Article

Differential marking, investigation and motor activity in presence of conspecific odours differing on their population of origin in bank voles

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Abstract

Odours emitted by rodent species convey cues about their overall body conditions and provide valuable information intervening in many aspects of their social relationships such as territorial and mating activities. Although bank vole is one of the primary models for studying chemical communication in wild rodents, literature is scarce about its reactivity to odours of conspecifics from its population compared to those of conspecifics from a different population.

Here we tested the effect of the population of origin on the behaviour of wild bank voles (*Myodes glareolus*) through 30min tests in laboratory. We observed both males and females differential marking (i.e. by urine or glandular secretions), motor activity and investigation (i.e. sniffing events) in presence of conspecific whole body odours coming from either the Same Population of Origin (SPO) or from a Different Population of Origin (DPO).

Our results showed that both male and female bank voles react differently to odours of conspecifics according to the population of origin of the latter. Both motor activity and marking were more important when voles were confronted to odours from DPO donors than SPO ones. These effects were independent of the sex of the subjects. Moreover, male subjects tended to investigate more odours from DPO conspecifics than odours from SPO ones. Causes underlying apparent between-populations differences in the bank voles' body odours are discussed.

Keywords *Myodes glareolus*; population recognition; wild rodents; chemical signals; olfactory communication.

1 Introduction

Chemical signals are probably the most widespread means of communication of virtually all mammal societies other than primates. They affect almost all aspects of their social biology in providing information about identity (e.g. species, kinship, sex, age) and overall body conditions (e.g. dominance, reproductive status,

health) (Alberts, 1992; Brown and MacDonald, 1985; Hurst, 2005; Schellinck et al., 2008; Seyfarth and Cheney, 2003; Wyatt, 2003).

To what concerns social species, the population membership is another valuable information that could be given and obtained through olfactory cues. A population is defined by a collection of inter-breeding organisms of a particular species living in the same place and time (Miller and Ricklefs, 1999). It is indeed of great interest for individuals to detect the presence of a novel immigrant in their population through its odorant cues, before encountering it. Hence, it could allow to avoid surpopulation as well as members depletion by chasing or accepting new immigrants respectively (Krebs and Davies, 1993). But also, it could help to choose the best mates and to prevent agonistic encounter if the immigrant turns out to be of interest or stronger respectively (Hoffmeyer, 1982; Rich and Hurst, 1998).

Bank vole, *Myodes glareolus* Schreber 1785, is one of the primary models for studying chemical communication in wild rodents; thus, much information is available about that species' discrimination and recognition abilities (Kruczek, 1994; Kruczek, 2007; Kruczek and Golas, 2003; Lopucki and Szymroszczyk, 2003; Rozenfeld and Rasmont, 1991). However, as far as the authors know, its reactivity to odours of conspecifics from its population of origin compared to those from a different population has never been tested under laboratory conditions. Nonetheless, such abilities of population discrimination through olfactory cues have already been described in other rodent species such as mole rat, *Spalax ehrenbergi* (Heth et al., 2002); steppe mouse, *Mus specilegus* (Heth et al. 2001); and house mouse, *Mus musculus* (Cox, 1989). Those studies establish therefore a valuable background for the present experiment.

In this paper, we report on a behavioural experiment under laboratory conditions with wild born bank voles. We aimed to study their reactivity (i.e. marking, motor activity, and investigation) to conspecific odours differing on their population of origin without any habituation procedure. Bank vole is a wild rodent widespread in Europe (Corbet and Harris, 1991). It forms intersexual groups of close relatives in winter, consisting of two to four females with some of their last litter young and one or two males. During the breeding season, females become territorial and mature males form hierarchical groups and compete for mates (Gipps, 1985). Their urine, faeces, saliva and other glandular secretions are their main vehicles of information for intraspecific communication and behavioural interaction (Marchlewska-Koj, 2000; Osipova and Rutovskaya, 2000).

We predicted that voles react more intensively (i.e. more marking, activity and investigation) when confronted to odours of conspecifics from a Different Population of Origin (DPO) than to conspecific odours from their own population (i.e. Same Population of Origin (SPO)), since DPO odours represent novelty (Carter et al., 1988; Johnston et al., 1997).

2 Method

2.1 Trapping

During October 2004, two trapping sessions were performed in two very distant fields (i.e.>100km). One was located in the Cedrogne forest (50°12'N-5°47'E; Houffalize, Ardenne, south east Belgium) and the other one in the Lauzelle forest (50°40'N-4°37'E; Louvain-la-neuve, Walloon Brabant, central Belgium). Both fields had a dense, but low vegetation cover representing prime bank vole habitat (Geuse, 1985).

