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Females do it better. Individual recognition experiments reveal sexual dimorphism in *Lemur catta* (Linnaeus 1758) olfactory motivation and territorial defence

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Summary

In this paper, we aim at demonstrating individual recognition of female genital marking in *Lemur catta*. By gas chromatography and behavioural trials we verified the occurrence of the three components of recognition systems. We showed that each female has a unique chemical signature (expression component), and males and females perceive female individuality (perception component). To verify the presence of the action component (the last component of recognition systems), we designed a bioassay based on territorial competition to verify the functional response to female odours. Only females identified other females on the basis of their scents. The lack of a territorial functional response by males to female secretions may not indicate a male inability to identify females by their scents. In fact, sexual dimorphism in motivation and territorial defence may explain the response by males in the functional experiment. Actually, game theory predicts that males defend their own territories more vigorously against males compared with females. Therefore, the result of individual recognition bioassays of female odours may open interesting scenarios in the evaluation of the territorial defence investment across the different sex combinations.

Key words: female genital secretions, gas chromatography, scent tests, individual recognition, sexual dimorphism, *Lemur catta*.

Introduction

Female fitness is mostly linked to the access to food resources whereas that of males should be limited by the access to females (Trivers, 1972; Wrangham, 1980). Consequently, costs and benefits of territorial defence should vary as a function of the sex of resident and foreign individuals, which meet inside a territory (Boydston et al., 2001). Generally, mammals defend their own territories most vigorously against same-sex intruders (King, 1954; Rood, 1983; Heinsohn and Packer, 1985). By contrast, it is difficult to predict the outcome of the encounters between conspecifics of the opposite sex. In that case, additional factors, such as reproductive opportunities, may interact with territoriality and force animals to evaluate costs and benefits of a potential response (Cant et al., 2002). The relative amount of costs and benefits may be determined by the social and biological characteristics of the species (social and kin structure, male or female dominance, male or female philopatry, seasonal reproduction, group size) and by the particular social context during which the encounter takes place (number of animals engaging in the conflict, their ages and social status) (Krebs and Davies, 1991).

During the inter-group encounters, animals have to categorize conspecifics as males or females, group-mates or aliens on the basis of several cues before modulating the possible response. This information may also be present when functional cues (even those decoupled from the sender, as in the case of some chemical cues) are perceived by the resident animal (Bradbury and Veherencamp, 1998; Hebets and Papaj, 2005). Consequently, the response given in the absence of the cue bearer often matches the response given when the bearer is present (Palagi and Dapporto, 2006; Scordato and Drea, 2007). For this reason, when a cue carries messages involved both in reproductive strategies and in inter-group competition (i.e. genital secretions of alien females), the reaction of the receiver to such a cue should also predict the outcome of the encounters between conspecifics of different sexes and groups. To clarify this issue, we selected *Lemur catta* as a model species since its social life history and communication systems are well known. Ring-tailed lemur communication is strongly scent oriented, with chemical signals playing a pivotal role both in reproductive strategies and in territorial competition (Kappeler, 1998; Gould and Overdorff, 2002; Palagi et al., 2005).

In a recent paper, we demonstrated that both male and female ring-tailed lemurs are able to recognize male conspecifics on the basis of their highly specialized brachial secretions (Palagi and Dapporto, 2006). In that paper, we verified the occurrence of the three components of recognition systems: (1) the expression component (the presence of diversification of some cues), (2) the perception component (the perception and discrimination of such cues) and (3) the action component (the functional response to the perception of such cues). This last component is crucial to demonstrate that recognition goes beyond odour

discrimination and that animals are able to form a mental image of the sender by perceiving its scent (Johnston and Bullock, 2001; Thom and Hurst, 2004; Palagi and Dapporto, 2006). We demonstrated the occurrence of the action component on *Lemur catta* male secretions by designing an experiment based on the hypothesis that male scent should be involved in territorial competition. Ring-tailed lemurs of both sexes usually prefer to smell unfamiliar odours compared with familiar ones, but when a well-known odour belonging to a competitor is proposed this is preferred (Palagi and Dapporto, 2006).

Individual recognition of female scent marks has not yet been demonstrated. *Lemur catta* females exclusively use genital secretions to mark the environment (Jolly, 1966; Sauther et al., 1999). Female marking is widely used in inter-group (between competing groups) and intra-group communication (communication of reproductive status and maintenance of linear hierarchical relationships among females which always dominate over males) (Mertl-Millhollen, 2006; Palagi et al., 2003; Palagi et al., 2004). Due to the short receptive period of females (a few hours per year) (Van Horn, 1975; Van Horn and Resko, 1977; Van Horn and Eaton, 1979; Sauther, 1991) and to qualify seasonal variations in their genital markings, it is crucial for males to focus their investigation of female odours during the reproductive period (Hayes et al., 2004; Hayes et al., 2006; Palagi et al., 2004; Scordato and Drea, 2007).

To search for individual recognition of female genital marking, we applied the same approach described in Palagi and Dapporto (Palagi and Dapporto, 2006). The occurrence of individual recognition of female secretions is not obvious due to theoretical complications and confounding empirical observations regarding the three components: (1) the vaginal secretion, a non-specialized scent, may vary as a function of physiological and environmental factors, which may make the expression component unstable (Thom and Hurst, 2004); (2) habituation/dishabituation tests on female secretions have failed to demonstrate the occurrence of the perception component (Mertl-Millhollen, 2006) and (3) unlike the response to alien males, which are competitors for both sexes, alien females may be considered by resident males not as competitors but as possible sexual partners. In this case, the action component may remain undetected by experiments based on territorial defence. Therefore, the outcome of individual recognition experiments on female odours may also open interesting scenarios to evaluate the territorial defence investment within and between sexes.

