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Family identity of the sub-social desert terrestrial isopod *Hemilepistus reaumurii*

Anas Ayari [a, *], Freddie-Jeanne Richard [b], Catherine Souty-Grosset [b], Karima Nasri-Ammar [a]

[a] Université Tunis El Manar, Faculté des Sciences de Tunis, Unité de recherche de Bio-Ecologie et Systématique Evolutive, 2092 Tunis, Tunisia
[b] Université de Poitiers, UFR Sciences fondamentales et appliquées, Laboratoire Ecologie et Biologie des interactions UMR CNSR 7267, Equipe Ecologie Evolution Symbiose, Poitiers, France

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ABSTRACT

Terrestrial isopods (Oniscidea) are crustaceans whose ancestors have left the water to conquer land even in arid regions where *Hemilepistus reaumurii* is living. This species is the only terrestrial isopod conducting a real sub-social life as a monogamous semelparous species forming families. The chemical signature of five family units from this population was investigated by gas chromatography. Results showed highly significant differences among the family units according to: (i) the cuticular chemical profiles which confirm that the cuticle is one of the most important organs involved in family chemical signature and recognition; (ii) the cuticular chemical distances and (iii) the faeces chemical profiles which suggest that these droppings help individuals of the same family to find their burrows and deter intruders. Moreover no significant correlation was shown between faeces chemical distance and the distance between burrows from where the family units were collected.

1. Introduction

In crustaceans, chemical signals play an important role during various life stages and according to the habitat (Thiel and Breithaupt, 2011). The terrestriality often implies land marking to display chemical signals by depositing gland secretion, urine or faeces into the substratum (Thiel and Breithaupt, 2011). Aggregates of individuals also produce stronger chemical signals. Moreover the evolution of the social organization complexity is associated with an evolution of the chemical communication between congeners to maintain the group cohesion (Wyatt, 2005; Richard and Hunt, 2013). Communication between congeners of a social group is indispensable to define the group membership, to coordinate activities and identify individuals and their roles in society (Wyatt, 2005).

Terrestrial isopods are crustaceans whose ancestors have left the water to conquer land. Most species are gregarious, and their burrows or communal dwellings exhibit kin or species-specific scents. From all the isopods studied so far, *Hemilepistus reaumurii* (Milne-Edwards, 1840) is one of the few Oniscidea that conducts a real sub-social life (Linsenmair, 1985b, 2007; Schildknecht et al., 1988). This isopod exhibits one of the highest levels of terrestrial adaptation (Wägele, 1989) because of its capability to live in desert. Among the defined seven degrees of sociality levels (Wilson, 1971), it belongs to the second level (Wheeler, 1928; Michener, 1953; Linsenmair, 1985b).

Hemilepistus reaumurii is a monogamous species in which pairs together with their progeny form strictly exclusive family units. In terms of ecological impacts, this desert isopod is considered as the most efficient herbivore and detritivore of the arid regions of North Africa and Asia Minor (Linsenmair, 1974; Schmalfuss, 1984; Wieser, 1984; Warburg et al., 1984; Coenen-Stass, 1984). It affects soil erosion, desalinization and decomposition process by surface deposition of faeces which contain high amounts of mineral soil and relatively high concentrations of soluble salt and organic carbon (Shachak and Yair, 1984). It shows homing behaviour towards its burrow; the average foraging excursion is about 2–6 m, the longest distance being 20 m (Hoffmann, 1984). Linsenmair (1984) showed that the final identification of the burrow was related to a ‘family badge’, also called family odour, which is a mixture of compounds from all family members that enables each member of

* Corresponding author.
E-mail address: ayari.anas88@gmail.com (A. Ayari).

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the family to identify its burrow. It is likely that signature mixtures, as they involve learning, are processed differently from pheromones though this is still not fully understood (Wyatt, 2010). Moreover *H. reaumurii* uses its faeces to build an embankment around the burrow entrance in the form of a ring used as nest marking e.g. as a landmark for burrow recognition (Linsenmair, 1985a). In this semelparous annual species, the yearly life cycle (only one offspring followed by the death of parents) has been investigated by Shachak (1980), Shachak and Yair (1984) in the Negev desert (Palestine), Kacem and Rezig (1995) and Nasri et al. (1996) in Fatnassa (Tunisia). The locomotor rhythm in *H. reaumurii* has been studied by Nasri-Ammar et al. (2015). These authors showed that individuals of *H. reaumurii* exhibited a seasonal variation of its locomotor activity rhythm controlled by an endogenous circadian period.

Linsenmair (1985b) described how the species has highly developed individual and kin identification and recognition systems. In this desert isopod, the cohesion of family units is based on the existence of a system of individual or family specific signals. From behavioural experiments, the specificity of these signals was suggested to be determined genetically (Holdich, 1984; Linsenmair, 1972, 1984, 1985b). The headquarters of this communication system is located at the apical chemoreceptor cones of the last antennal segment (Seelinger, 1977, 1983). Schildknecht et al. (1988) analyzed for the first time this highly family-specific recognition from the chemical point of view: pheromonal compounds were extracted from surface washings of individuals and also from their exuvia. They found that the discriminators are strongly polar, practically non-volatile compounds of low molecular weight and can easily be transferred from one individual to another by direct contact. Since that work, nothing else was continued and no chemical analysis of faeces was performed.

