (Bencherif, 2011).

The investigation was conducted in two distinct regions: (1) Aflou:  $(34^{\circ}06'N \ 02^{\circ}06'E)$  which is located on the mountains of the Saharan Atlas, notably in the massive heart of Djebel Amour, at an altitude between 1,000 and1,500 m a.s.l. with slopes of 12,5 to 25%; and (2) Laghouat:  $(33^{\circ}47'N \ 02^{\circ}51'E)$  which is located in the southern foothills of the Saharan Atlas, at an altitude between 700 and 1,000 m a.s.l. and slopes from 0 to 3% (Fig 1).

The research was carried out in three types of habitats, the distance between them being up to 100 km: (i) Pine Forest ( $34^{\circ}07$ 'N 02°05'E): located on the high plain of the Aflou region, at an altitude of 1,450m a.s.l. This habitat is a planted area aiming to reduce the creep of desertification and its spread to the fertile northern part of the country; it includes different types of plants, including Aleppo pine (*Pinus halepensis* Mill.) associated with a formation of halfah grass (*Stipa tenacissima* L.); (ii) Dry River (33°08'N 02°53'E): situated in M'Zi, Laghouat region. The study site was a wadi (dry river), at an altitude of 760m a.s.l., characterized by herbaceous plants and represented mainly by the aristide grass (*Aristida pungens* Desf.) dispersed on sandy soil; (iii) Dhaya (33°9'N 03°20'E): located in Tilghimt, 100 km south of Laghouat, at an altitude of 700m a.s.l. This station is a closed depression where non saline water accumulates and then evaporates or infiltrates very slowly into fine soils (Pouget, 1992). The Dhaya are mainly marked by the presence of the Atlas pistachio (*Pistacia atlantica* Desf.) and the wild jujube (*Ziziphus lotus* (L.) Lam.) (Fig 2).

### Ant sampling

Ant sampling was carried out using two collecting techniques. The first one was the quadrat method, which consists of manually counting and capturing ant species over an area of 100 m<sup>2</sup> (10 m x 10 m) (Cagniant, 1973; Suguituru et al., 2011), noting that the quadrat is randomly selected with three repetitions per station.

The second method used was pitfall traps. This process consists in burying metal pots (7.5cm in diameter and 10.5cm deep) up to ground level; they are placed on a transect plane of 10 traps, with a space of 5m. Two-thirds of the buried pots are filled with an attractive mixture (water with detergent) and left in place for 2 days (48 hours) (Berville et al., 2016; El Keroumi et al., 2012).



Fig 1. Geographic situation of study area (steppe of Algeria) and distribution of sampling sites.



**Fig 2.** Photographs showing the physiognomy of the three prospected stations (a) Pine forest, (b) Dry River and (c) Dhaya.

It should be noted that ants were sampled once a month for one year, from 2013 to 2014. Ant species were counted by the quadrat method from early sunrise to noon, while the pitfall trapping was done from noon to noon on the second day. In each station, the total number of samples is therefore 3 x 12 quadrats and 10 x 12 pitfalls. As there are three stations, our whole study corresponds to 460 samples of ants. All ants were placed in vials, stored in 70% ethanol and labeled according to the type of collecting, trap number and any ecological information.

Ants were identified using the keys of Cagniant (1996, 1997, 2009), Cagniant and Espadaler (1997) and the Internet site of B. Taylor ("Ants of Africa"). Part of the ants was sent to Professor Henri Cagniant (Paul Sabatier University, Toulouse, France) for identification. Voucher specimens of the ants were deposited in the collections of H. Cagniant and Zoology Department of the National School of Agricultural Sciences (Algeria).

## Data analysis

Despite the great sampling effort, when we analyzed our data, our samples showed a fairly low independence and we preferred to consider the abundance rather than the frequency of occurrence of the collected ants. To analyze the ant diversity, the data of the pitfall traps of the various prospected habitats are evaluated by the following indices: Total species richness index (S), relative abundance (RA%) is calculated as (RA = ni / n\*100) where ni is number of individuals of taxon i and n is the total number of individuals of all species, dominance (D) it was calculated as  $D=\Sigma(ni/n)^2$ and Occurrence frequency (O %) was calculated according to Dajoz (1985): (O = pi / p\*100) where pi is the total number of samples containing the species taken into consideration and p is the total number of samples.

From the ant occurrence frequency (O %), we distinguished: constant species ( $O \ge 50\%$ ), accessory species (25% < O < 50%), accidental species ( $O \le 25\%$ ).