A 30 x 30m grid containing 40 Ugglan traps was established in each site. Ugglan is a multiple-capture live-trap with a contra-weight platform device. Once the platform lowers, the animal can go to the bait and when

leaving the platform, it goes up and the animal is trapped (Jacob et al., 2002). Traps were placed at approximately 5m distance in most suitable zones (e.g. along logs, under branches, ferns, etc…) and baited with muesli and apple for the hydro-supplementation. Traps were checked twice a day after the activity peaks of voles (i.e. at dawn and at dusk) (Lode 1995). Sixteen adult bank voles (8 males and 8 females) were caught in each field. The 32 individuals selected overall were still in reproductive status but females were non-lactating.

2.2 Animals and housing conditions

The voles were housed in individual polyurethane cages (34 x 17 x 19cm; L x W x H) at 20°± 2°C and placed in two separated rooms (according to their population of origin). The photoperiod was set in both rooms at 16h light/8h dark (lights on at 07am). Corn and wheat were provided as food, supplemented with a quarter of an apple and some dandelion leaves twice a week. Water was available *ad libitum*. Sawdust, small branches and paper were supplied as nesting material and changed every two weeks. To enrich their environment and to allow physical exercises, a metal wheel was also provided.

2.3 Experimental procedure

Polyurethane cubes of 1cm side were used as substrate for the olfactory cues. Preliminary to the experiment, each bank vole (N=32) was isolated during four hours in a jar containing 20 cubes. As no particular odour linked to the population of origin has been described so far in literature, the whole body of bank vole was used as the source of olfactory cues. After this period of close contact, the cubes could be considered as impregnated with the whole body odours of the individual. To preserve odour properties, the cubes were stored at -21°C in individual bags (Andrzejewski and Owadowska, 1994). According to the sex and the population of origin of the donor, four different treatment groups were obtained: male and female from the SPO, male and female from a DPO.

From the 16 adult bank voles trapped in each field, 10 (5 males and 5 females) were randomly chosen and used for the experiment. The six remaining were kept as back-up.

The behavioural observations were performed in a Plexiglas® arena (100 x 30 x 45cm; L x W x H) and filmed with a black and white camera hanging over the arena and connected to a video recorder.

Each trial lasted 30 minutes and took place as follows: an impregnated polyurethane cube was fastened in the middle of an A4 sheet of white copy paper, scotched in the centre of the arena. This scotched sheet was considered as the zone of interaction with the target cube. A vole was then introduced in the arena, with a small beaker, but outside the A4 sheet, and filmed during 30 minutes. When time was over, the vole was returned to its individual cage and the sheet of paper was removed from the arena. Between two trials, the arena was thoroughly cleaned with Norvanol® (i.e. Ethanol denatured with ether). The experimenters were permanently wearing rubber gloves that were changed after each trial.

Prior to testing, every tested bank vole was put in the arena with an unscented cube fastened on an A4 paper for 15 minutes. This session aimed to eliminate the effect of novelty (O'Keefe and Nadel, 1978).

Each vole (N=20) was tested 5 times with one cube from each of the 4 treatment groups (i.e. male and female SPO, male and female DPO) for a total of 20 trials. The 5 repeated cubes were picked from 5 different voles, randomly chosen among the 8 donors of the concerned treatment group. So that, one subject was never tested twice with the same donor odour. The rate of testing for each vole alternated from two to three times per week, inducing a minimum interval of 48 hours between each trial. This procedure was set up to prevent habituation and boredom. Although this experimental procedure does not provide direct information about the

chemical structure or composition of the odorants, it does provide useful information about quantification of behavioural reactivity and how animal perceive the odours in terms of discriminable differences between them.

It took 7 weeks for the procedure to be completed with the 20 voles. At the late December 2004, all the individuals (N=32) were released at their respective place of capture in the field.

2.4 Data collection

(1) Marking. Each of the A4 papers was observed under UV and natural lights to count the urine and glandular marks (Desjardins, Maruniak, & Bronson 1973) and the faeces respectively, that were deposited by voles during trials.

Thereafter, the filmed sequences of the 400 trials of 30 minutes were examined and the behavioural events were recorded using the Noldus - The Observer® 5.0 for Windows (Noldus information Technology, Wageningen, The Nederlands). The Observer is a professional package devised for the collection, sequence, analyses and presentation of observational data such as activities, postures, gestures, facial expressions, movements, and social interactions.