However Hansson et al. (2011) highlighted how *H. reaumurii* is an interesting model system for chemical ecology and kin recognition. According to Breithaupt and Thiel (2011), their chemical signatures need to be more studied in order to understand how family members recognize each other and defend their burrows against non-related individuals.

We hypothesise that: (i) cuticular compounds of *H. reaumurii* are involved in kin recognition; (ii) faeces chemical compound are involved in nestmate recognition; and (iii) cuticular chemical distance increases proportionally with the distance between burrows, which support the hypothesis that the composition of cuticular compounds produced by individuals of the same family is genetically determined (Holdich, 1984; Linsenmair, 1972, 1984, 1985a, 1985b).

The present work aims to study the family network recognition in the subsocial xerophilous species *H. reaumurii* considering both cuticle and faeces of individuals sampled during the growth period of surface active offspring.

2. Materials and methods

2.1. Study area

The present study was conducted in Bchachma locality (35°49′N–10°10′E) near Kairouan (Tunisia) at an altitude of about 23 m (Fig. 1). The study area, situated in the marginal area of a salt lake which is covered by small dunes called hillocks covered by halophytic plants such as *Halocnemum strobilaceum* and *Suaeda mollis* (Ayari et al., 2016). Temperatures are usually mild in winter (range 6°C–17 °C) and highest in summer months (range 25°C–42 °C). The average annual rainfall is about 26 mm (range 6.7–49.2) and the driest months are July and August. Kairouan climatic data were taken from http://french.wunderground.com/ website.

2.2. Biological model

Unlike other terrestrial isopods, which are lucifuginous, *Hemilepistus reaumurii* exhibits a daily activity pattern and its above ground activity was observed from February to November (Shachak, 1980; Ayari, unpublished data). At the end of this month individuals entered into a quiescence period and remained underground in their burrows during December and January (Shachak, 1980; Ayari, unpublished data). The dispersal phenophase starts at the end of February and is followed by the pair formation period occurring from the end of March until April (Ayari, unpublished data). The reproduction period begins in May and is characterized by the presence of a reproductive female which realize its only brood per life cycle. In June and July, a difference in size between adults and juveniles is clearly observed. From August to November the growth of juvenile is increases whereas a high percentage of mortality of adults was noted (Fig. 2) (Ayari, unpublished results).

Five family units of *H. reaumurii* (Family A ($N = 5$), Family B ($N = 9$), Family C ($N = 10$), Family D ($N = 12$), Family E ($N = 9$)), were collected as they exited their burrows in November 2013 coinciding with the juvenile growth period (Fig. 3). Faeces deposits were collected from the entrance of each family burrow. The exact location of the burrows from where specimens were collected is shown in Fig. 3. Many other burrows of other families were also present between our chosen burrows.

2.3. Chemical analysis

We compared the chemical profiles between *H. reaumurii* individuals per family unit and between units. Each individual was immersed in 4 ml of dichloromethane for 24 h. We also did chemical extraction of faeces collected at the entrance of the five nests. For each nest we prepared five extracts of 200 mg that were immersed in 200 μl of dichloromethane during 24 h (in total $N = 25$). Extracts were stored at −20 °C until analyzed. Before analysis, any remaining dichloromethane was allowed to evaporate, and dried extracts were dissolved again in 50 μl of dichloromethane. Two microliters of these mixtures were injected into an Agilent Technologies 7890 A gas chromatograph, equipped with an Agilent capillary column DB-5 (30 m × 0.250 mm, film = 0.50 μm). The initial temperature was 100 °C for 2 min with a subsequent gradual increase of 5 °C/min until 300 °C and maintained for 10 min.

Chemical analyses were similar to those described by Richard et al. (2007).

2.4. Statistical analysis

Qualitative chemical profiles were compared using GC peak integration and the relative abundance of the various peaks. To test for differences in chemical profiles between family individuals and also between faeces of the different nest, we used a stepwise discriminate analyses using (Statistica 6.0; Statsoft Inc.) as in Richard et al. (2007). Individual cuticular chemical distance and faeces chemical distance were respectively compared with geographical distance between nests with Pearson's correlations.