In addition, the diversity of the three habitats was estimated using the Shannon's index (H) it was estimated as  $H = -\Sigma(pi \log pi)$ , where pi is the proportion of individuals of the *i* species (pi = ni / n;),  $H_{max}$  is the maximum possible value of H, and is equivalent to (log<sub>2</sub>S) and Pielou's evenness index (J), it is calculated as  $J = H / H_{max}$  (the value of J varied between 0 (a single species dominates) and 1 (all species are equally abundant)).

Finally, the data were processed via Correspondence Analysis, in order to determine the activity of myrmecofauna during one year of study using PAST software version 2.17 (Hammer et al., 2001)

### Results

## Myrmecofauna

We found a total of 20 species of ants in the three studied stations (Table 1), belonging to three sub-families: Dolichoderinae represented by a single species: *Tapinoma nigerrimum* (Nylander, 1788), Myrmicinae represented by *Messor arenarius* (Fabricius, 1787), *Messor aegyptiacus* (Emery, 1878), *Messor sanctus* Emery, 1921, *Messor medioruber* Santschi, 1910, *Messor capitatus* (Latreille, 1798), *Tetramorium biskrensis* Forel, 1904, *Tetramorium sericeiventre* Emery, 1877, *Monomorium salomonis* (Linnaeus, 1758), *Monomorium subopacum* (Smith, 1858), *Pheidole pallidula* (Nylander, 1848) and *Cardiocondyla batesii* Forel, 1894. The Formicinae sub-family is represented by two genera only: i) *Camponotus* with *Camponotus thoracicus* (Fabricius, 1804), *Camponotus foreli* Emery, 1881, *Camponotus alii* Forel, 1890 and *Camponotus barbaricus* Emery, 1905; ii) *Cataglyphis*, represented by four species, namely *Cataglyphis bicolor* (Fabricius, 1793), *Cataglyphis bombycina* (Roger, 1859), *Cataglyphis albicans* (Roger, 1859) and *Cataglyphis rubra* (Forel, 1903). The abundance of each ant species was different according the sampling techniques used, since certain species were occurred only in the quadrat method, as it is the case of *M. aegyptiacus*, *T. sericiventre*, *M. subopacum*, *C. thoracicus*. The difference between the number of ant species taken by the two sampling methods was yet not statistically significant (Wilcoxon signed-rank test; pitfall traps: p > 0.05, quadrat traps: p = 0.65)



**Fig 3.** Occurrence frequency (O%) of ant species in the three habitats. Total specimens (Pin forest: 2264; Dry river: 2511; Dhaya: 1772) number of pitfalls, 10.

A greater richness was recorded with the use of pitfall traps for pine forest, with nine species: *M. capitatus, M. salomonis, T. biskrensis, C. foreli, C. barbaricus, C. alii, C. bicolor, C. albicans* and *C. rubra*. In the Dhaya of Tilghimt, eight species of ants were identified, including *M. sanctus, M. medioruber, T. biskrensis, M. salomonis, P. pallidula, C. batesii, C. thoracicus* and *C. bicolor*. In the dry river of M'zi, only five species were detected: *T. nigerrimum, M. arenarius, M. salomonis, C. bombycina* and *C. bicolor*.

Sometimes abundance reflects better the ant activity in the locations we studied according the ant sampling mode. In the 3 habitat types (Table 2), the pitfall traps revealed that *M. capitatus* is especially abundant exclusively in forest, while the highest relative abundance was noted for *T. nigerrimum* (39.3% of the whole individuals in the traps used for sampling) in the dry river station, followed by *C. bombycina* (36.6%). In the Dhaya of Tilghimt, *C. bicolor* is dominant (41.5% of the whole individuals in the traps used for sampling), followed by *P. pallidula* (20.4%) (Table 2).

For the frequency of occurrence (O %) of ants species recorded by pitfall, in the pin forest, on the nine species of ants reported, *C. bicolor* is considered as the only constant species, the rest of the ants are presented in the category of accessory species in the dry river *T. nigerrimum* with *C. bombycina* are constant ants while *C. bicolor* is classified in the category of accessory species; however *M. arenarius* and *M. salomonis* have appeared less in dry river. The rates of occurrence of ants in the daya are as follows: *C. bicolor* and *P. pallidula* have appeared consistently, the species of *Messor* and *C. batesii* are classified as accessory species and the last species represented by *C. thoracicus* and *M. salomonis* appeared accidentally.