The two following behaviours were identified:

(2) Investigation. It was defined by the number of sniffing events exhibited by the subjects towards the cubes. Sniffing is shown when an individual is aroused to explore by olfactory stimulation. The olfactory input affects sniffing activities by regulating the degree of their persistence; the duration being affected by the character of the olfactory stimuli encountered. Thus, known stimuli are contacted only briefly, whereas, unknown stimuli elicit prolonged sequence of sniffing (Todrank et al., 1999; Welker 1964). A sniffing event was recorded when the vole brought its nose on the polyurethane cube and appeared clearly to sniff this one in a sequence of generally 3 to 5 successive nose movements.

(3) Motor activity. Motor activity of the voles during trials was determined by counting the number of entries (i.e. at least with fore paws) on the A4 copy paper containing the impregnated cube. The motor activity is proportional to the arousal induce by the olfactory stimulus (Schapiro and Salas, 1970).

2.5 Statistical analysis

Number of marks counted on the A4 papers, investigation as well as the motor activity of the voles were analysed with ANOVAs of 4 factors (donor origin, donor sex, subject origin, subject sex) without repeated data as the donors were different each time. The null hypothesis stated that the origin of the donor had no effect. Significant differences ($p<0.05$) in behaviours exhibited by voles while submitted to odours from different origins indicate that subjects discriminate between them. The analyses were done with JMP® 7.0 (SAS Institute, Cary, NC), allowing computing ANOVAs with factors greater than 3. *Post-hoc* comparisons of the reactions of voles towards odours of DPO vs SPO males and DPO vs SPO females were made by Tukey-Kramer Hsd Student tests with SAS® 9.1 (SAS Institute, Cary, NC).

3 Results

3.1 Urine and glandular marking

The number of urine and glandular marks laid by the subjects on the zone of interaction during trials, differed with the population of origin of the donor ($F_{12,384}=3.942$; $p<0.0001$) (Fig.1). Comparisons of marks laid on the A4 paper during trials towards DPO versus SPO odours revealed that all subjects marked more when confronted to DPO cubes. However, females from the Lauzelle wood marked less abundantly than other subjects when confronted to female odours (Fig.2).