3. Results

3.1. Cuticular chemical signature

The following study was performed to determine if the changes

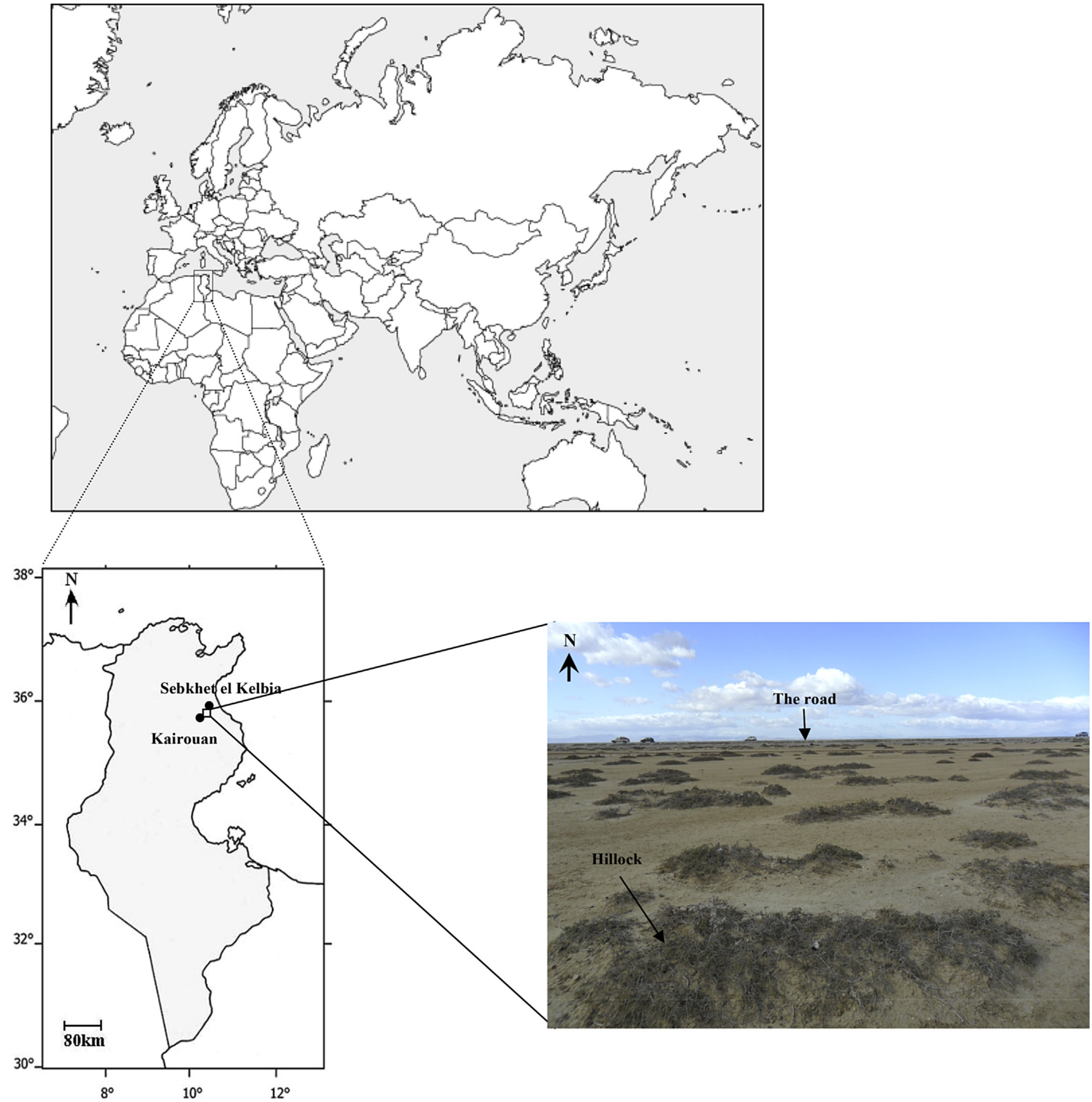

Fig. 1. Location of the study site Bchachma locality (35°49′N–10°10′E).

in chemical profiles associated with cuticles are the origin of the family chemical signature. The discriminate analyses (Fig. 4) revealed that four variables explain 100% of compensation (Variable 1 = 51%; Variable 2 = 25%; Variable 3 = 13%; Variable 4 = 11%). The global analysis revealed a highly significant difference between the chemical profiles of the five family units ($F_{36.12} = 10.639$, $P < 0.00001$. Cuticular chemical distances between the five families of *Hemilepistus reaumurii* were highly significantly different ($MD > 15.19$; $P < 0.0001$).

Furthermore cuticular chemical distance was significantly positively correlated with the distance between the burrows from where the five families were collected ($R^2 = 0.545$; $P = 0.015$) (Fig. 6a).

3.2. Faeces chemical signature

The discriminate analyses of faeces (Fig. 5) revealed that two variables explain 90% of compensation (Variable 1 = 55%; Variable 2 = 35%). The global analysis revealed a highly significant difference between the chemical profiles of the five family units ($F_{44.36} = 19.55$, $P < 0.00001$. Faeces chemical distances between the five family units of *Hemilepistus reaumurii* were significantly

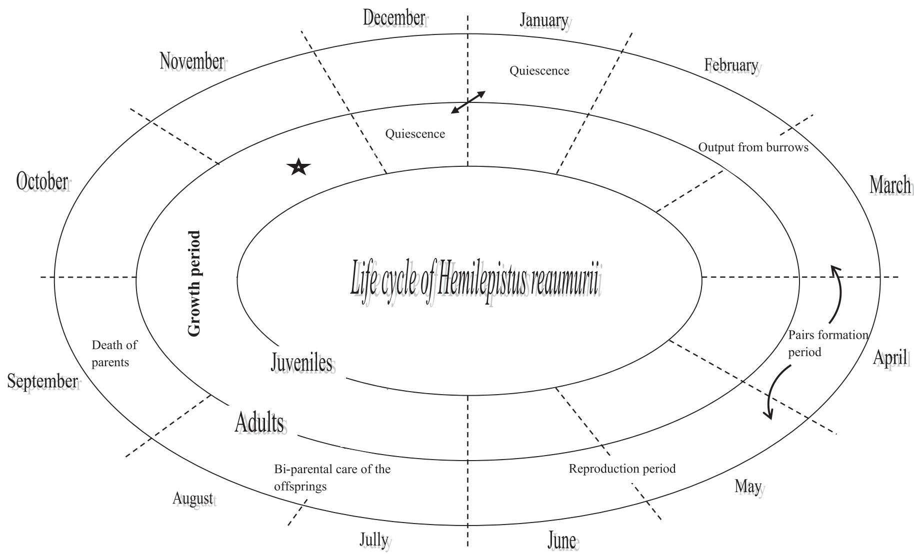

Fig. 2. Life cycle of *Hemilepistus reaumurii* from Bchachma locality ★ Sampling period.