Subfamily	Species	Pitfall	Quadrat
Dolichoderinae	Tapinoma nigerrimum (Nylander, 1788)	986	1,095
	Messor capitatus (Latreille, 1798)	763	241
	Messor arenarius (Fabricius, 1787)	13	298
	Messor aegyptiacus (Emery, 1878)	0	192
	Messor medioruber Santschi,1910	288	678
Myrmicinae	Messor sanctus Emery, 1921	221	552
	Tetramorium biskrensis Forel, 1904	184	95
	Tetramorium sericeiventre Emery, 1877	0	17
	Monomorium salomonis (Linnaeus, 1758)	430	359
	Monomorium subopacum (Smith, 1858)	0	23
	Pheidole pallidula (Nylander, 1849)	362	468
	Cardiocondyla batesii Forel, 1894	149	133
	Camponotus barbaricus Emery, 1905	296	5
	Camponotus foreli (Roger, 1859)	126	132
	Camponotus alii Forel, 1890	116	282
г · ·	Camponotus thoracicus (Fabricius, 1804)	1	12
Formicinae	Cataglyphis rubra (Forel, 1903)	224	67
	Cataglyphis albicans (Roger, 1859)	76	43
	Cataglyphis bicolor (Fabricius, 1793)	1,421	1,322
	Cataglyphis bombycina (Roger, 1859)	918	823
Total richness		17	20

Table 1. Abundance of ant species collected at the steppe of Algeria by two sampling methods

The study areas are very different from the points of view of their floristic nature and their physiognomic and even edaphic aspects, and seem to directly influence the ant community ecology and distribution, particularly the 17 species captured by pitfall traps. However, there are only two species common in the three types of vegetation, namely *C. bicolor* and *M. salomonis*. The other ants are considered as characteristic to each region (Table 2).

Table 2. Ant species collected by pitfall trapping in the three habitats.

Seek for an iler	Species	Pine Forest		Dry River		Dhaya	
Subtaininy		ni	RA%	ni	RA%	ni	RA%
Dolichoderinae	Tapinoma nigerrimum (Nylander, 1788)	-	-	986	39.3	-	-
Myrmicinae	Messor capitatus (Latreille, 1798)	763	34	-	-	-	-
	Messor arenarius (Fabricius, 1787)	-	-	13	0.5	-	-
	Messor medioruber Santschi,1910	-	-	-	-	288	16.3
	Messor sanctus Emery, 1921	-	-	-	-	221	12.5
	Tetramorium biskrensis Forel, 1904	38	6.5	-	-	38	2.1
	Monomorium salomonis (Linnaeus, 1758)	298	12.8	92	3.7	49	2.8
	Pheidole pallidula (Nylander, 1849)	-	-	-	-	362	20.4
	Cardiocondyla batesii Forel, 1894	-	-	-	-	149	8.4
Formicinae	Camponotus barbaricus Emery, 1905	269	11.9	-	-	-	-
	Camponotus foreli (Roger, 1859)	126	5.6	-	-	-	-
	Camponotus alii Forel, 1890	116	5.1	-	-	-	-
	Camponotus thoracicus (Fabricius, 1804)	-	-	-	-	1	0.1
	Cataglyphis rubra (Forel, 1903)	224	9.9	-	-	-	-
	Cataglyphis albicans (Roger, 1859)	76	3.4	-	-	-	-
	Cataglyphis bicolor (Fabricius, 1793)	255	11.3	255	20	664	37.5
	Cataglyphis bombycina (Roger, 1859)	-	-	918	36.6	-	-

ni: number of individuals, RA%: relative abundance

#### Species diversity

The high total specific richness of ants in forest environment (9 species) also matched with the results obtained for the Shannon index of diversity. The results showed that this environment is the most diversified (H=1.96), followed by Dhaya (H=1.64) and the dry river (H=1.20). On the other hand, the dominance index in the three habitats studied is slightly high in the dry river of M'Zi (D=0.3) compared to that of the Dhaya (D=0.2) and the pine forest (D=0.1). The Pielou's evenness index varies between J= 0.74 to J=0.89 at the three locations. The values tend towards 1, which means that the number of species remains in equal proportion and tends to be stable (Table 3).

Table 3. Diversity indexes and Evenness for the three habitats.

	<b>Pine Forest</b>	Dry River	Dhaya
Taxa (S)	9	5	8
Individuals	2264	2511	1772
Dominance (D)	0.17	0.32	0.23
Shannon Index (H')	1.96	1.20	1.64
Simpson (1-D)	0.82	0.67	0.76
Evenness Index (J)	0.89	0.74	0.78

### Seasonality effect on ants' activity

Most species show a variation in their seasonal activity according to their habitats (Fig 4). The overall average abundance



Fig 4. Seasonal variation in ant community trapped by pitfall in the three habitats prospected.

of ant populations recorded by the pitfall traps was calculated for each season in all studied stations to better understand the activities of the ants living in Algerian steppe.