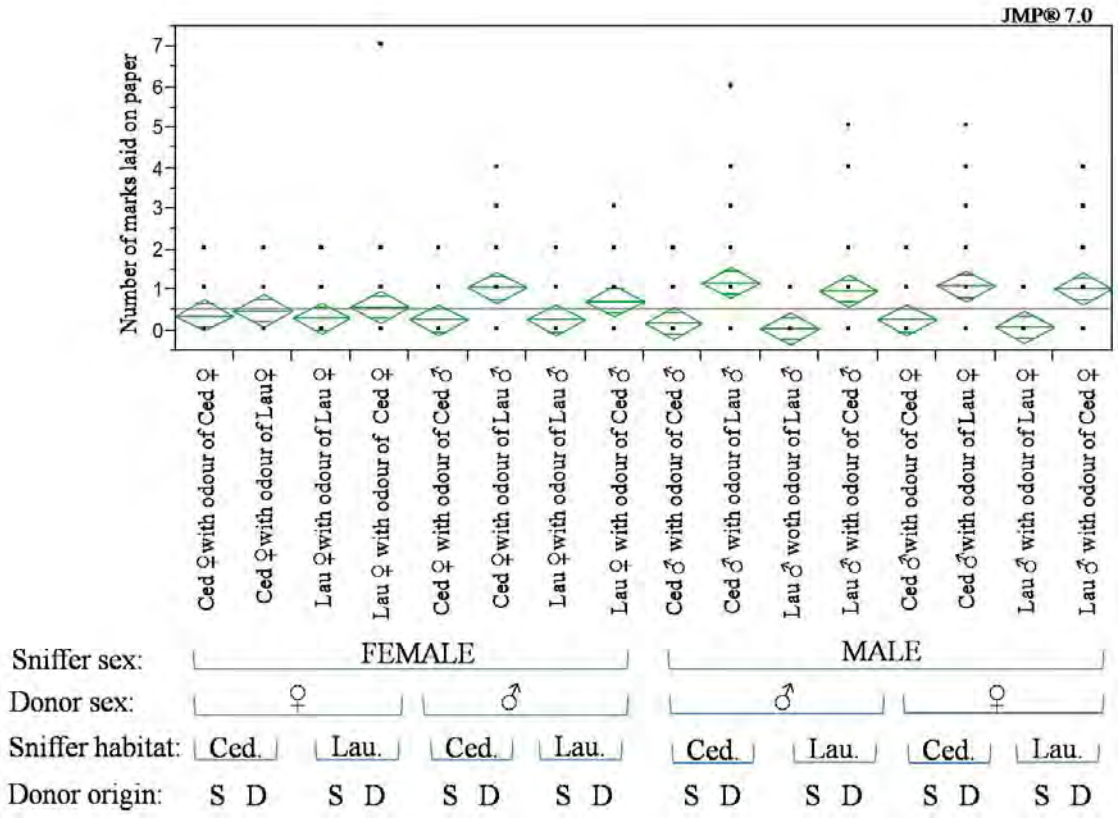

Fig. 1 Number of marks laid on the zone of interaction by male and female voles from the habitats of Cedrogne and Lauzelle confronted to conspecific odours from their population of origin (SPO) and from a different population (DPO) and of same-/opposite-sex. SPO and DPO results were joined side by side for each combination of donor and subject. Diamond pikes are 95% of confidence interval and transverse line is the overall mean. Abbreviates: Lau.=Lauzelle wood, Ced.=Cedrogne wood, S=Same population of origin and D=Different population of origin.

3.2 Guidelines for the analysis of the figure 1 and the following figures 3 & 5 obtained with JMP® 7.0

The figure is composed by 16 diamonds and has to be read as follows:

The 8 first diamonds concern female subjects. The 4 first diamonds concern female subjects and female donors. The 2 first diamonds concern female subjects from the Cedrogne wood. It shows the number of marks they laid when confronted to an odour from a SPO female (i.e. the first diamond) versus a DPO female (i.e. the second diamond).

All the 16 diamonds have to be analysed similarly, two by two, in order to obtain a comparison of each of the tested combination of subject and donor.

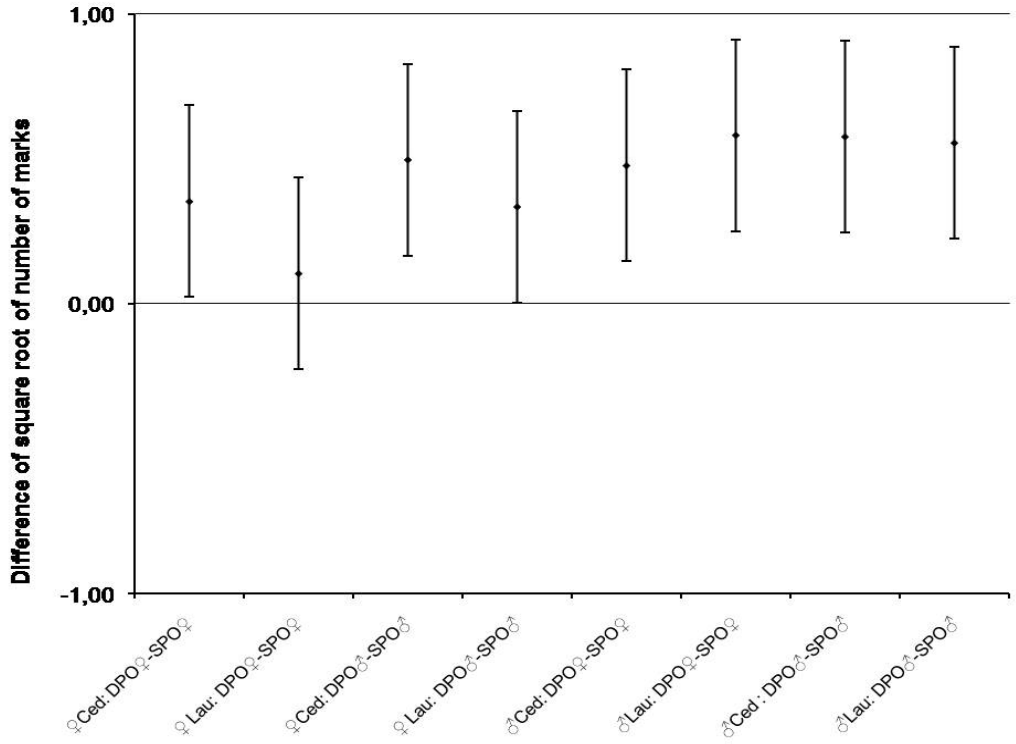

Fig. 2 Differences of square root number of marks (i.e. glandular and urine) laid by the subjects on the zone of interaction when in presence of odours from conspecifics from a different population of origin (DPO) versus odours from conspecifics from their own population of origin (i.e. same population of origin (SPO)) for each sex and origin of the subject.