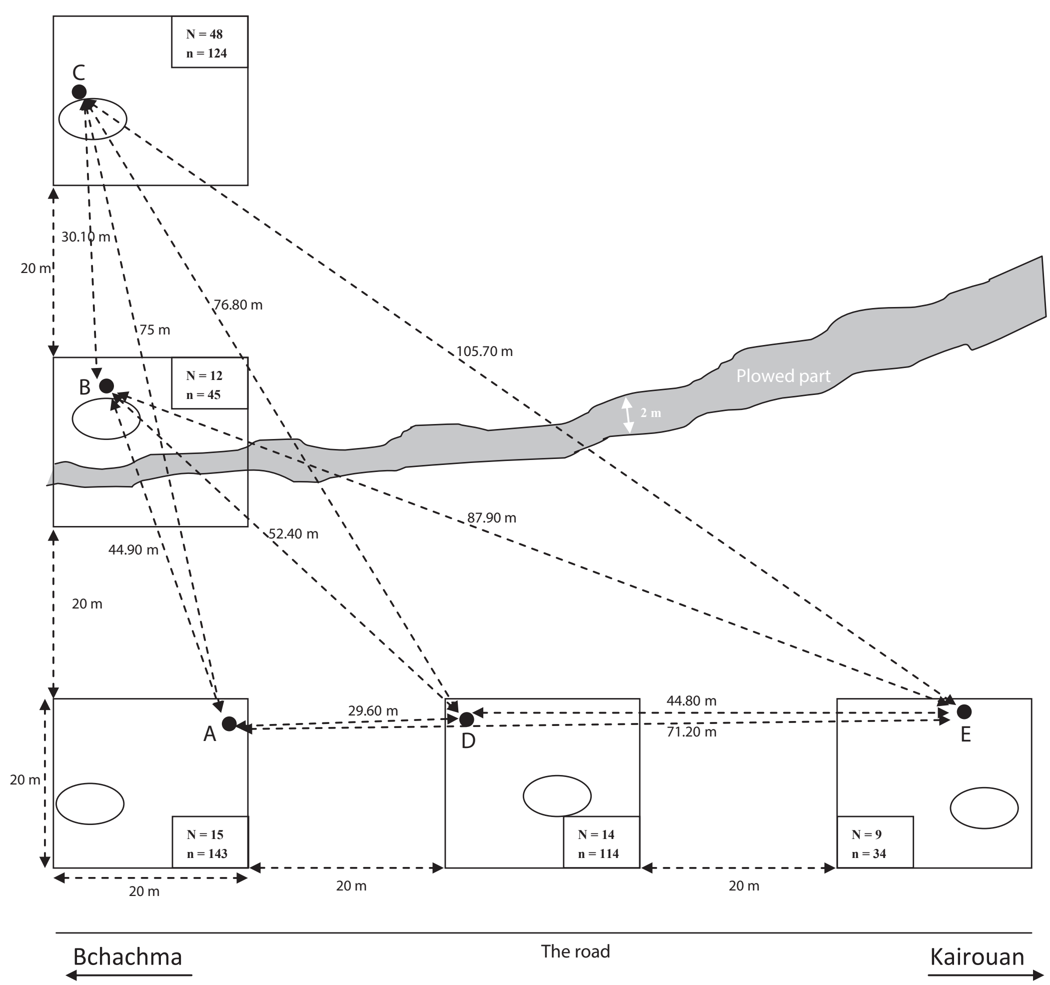

Fig. 3. Diagram showing the field distances between burrows from which the five families and faeces were collected (A, B, C, D and E). ● Marked hillock (Localisation of the studied sections). ◯ Exact location of the burrow from which the family units and faeces were collected. N = Total number of hillocks during the studied month. n = Total number of burrows during the studied month.

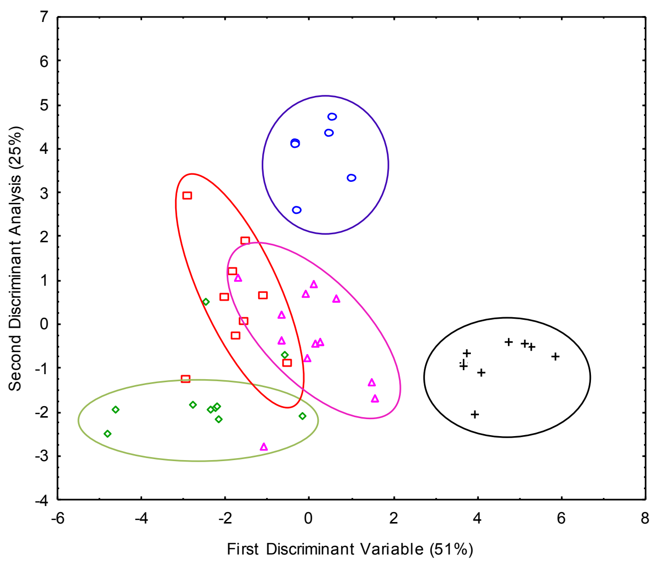

Fig. 4. Discriminate analysis of the five family unit's cuticular compounds of *Hemilepistus reaumurii*. Family unit collected from: ○ section A, □ from section B, ◊ from section C, △ from section D, +d from section E.