In Figure 1, we can observe the maximum activity peak of each ant species in each habitat. In the pin forest, the peak activity of ants is recorded mainly for the spring and summer months. This is not the case in the Dry River and the Dhaya, there are some species which have the peak in spring, other in summer and also in autumn.

In the pine forest, there is less seasonality than in the other two habitats.

The activity of myrmecofauna during one year is illustrated by a factorial analysis of correspondence (Fig 5). The analysis is satisfactory since the sum of the variables' projections on the plane F1 and F2 is greater than 50% of the total variance.

The correspondence analysis of ant showed that the seasons are represented in three quadrants. Each quadrant reflects a different spatial and temporal distribution of ant species. The first quadrant corresponds to the ant populations that are active in the spring season, represented by *T. nigerrimum, C. albicans, C. alii, C. foreli* and *C. batesii*. The second quadrant concerns the most abundant ants during the summer, namely *C. bicolor, C. bombycina, C. rubra, C. barbaricus, C. thoracicus, M. capitatus, T. biskrensis* and *M. salomonis*. Finally, the third quadrant is characterized by ants observed during autumn period. It includes the following species: *Messor (M. sanctus, M. medioruber, M. arenarius)* and *P. pallidula* (Fig 5).



Fig 5.Correspondence Analysis of ant activity according to season.

### Discussion

#### Diversity and distribution of ants

Based on the steppe inventory, a total of 20 ant species were recorded using the quadrat method and 17 species using the pitfall trapping. The difference between the richness values of the two sampling techniques was evident, particularly for species of the genus *Messor*, *C. barbaricus*, *C. thoracicus*, *M. subopacum* and *T. sericeiventre*. This can be explained by some behavioral traits of these species. *Messor* spp., for example, are more abundant in quadrats than in pitfalls probably due to the use of trails for foraging, and it is less likely than the workers fall into traps except when a trail ends on a pitfall. In this case, they fall in large number and it seems to be the case of *M. capitatus* (X. Cerdá, personal communication). As many *Camponotus*, *C. barbaricus* and *C. thoracicus* are mostly nocturnal, and this is certainly the reason why they are less detected in quadrats (Cagniant, 2009).

Bernard (1958) identified 16 species of ants living in the Algerian-Tunisian steppes, close from the location of the present study, Souttou et al. (2011) reported 15 species of ants in the steppe of the Djelfa region, while in another part of Djelfa, Bouzekri et al. (2015) recorded nine species of ants only. Until this moment, the single study on an Algerian steppe ant community showing a higher richness (S = 24 species) is that of Barech et al. (2016). Furthermore, between12 and 14 species were found in the Tunisian steppe (Heatwole & Muir, 1989) while in Iran, from 7 to15 species were sampled in several steppe locations (Paknia & Pfeiffer, 2011). The richness of the forest environment (Pine forest) is consistent with Djioua et al. (2014) with S= 15, including 13 species nesting in forest environment. Furthermore Bougherara (2009) studied an oak grove at Chréa (Algeria) (1,450 meters a.s.l.) where he reported the occurrence of 9 ant species.

The study on the heterogeneity of the distribution of ant fauna between study stations is consistent with Cagniant (1973). The author noted that this heterogeneity can be explained by the influence of climate and composition of the vegetation cover. Similarly, Gaspar (1972) showed that climatic and soil factors directly influence the ant distribution. At Salt Lake Chott El Hodna (Algeria), Barech et al. (2016) also noted that the distribution of ants is dependent not only to soil texture but also to its composition (salinity).

Our study suggests that the distribution of Formicidae can be classified into two groups. The first one is represented by *eurytopic* species, which have a wide distribution and occupy various biotopes. This is the case of *C. bicolor*, common in the three stations surveyed. This observation corroborates Cagniant (1969, 1970) who indicated that this *Cataglyphis* is common throughout Algeria as well as in the Sahara Oases with color variability; the darkest forms are those of the Saharan Atlas nesting in open areas. *M. salomonis* is a second species that can be attributed to this group. According to Bernard (1958) this omnivorous ant is dominant especially in the arid steppe and desert environments.

The second group includes stenotopic species, frequently localized in a specific area; this is the case of *Camponotus* spp., which use to climb trees and are widespread in all forests (Cagniant, 1996). On the other hand, Bernard (1945, 1958) reported that *T. nigerrimum* are found near wadis. This statement is in agreement with our own observations since this species has been recorded only in the dry river at M'Zi station. According to Bernard (1968), *T. nigerrimum* is sensitive to soil nature and its nests are dug in moist, clayey soils or highly permeable sand.