3.3 Investigation

Investigation varied with the population of origin of the donor ($F_{12,384}$=3.214; P=0.0035) and with the sex of the subjects ($F_{12,384}$=3.672; p=0.0014**) (Fig.3). Differences in the number of sniffing events exhibited towards DPO minus SPO cubes were analysed (Fig.4). Female subjects tended to sniff less often DPO than SPO cubes with the exception of females from Lauzelle which sniffed more frequently cubes impregnated with the odour of Cedrogne males. Male subjects sniffed more frequently DPO than SPO cubes with males from Lauzelle more frequently than males from Cedrogne.

3.4 Motor activity

The motor activity of the subjects differed with the population of origin of the donor ($F_{12,384}$=4.353; p<0.0001) (Fig.5). All subjects entered more often the A4 paper (i.e. the zone of close contact with the cube) in the presence of DPO odours than SPO ones, from both sexes of donors. However, females from Lauzelle entered less often the paper than other subjects and Cedrogne females entered less often the copy paper than other subjects in presence of males' impregnated cubes only (Fig.6).

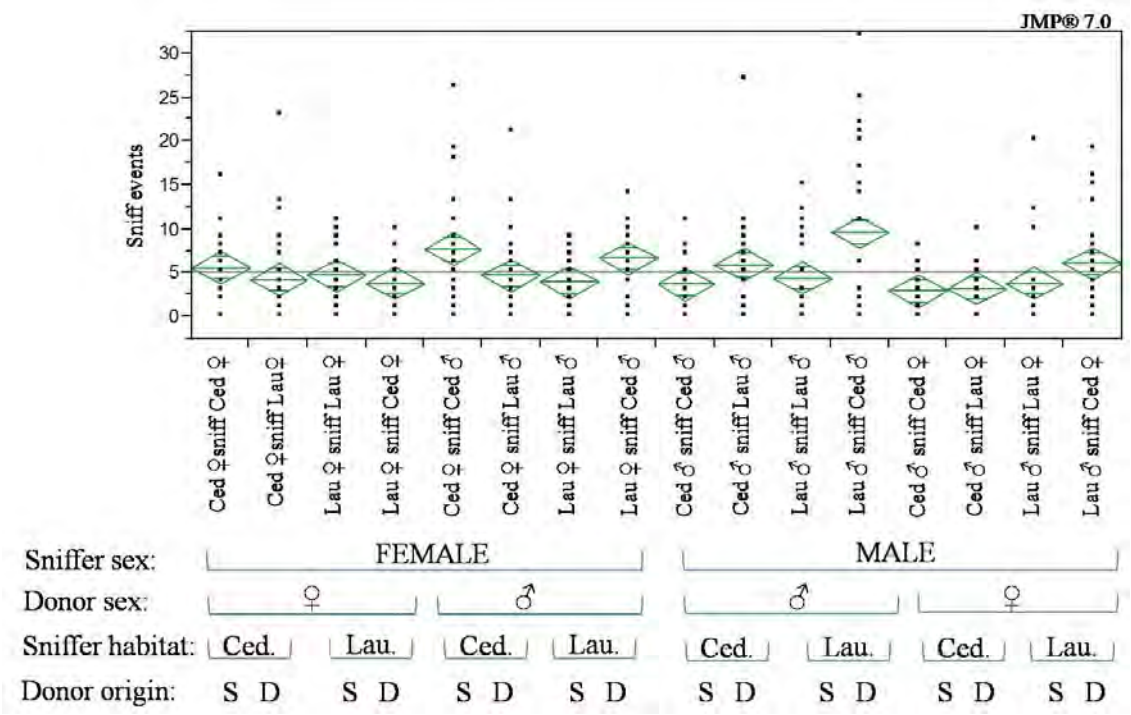

Fig. 3 Number of sniffing exhibited on the impregnated cubes by male and female voles from the habitats of Cedrogne and Lauzelle towards odours of conspecifics from their population of origin (SPO) and from a different population (DPO) and of same-/opposite-sex. SPO and DPO results were joined side by side for each combination of donor and subject. Diamond pikes are 95% of confidence interval and transverse line is the overall mean. Abbreviates used: Lau.=Lauzelle wood, Ced.=Cedrogne wood, S=Same population of origin and D=Different population of origin.