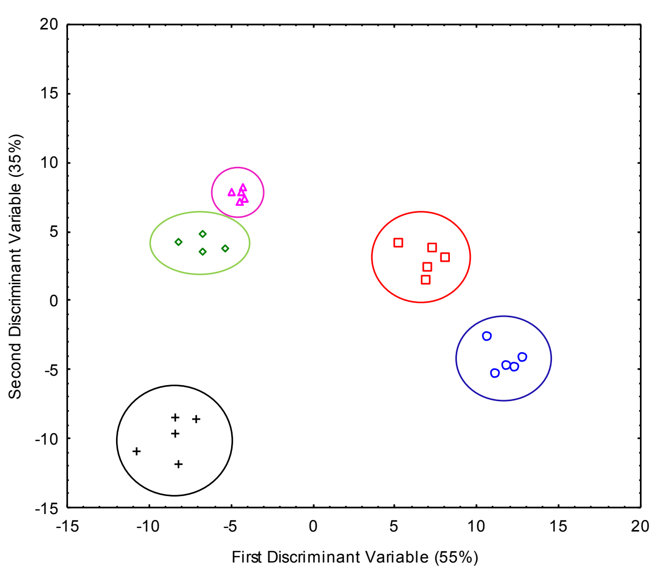

Fig. 5. Discriminate analysis of the five family unit's faeces compounds of *Hemilepistus reaumurii*. Family unit faeces collected from the burrow: ○of section A, □ of section B, ◊ of section C, △ of section D, + of section E.

different ($MD > 42.9$; $P < 0.02$).

Furthermore no significant correlation was shown between faeces chemical distance and the distance between burrows from where the five family units were collected ($R^2 = 0.000$; $P = 0.978$) (Fig. 6b).

4. Discussion

Family recognition of the subsocial desert detritivore *Hemilepistus reaumurii* collected from the zone of Bchachma has been tested. Our study demonstrated a highly significant difference between the cuticular chemical profiles of the five families, confirming that the cuticle is one of the most important organs involved in family chemical signature and recognition. Therefore, these results confirm the hypothesis that cuticular compounds of

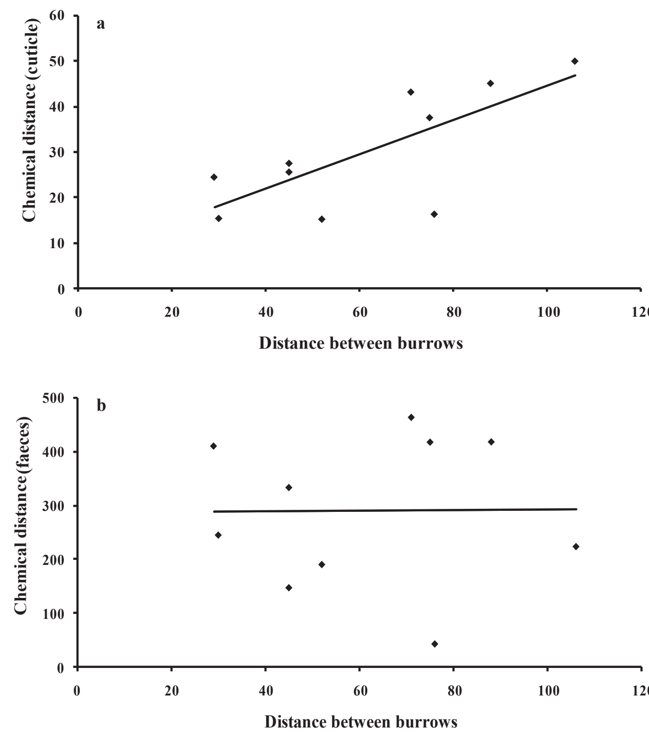

Fig. 6. Correlation of the distance between burrows and the chemical distance of individuals' cuticle (a) ($R^2 = 0.545$; $P = 0.015$) and faeces (b) ($R^2 = 0.000$; $P = 0.978$).

H. reaumurii are involved in kin recognition.

Furthermore, results showed that cuticular chemical distances between the five families of *H. reaumurii* were highly significantly different suggesting that each family of *H. reaumurii* has its own specific cuticular chemical signature. Linsenmair (1987, 2007) in a behavioural study, mentioned that the desert isopod *H. reaumurii* showed a recognition of its family members by identifying the smell (chemical compounds) of their cuticle with a direct contact. These cuticular chemical compounds seem to be a mixture of compounds specific to each family (Schildknecht et al., 1988). For most social insects, congener discrimination is generally based on a complex mixture of cuticular hydrocarbons (Boomsma and Franks, 2006). Mixtures of cuticular hydrocarbons are various; however, generally each species has its own profile of hydrocarbons (Richard and Hunt, 2013). Species chemical profile is genetically determined and can differ also at the individual level. Additionally, individual chemical odour can also change over time depending on the environment (Richard et al., 2004, 2012) and is homogenized between colony members by social interactions (Dahbi et al., 1999).