The genus of harvester ants *Messor*, represented by five species in our study, includes *M. capitatus* which is frequent in forests and mountains at an altitude between 1,000 and 1,700 m (Cagniant & Espadaler, 1997). Cagniant (1997) corroborates our observation about *M. arenarius* since he noted that this ant is a *sabulicolous* species found in the Saharan ergs, wadi sands, High Plains and Sahara Atlas. The distribution of *M. aegyptiacus* is observed mainly in the northern edges of the Sahara (Cagniant, 1997), which corresponds to one of the locations of this study.

Two species of the genus *Cataglyphis* were common in the pine forest: *C. albicans* and *C. rubra*. This result agrees with Bouzekri et al. (2015) and Bernard (1958), who reported the dominance of *C. albicans* in the Algerian-Tunisian steppes where it lives in dry, hard and steppe-like habitats (Wehner, 1983). Cagniant (2009) confirmed the occurrence of *C. rubra* in the entire pre-Saharan region of Morocco in the steppes and other stony areas between 800 and 1,400 m a.s.l., as well as in the Algerian high lands. Sheltered by tufts of *Aristida pungens*, the nests of *C. bombycina* are dug in pure sand and can occupy a very large area. This "silver ant" is common on dunes and other sandy areas (Cagniant, 2009).

The ants' diversity is reported to be more variable in forest areas (Sommer & Cagniant, 1988). Indeed, this diversity uses to be high when it is not subjected to any external disturbance (Faurie et al., 2006). This is consistent with the results of this study (Table 3) and with Barech et al. (2016), with a diversity of H= 1.4 and H = 1.35, respectively. On the other hand, a low diversity (H between 0.02 and 0.7) was observed in Algerian cultivated zones as a citrus orchard by Fekkoun et al. (2011) and in cultivated areas by Bouzekri et al. (2015) and Dehina et al. (2007).

#### Seasonal activity of ants

According to the Correspondence Analysis, the temporal dynamics of the ants in the different habitats sampled here was categorized into three groups. As a result, temperature is the most important factor which affects the spatial and temporal variation of ants which can be then considered as thermophilic (Hölldobler & Wilson, 1990). Pfeiffer et al. (2003) also noted that the distribution of the ants in the Mongolian steppes depends on temperature amplitude.

Furthermore, seed-harvesting ants, such as *M. sanctus*, *M. medioruber*, *M. arenarius* and *P. pallidula*, seem to be more abundant and active in autumn. These species are important seed consumers in several desert ecosystems (Cagniant, 1973; Pirk et al., 2009). This explains their dominance during this period coinciding with seed maturation when they found an amount of this interesting trophic resource. Similarly, Cros et al. (1997), in a study on the activity of Mediterranean ants, reported a maximum foraging activity of ants of the genus *Messor* and *P. pallidula* during autumn (September and October), except for *M. capitatus* which is more active during summer. In addition, Cros et al. (1997) observed that this species is mainly active at dusk and at night during the summer months, as well as *C. thoracicus* and *C. barbaricus*, also observed in this study.

In the case of the xerophilic genus *Cataglyphis*, sunlight and temperature rise seem to be the main factors determining worker foraging (Tohmé et al., 1985; Cerdá et al., 1994; Lenoir et al., 2009). This is the case of *C. bicolor*, *C. bombycina*, *C. rubra* and *C. albicans*.

A strictly springtime activity were observed in *T. nigerrimum*, *C. batesii* and two species of *Camponotus*, represented by *C. foreli* and *C. alii*.

Our observations of the ant seasonal activity corroborates a study on the impact of the seasons on the abundance, diversity and species composition of an ant community in a semi-arid zone of Australia (Andersen, 1983). Similarly, Basu (2008) observed significant seasonal fluctuations in ants' activity in a tropical forest in the Western Ghats (India).Consequently, ants' activity in Algerian steppe strongly seems to be influenced by seasonal variations, which are often correlated with temperature variations (Retana & Cerdá, 2000; Bollazzi & Roces, 2002) and trophic availability (Steinberger et al., 1992).

## Acknowledgments

We would particularly like to acknowledge the reviewers and express our gratitude to Professor Xim Cerda for his valuable advice. Special thanks to Jacques Delabie and Elmo Koch for their revisions on earlier versions of the manuscript. We also extend our gratitude to Professor Henri Cagniant for the confirmation of ant identifications.

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