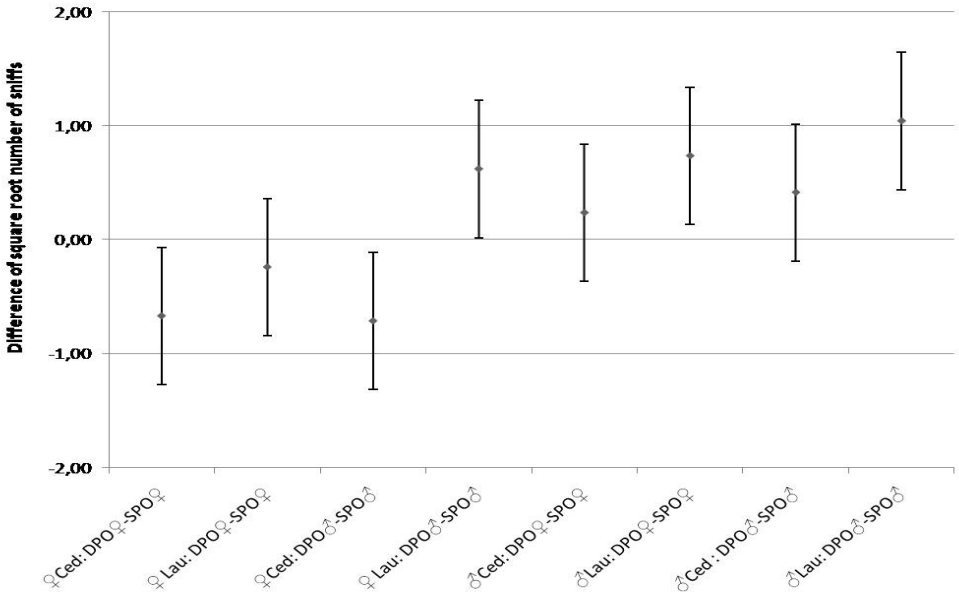

Fig. 4 Differences of square root number of sniffing exhibited on the impregnated cubes by sniffer voles towards odours from conspecifics from a different population of origin (DPO) minus towards odours from conspecifics from their own population of origin (i.e. same population of origin (SPO)) for each sex and origin of the subject.