Chemical signatures correspond to mixtures of very small volatile chemical compounds that may be transmitted between individuals through direct contact. In fact the perception of cuticular chemical compounds is generally possible within a short distance, but may require direct contact that will allow the perception of components without or with low volatility in honey bees (Brockmann et al., 2003) and in ants (Brandstaetter et al., 2008). However analyses at high temperatures showed volatile properties for alkanes composed of up to 29 carbon atoms in foraging bees (Schmitt et al., 2007). Schildknecht et al. (1988) suggest that the compound most involved in the chemical communication in *H. reaumurii* could be terpenoids.

The specific smell of each family allows individuals to distinguish family members from intruders and can trigger defensive and aggressive behaviours to these intruders. Defensive behaviour seen between *H. reaumurii* individuals in the field were generally used to protect burrows and offspring against intruders. The ability to discriminate between kin and non-kin promotes the evolution of sociality. Such behaviour could be a precursor compared with the nestmate recognition between individuals with different level of kinship in social insects. Nestmate recognition prevents alien colony member entry to their nest and only allows individuals belonging to their colony to entry (Richard and Hunt, 2013). Both kin and nestmate recognition and discrimination are important to protect resources and brood. In *H. reaumurii* both parents protect the burrow entrance until they die. Studying the ultrastructure of *H. reaumurii* cuticle, Ayari et al. (2016) have demonstrated the existence of secretory canals serving as potential transporters of chemical substances from the exocrine glands to the surface of the cuticle.

Our results showed that cuticular chemical distance and distance between burrows from the five families were significantly positively correlated. These results confirm the hypothesis that cuticular chemical distance increases proportionally with the distance between burrows. Our results strongly support the hypothesis that the composition of cuticular compounds produced by individuals of the same family is genetically determined (Holdich, 1984; Linsenmair, 1972, 1984, 1985a, 1985b). Large distances (over 100 m) i.e. between burrows minimize the chances of encounters between individuals of different families: the higher the geographical distance, the lower is the probability that individuals may form a mating pair. Genetic analysis to determine individual relatedness would be necessary to totally demonstrate individual dispersion and mating strategy in this species. Moreover, even if individuals of the same family differ in chemical profile, they form a family-specific signature. The signature is the result of chemical transfer between family members by direct contact (Hansson et al., 2011) as observed in social insects.

Faecal analysis, studied for the first time, revealed highly significant differences between the chemical profiles of the five families which prove that each family has its specific faeces odour. These findings confirm the hypothesis that faeces chemical compound are involved in nestmate recognition. In fact, faeces deposited at the entrance of burrows are used as a marking system of the family burrow (Linsenmair, 1985a). These droppings help individuals of the same family to find their burrows and warn intruders. Linsenmair (2007) mentioned that other species mark their nest entrance using deposited faeces. For example, before starting foraging excursions, the xeric isopod *Porcellio albinus* scrape out sand from the burrow floor and pile it up before the entrance (Medini-Bouaziz, 2002; Linsenmair, 2007). This sand pile is much larger than the burrow entrance itself, thus greatly facilitating the relocation of its burrow by a homing isopod (Linsenmair, 2007). Linsenmair (1987) mentioned that *H. reaumurii* piles up a permanent, conspicuous faeces embankment around its burrow entrance, marked with a family-specific signature. These results are similar to that described in many species of insects. For example, in ants, the burrow substrate is also involved in the smell of the colony (Pfennig et al., 1983; Gamboa et al., 1986; Singer and Espelie, 1996).

Faeces and cuticular chemicals present different profiles. Our results showed that faeces chemical distance and distance between burrows of the five families were not correlated (a new finding). That could be explained by the fact that faeces composition was dissimilar to that of cuticle. In addition to the chemical compound (Schildknecht et al., 1988) used for recognition and chemical communication, faeces contain digestive material, soil substrate, bacteria and dietary compounds shared between family members. This material is common for all individuals of this population which makes faeces chemical distance and distance between burrows not correlated.

Comparisons between cuticular and faeces chemical signatures of the monogamous couples of *H. reaumurii* at the start and end of the pair formation period is under study in order to better understand the function of chemical recognition during the life cycle of this species. Another aim is to identify the blend of compounds used for nest marking; also to better understand whether they learn the location or the chemical odour, or both?

5. Conclusion

Our finding highlights the existence of a family cuticular and faeces chemical signature for *H. reaumurii*. Furthermore, chemical distances increase proportionally with the distance between burrows. These results may suggest that individuals of *H. reaumurii* avoid consanguinity during the pair formation period. In other hand, the existence of a cuticular and faeces chemical signature allows congeners to identify their nest, to recognize and to find their burrows. This will lead to; (i) increase the reproductive success, (ii) better protect the offspring and (iii) protect the family burrow which is crucial for the survival of this species in an arid environment.