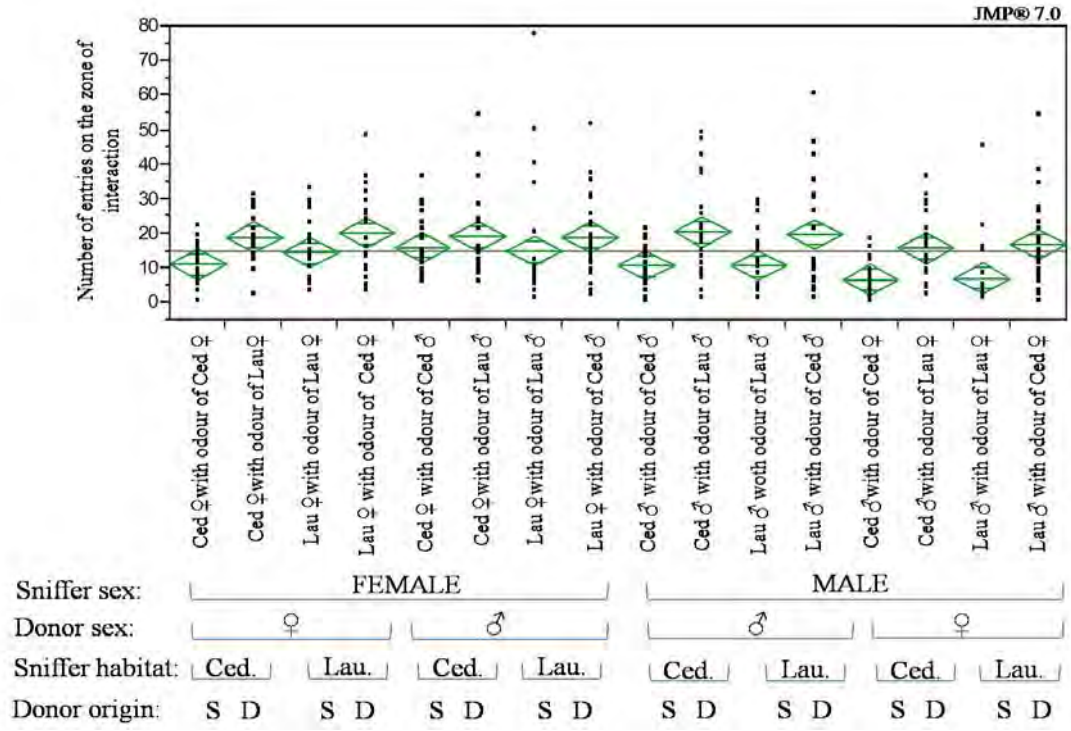

Fig. 5 Number of entries done on the zone of interaction by male and female voles from the habitats of Cedrogne and Lauzelle, in the presence of odours of conspecifics from their population of origin (SPO) and from a different population (DPO) and of same-/opposite-sex. SPO and DPO results were joined side by side for each combination of donor and subject. Diamond pikes are 95% of confidence interval and transverse line is the overall mean. Abbreviates: Lau.=Lauzelle wood, Ced.=Cedrogne wood, S=Same population of origin and D=Different population of origin.

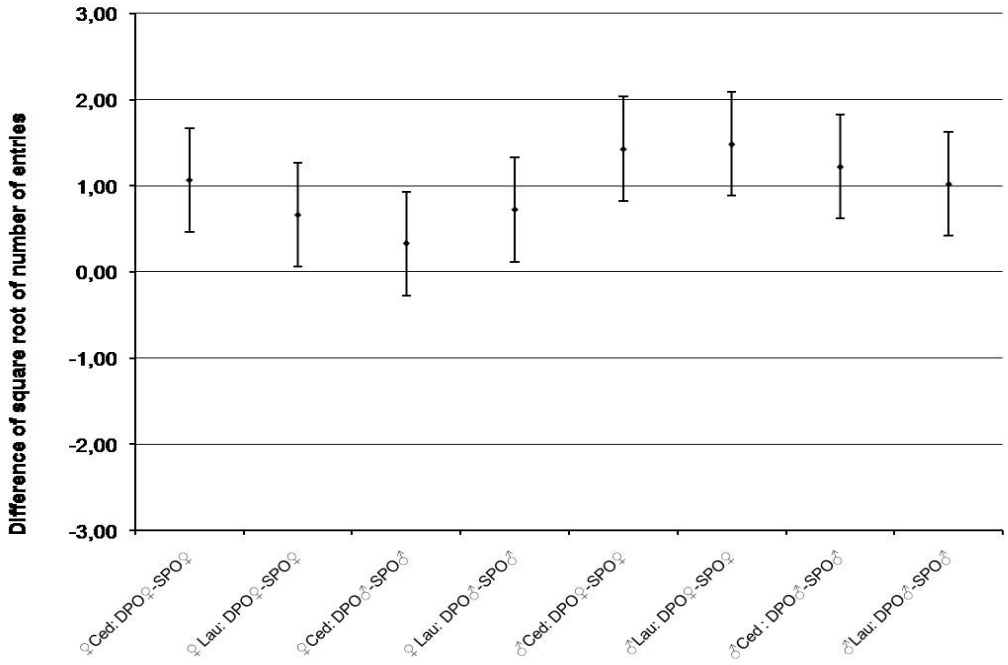

Fig. 6 Differences of square root number of entries done by the subjects on the zone of interaction when in presence of odours from conspecifics from a different population of origin (DPO) versus odours from conspecifics from their own population of origin (i.e. same population of origin (SPO)) for each sex and origin of the subject.

4 Discussion

In this study, we compared the behaviours (i.e. investigation, motor activity and marking) displayed by bank voles in presence of a polyurethane cube bearing conspecific odours differing on their population of origin.

Results of both marking and motor activity demonstrated that male and female bank voles reacted differently to odours depending on the population of origin of the donor. These results supported our hypothesis that behaviours should be enhanced in the presence of DPO conspecifics odours compared to those exhibited while exposed to odours of SPO donors. Abundant marking as well as high motor activity have been suggested to be a form of self-advertisement, which maximises individual identity, by odours and gestures respectively (Ferkin, 1999). This significant self-advertisement is induced, in the present case, when voles are in presence of conspecific odours from a different population of origin.

Even if faeces are olfactory signals in mammals (Viitala and Hoffmeyer, 1985), they were not taken into account in this study because of the lack of reliability of their counting at the end of each trial. Indeed, as faeces were movable and consequently scattered throughout the arena by voles during trials, they were too susceptible to be erroneously located by the experimenter on the zone of interaction.