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References

Ayari, A., Raimond, M., Souty-Grosset, C., Nasri-Ammar, K., 2016. Hierarchical organization of the cuticle of the subsocial desert isopod; *Hemilepistus reaumurii*. J. Struct. Biol. 193, 115–123.
Boomsma, J.J., Franks, N.R., 2006. Social insects: from selfish genes to self-organization and beyond. Trends Ecol. Evol. 21, 303–308.
Brandstaetter, A.S., Endler, A., Kleineidam, C.J., 2008. Nestmate recognition in ants is possible without tactile interaction. Naturwissenschaften 95, 601–608.
Breithaupt, T., Thiel, M., 2011. Chemical Communication in Crustaceans. Springer Press, New York. http://dx.doi.org/10.1007/978-0-387-77101-4_1.
Brockmann, A., Groh, C., Frohlich, B., 2003. Wax perception in honeybees: contact is not necessary. Naturwissenschaften 90, 424–427.
Coenen-Stass, D., 1984. Observation on the distribution of the desert woodlouse *Hemilepistus reaumuri* (Oniscidea, Isopoda, Crustacea). In: Sutton, S.T., Holdish, D.M. (Eds.), Biology of Terrestrial Isopods, Symposia of the Zoological Society of London, 53. Cambridge University Press, pp. 369–380.
Dahbi, A., Hefetz, A., Cerda, X., Lenoir, A., 1999. Trophallaxis mediates uniformity of colony odor in *Cataglyphis iberica* ants (Hymenoptera, Formicidae). J. Insect Behav. 12, 559–567.
http://french.wunderground.com/.
Edwards, M.H., 1840. Filter-feeding by the marine boring isopod, *Sphaeroma Quoyanum*. Crustaceana 28, 7–10.
Gamboa, G., Reeven, H., Ferguson, D., Wacker, T., 1986. Nestmate recognition in social wasps: the origin and acquisition of recognition odours. Anim. Behav. 34, 685–695.
Hansson, B.S., Harzsch, S., Knaden, M., Stensmyr, M., 2011. The neural and behavioral basis of chemical communication in terrestrial crustaceans. In: Breithoupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans, pp. 149–173.
Hoffmann, G., 1984. Orientation behavior of the desert woodlouse *Hemilepistus reaumuri*: adaptations to ecological and physiological problems. In: Sutton, S.T., Holdish, D.M. (Eds.), Biology of Terrestrial Isopods, Symposia of the Zoological Society of London, 53. Cambridge University Press, pp. 405–422.
Holdich, D.M., 1984. The cuticular surface of woodlice: a search for receptors. In: Sutton, S.T., Holdish, D.M. (Eds.), Biology of Terrestrial Isopods, Symposia of the Zoological Society of London, 53. Cambridge University Press, pp. 9–48.
Kacem, H., Rezig, M., 1995. Cycle biologique d'*Hemilepistus reaumuri* (Audouin et Savigny, 1826) (Crustacé, Isopode, Oniscoïde). Bull. Soc. Sc. Nat. Tunis. 24, 56–65.
Linsenmair, K.E., 1972. Die Bedeutung familienspezifischer "Abzeichen" fûr den Familienzusammenhalt bei der sozialen Wiistenassel *Hemilepistus reaumuri* (Crustacea, Isopoda, Oniscoidea). Z. Tierpsychol 31, 131–162.
Linsenmair, K.E., 1974. Some adaptations of the desert woodlouse *Hemilepistus reaumuri* (Isopoda, Oniscoidea) to desert environment. Verhandlungen Ges. für Ökologie 4, 183–185.

Linsenmair, K.E., 1984. Comparative studies on the social behaviour of the Desert Isopod *Hemilepistus reaumuri* and of a *Porcellio* species. In: Sutton, S.T., Holdish, D.M. (Eds.), Biology of Terrestrial Isopods, Symposia of the Zoological Society of London, 53. Cambridge University Press, pp. 423–454.

Linsenmair, K.E., 1985a. The influence of landmarks on the systematic search behaviour of the desert isopod *Hemilepistus reaumuri*. Behav. Ecol. Sociobiol. 4, 325–334.

Linsenmair, K.E., 1985b. Individual and family recognition in subsocial arthropods, in particular in the desert isopod *Hemilepistus reaumuri*. In: Hölldobler, B., Lindauer, M. (Eds.), Fortschritte der Zoologie 31. Experimental Behavioral Ecology and Sociobiology. G. Fisher Verl, Stuttgart, pp. 411–436.

Linsenmair, K.E., 1987. Kin recognition in subsocial arthropods, in particular in the desert isopod *Hemilepistus reaumuri*. In: Fletcher, D.J.C., Michener, C.D. (Eds.), Kin Recognition in Animals. John Wiley and Sons Ltd, Chichester, pp. 121–208.

Linsenmair, K.E., 2007. Sociobiology of terrestrial isopods. In: Duffy, J.E., Thiel, M. (Eds.), Evolutionary Ecology of Social and Sexual Systems – Crustaceans as Model Organisms. Oxford University Press, New York, pp. 339–364.

Medini-Bouaziz, L., 2002. Systématique, biologie et biogéographie du genre *Porcellio* en Tunisie (Crustacés, Isopodes Oniscidea). Thèse de l' Université de Tunis el Manar, pp. 1–228.

Michener, C.D., 1953. Problems in the development of social behavior and communication among insects. Trans. Kans. Acad. Sci. 56, 1–15.