Regarding investigation, male bank voles behaved in agreement with our predictions. Subjects sniffed more DPO odours than SPO ones, independently of the sex of the donor. Except for Lauzelle females which sniffed more frequently DPO male odours than SPO ones, female subjects investigate less frequently DPO odours than SPO ones. We found those results intriguing as several studies on voles have shown that sniffing is usually exhibited while investigating an unknown odour (Carte et al., 1988; Johnston, 2003; Johnston, 1997; Kruczek, 1998).

Two hypotheses can be put forward in regards to our results which tended to show that bank voles are able to discriminate odours of conspecifics differing on their population of origin.

First, odours (body odours and/or urine) emitted by bank voles bear information relative to their population of origin. Given the context of our experiment, the information should be delivered independently of the current housing conditions of the animals and should remain stable in time. Indeed, the tested bank voles were housed in individual cages in the laboratory for several weeks with their natural diet and forest litter replaced by a mix of grains and industrial wood shaving respectively. Therefore, to be reliable and remain stable in time, the olfactory cue ideally needs to be both genetically-determined and expressed independently of metabolic or environmental fluctuations. It has been shown that blind mole rats from the same population share similarities in their individual odours that covary with shared genetic similarities. That is, the closer their genetic relatedness, the more similar their odours will be (Heth and Todrank, 2000). Moreover, at the chemical level of analysis in other taxa, significant differences have already been found in sex pheromone blends and particularly among solitary bee populations. The difference in odour blends was correlated positively with geographic distance, suggesting that genetic difference among distant populations can affect sex pheromone chemistry in bees (Vereecken et al., 2007). Thus, it is likely that the variations of body odours in bank voles may be genetically determined. This would imply that voles determine the population of origin of a conspecific by comparing donor odours with their own, using a self-referent matching process. Such a process has already been demonstrated in golden hamster for kin recognition (Todrank et al., 1998) and has been suggested in blind mole rats (Heth et al., 1996).

Although a self-referent matching process is possible, a second hypothesis may be put forward. It is based on the familiarity (i.e. already met and/or smelled) that may exist between individuals belonging to the same

population. Indeed, social interactions may enable learning association between individuals and their respective odours (Johnston and Jernigan, 1994). Moreover, familiarity may facilitate mating, reduce agonistic behaviour between neighbours and influence inbreeding avoidance, and parent-offspring bonds (Ferkin, 1988; Murdock and Randall, 2001; Randall, 1989; Shapiro et al., 1986). Many mammals establish and maintain familiarity through olfactory communication (DeVries et al., 1997; Newman and Halpin, 1988; Zenuto and Fanjul, 2002). However, to study interactions of small rodents under field conditions is difficult as they are small animals with a secretive and mainly underground way of life. Moreover, they can be largely dispersed and often active only at night (Andrzejewski, 2002). So far, observations of interactions between bank voles have been mainly studied under artificial conditions in the laboratory (Marchlewska-Koj, 2000) or in semi-natural enclosures (Jedrzejewska and Jedrzejewski, 1990) which may elicit unnatural behaviours such as stereotypies—abnormal, repetitive, unvarying and apparently functionless behaviours— which are common in many captive animals (Garner and Mason, 2002). Those behaviours were not observed during this study (G.V. personal observations). But it cannot be neglected that voles may have already encountered conspecifics from their own population (SPO) (or their respective marking) before being trapped. If this has been the case, their respective odours became familiar and won't represent novelty while future encounters. Consequently, during our experiment, voles could have shown less interest and reacted less profusely to SPO conspecific odours than when confronted to unknown DPO conspecific odours (Dobly, 2005). Therefore, the variations of behaviour observed when voles were confronted to SPO and DPO odours would just be a matter of recognising an odour (i.e. from SPO conspecifics encountered in the wild) versus discovering a new one (i.e. odours from DPO conspecifics never met before) rather than a discrimination based on a self-referent matching process.

So far, none of the two hypotheses, that are self-referent matching process or familiarity, can be put forward. A fruitful area of research to determine which process is used by bank voles might be to carry out further laboratory and field studies involving genetic and behavioural ecology approaches (e.g. by using satellite radio-tracking with small transmitters) (Dammhahn and Kappeler, 2008). They will allow elucidating the causes underlying apparent between-populations differences in the bank voles' body odours. Moreover, to test more populations will be of great value as one of the limitations of our research was that only two populations were used. Though many points remained undeveloped and many improvements could be afforded to this study, this paper brings us a glimpse on the olfactory abilities of bank voles and thus how much is still to discover on wild rodents behaviours.

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