Nasri, K., Juchault, P., Mocquard, J.P., Souty-Grosset, C., 1996. Reproduction saisonnière chez *Hemilepistus reaumuri* (Audoin, 1826), isopode terrestre des zones semi-arides. Crustaceana 69, 223–236.

Nasri-Ammar, K., Jelassi, R., Ayari, A., Morgan, E., 2015. Seasonal changes of locomotor activity patterns in the desert isopod *Hemilepistus reaumuri*. Biol. Rhythm. Res. 47, 1–18.

Pfennig, D.W., Reeve, H.K., Shellman, J.S., 1983. Learned component of nestmate discrimination in workers of a social wasp, *Polistes fuscatus* (Hymenoptera: Vespidae). Anim. Behav. 31, 412–416.

Richard, F.J., Hunt, J.H., 2013. Intracolony chemical communication in social insects. Insectes sociaux 60, 275–291.

Richard, F.J., Hefetz, A., Christides, J.P., Errard, C., 2004. Food influence on colonial recognition and chemical signature between nestmate in the fungus growing ant *Acromyrmex subterraneus*. Chemoecology 14, 9–16.

Richard, F.J., Poulsen, M., Drijfhout, F., Jones, G.R., Boomsma, J.J., 2007. Specificity in chemical profiles of workers, brood and mutualistic fungi in Atta, *Acromyrmex*, and *Sericomyrmex fungus*-growing ants. J. Chem. Ecol. 33, 2281–2292.

Richard, F.J., Holt, H.H., Grozinger, C.M., 2012. Effects of immuno-stimulation on social behavior, chemical communication and genome-wide gene expression in honey bee workers (*Apis mellifera*). BMC Genomics 13, 558.

Schildknecht, H., Eßwein, U., Hering, W., Blaschke, C., Linsenmair, K.E., 1988. Diskriminîerungspheromone der sozialen Wüstenassel *Hemilepistus reaumuri*. Z. Naturforsch 43c, 613–620.

Schmalfuss, H., 1984. Eco-morphological strategies in terrestrial isopods. In: Sutton, S.T., Holdish, D.M. (Eds.), Biology of Terrestrial Isopods, Symposia of the Zoological Society of London, 53. Cambridge University Press, pp. 49–63.

Schmitt, T., Herzner, G., Weckerle, B., Schreier, P., Strohm, E., 2007. Volatiles of foraging honeybees *Apis mellifera* (Hymenoptera: Apidae) and their potential role as semiochemicals. Apidologie 38, 164–170.

Seelinger, G., 1977. Der Antennenendzapfen der tunesischen Wiistenassel *Hemllepistus reaumuri*, ein komplexes Sinnesorgan (Crustacea, Isopoda). J. Comp. Physiol. 11, 95–103.

Seelinger, G., 1983. Response characteristics and specificity of chemoreceptors in *Hemilepistus reaumuri* (Crustacea, Isopoda). J. Comp. Physiol. A 152, 219–229.

Shachak, M., 1980. Energy allocation and life history of the desert isopod *Hemilepistus reaumuri*. Oecologia 45, 404–413.

Shachak, M., Yair, A., 1984. Population dynamics and role of *Hemilepistus reaumuri* (Audouin and Savigny) in a desert ecosystem. In: Sutton, S.T., Holdish, D.M. (Eds.), Biology of Terrestrial Isopods, Symposia of the Zoological Society of London, 53. Cambridge University Press, pp. 295–314.

Singer, T.L., Espelie, K.E., 1996. Nest surface hydrocarbons facilitate nestmate recognition for the social wasp, Polistesmetricus say (Hymenoptera, Vespidae). J. Insect Behav. 9, 857–870.

Thiel, M., Breithaupt, T., 2011. Chemical communication in Crustaceans: research challenges for the twenty-first century. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans, pp. 3–21.

Wägele, J.W., 1989. Evolution und phylogenetisches system der Isopoda: stand der Forschung und neue Erkenntnisse. Zoologica 140, 1–262.

Warburg, M.R., Linsenmair, K.E., Bercovitz, K., 1984. The effect of climate on the distribution and abundance of isopods. In: Sutton, S.T., Holdish, D.M. (Eds.), Biology of Terrestrial Isopods, Symposia of the Zoological Society of London, 53. Cambridge University Press, pp. 339–367.

Wheeler, W.M., 1928. The Social Insects: Their Origin and Evolution. Harcourt Brace, New-York (NY).

Wieser, W., 1984. Ecophysiological adaptations of terrestrial isopods: a brief review. In: Sutton, S.T., Holdish, D.M. (Eds.), Biology of Terrestrial Isopods, Symposia of the Zoological Society of London, 53. Cambridge University Press, pp. 247–265.

Wilson, E.O., 1971. The Insect Societies. Belknap, Cambridge, MA, p. 548.

Wyatt, T.D., 2005. Pheromones: convergence & contrasts in insects & vertebrates. In: Mason, R.T., Le Master, M.P., Müller-Schwarze, D. (Eds.), Chemical Signals in 10 Vertebrates. Springer Press, NY, pp. 7–20.

Wyatt, T.D., 2010. Pheromones and signature mixtures: defining species-wide signals and variable cues for individuality in both invertebrates and vertebrates. J. Comp. Physiol. A 196, 685–700.