Materials and methods

Subjects and housing

The study was conducted in five captive groups of *Lemur catta* (Linnaeus 1758). The P1, P2 and P3 groups were housed in the Pistoia Zoo (Tuscany, Italy), the F group in the Falconara Zoo (Marche, Italy) and the L group in the Lignano Zoo (Friuli, Italy). P1 and L were multi-male/multi-female groups composed of eight individuals (two males and six females) and five individuals (two males and three females), respectively; P2 and P3 were single-male/single-female pairs; and F was an all-male group (eight males). All the subjects were healthy and fertile adults. All the groups lived in facilities composed of outside grassy enclosures and indoor halls [for details, see Palagi and Dapporto (Palagi and Dapporto, 2006)]. In particular, the P1 and P2 groups utilized the same outside grassy enclosure alternately for 4–6 h per day; the groups were always in olfactory and visual contact. P3 and P1/P2 groups were always separated from each other and were, consequently, unfamiliar.

Collection of genital secretions

We collected female genital secretions from seven females of P1, P2 and P3 groups from November 2003 to June 2006 during both reproductive and birth seasons. The secretions were collected by placing sheets of filter paper (50×50 cm^2) on the branches usually marked by lemurs. Prior to use, we washed the paper in organic solvents (methanol:pentane 1:1) to remove any volatile compounds occurring naturally in the paper. As a female marked the paper, we removed the area (~5×5 mm^2) soaked with genital secretions. In order to prevent chemical contamination, the samples were wrapped in an aluminium sheet. Each sample was labelled with the date and the name of the donor subject and was immediately frozen at –20°C (Hayes et al., 2002; Hayes et al., 2004). We used some of these secretions for scent trials (see below) and others for gas chromatography/flame ionization detection (GC/FID) analyses.

Experiment 1 – GC/FID analyses

Pieces of filter paper soaked with genital secretions were extracted in 300 μl of extraction solvent (1:3 v/v methanol:dichloromethane) for 20 min. The solution was then dried and re-suspended in 25 μl of solvent. We injected 2 μl of solution into a Varian 3900 gas chromatograph (Middelburg, The Netherlands) fitted with a Flame Ionization Detector (FID) and a fused silica capillary column coated with 5% diphenyl/95% dimethyl polysiloxane (Varian FactorFour VF-5ms; 30 m×0.25 mm×0.5 μm). Injector temperature was 280°C and detector temperature was 300°C. The carrier gas was hydrogen (at 12 psi; 1 psi=6.9 kPa). The temperature protocol was as follows: 70–150°C at a rate of 30 deg. min^{-1} (held for 5 min), and then 150–310°C at a rate of 5 deg. min^{-1} (held for 11.3 min).

Scent tests

Two pieces of filter paper soaked with genital secretions were fixed to the gates of the enclosure at a distance of 50 cm from each other using forceps. One of the two authors numbered the two pieces of paper. The other author performed a blind trial, presenting the filter paper to animals and registering olfactory responses without knowing the meaning of the two numbers. The observer waited until the animals spontaneously approached the samples. The experimental trials were considered valid only if the animal spent more than 10 s inspecting both samples and if both pieces of filter paper were detected by the subject. Each trial lasted three minutes for each animal; when two animals simultaneously approached the stimuli, the first author timed the three-minute trial of the two different animals (no more than two animals approached the stimuli simultaneously). Time spent investigating was tape-recorded, starting when the animal was about 2 cm from the scent stimuli and ending when the individual moved away. Since trials were performed on the whole group, we frequently changed the relative position (left/right) of the two samples

during the trials so that previous experience and copying behaviours did not bias the scent tests. Moreover, if a subject countermarked one of the two samples, we changed both samples at the end of the trial performed by that subject. During each trial, the names of individuals interacting and time spent sniffing and/or licking the samples were recorded. Since the animals showed a high variability in their motivation to investigate, we obtained different sample sizes for the different experiments performed. We performed one trial per animal.

Experiment 2 – scent discrimination

In the first experiment we compared the olfactory response elicited by the genital secretion and clean paper to verify whether animals actually perceived the scents (Experiment 2a).

To verify the occurrence of the perception component we performed habituation/discrimination tests as suggested by Johnston and Jernigan (Johnston and Jernigan, 1994) and Thom and Hurst (Thom and Hurst, 2004) (Experiment 2b). During four habituation trials, subjects were presented with two pieces of filter paper, both containing the secretions from an individual (individual A). The habituation response is usually observed in the form of a decrease in the inspection time. In the final trial, we presented two different odours, one belonging to the same individual (A) and one belonging to another individual (B). If the subject perceives the difference between the new scent (B) and the habituated scent (A), investigation of the former is expected to be higher when compared with the latter (Thom and Hurst, 2004). The habituation trials were followed by 1 min-intervals.

Experiment 3 – individual recognition by scent

To verify the occurrence of the functional component we performed a bioassay based on two experiments on the two groups competing for the same outside enclosure (P1 and P2). In the first experiment we presented the familiar odour of the female belonging to the competing group and the unfamiliar female from the P3 group (Experiment 3a). In the second experiment, we presented the familiar scent belonging to a group-mate and another one belonging to the unfamiliar subject from the P3 group (Experiment 3b). The scent tests were performed in the outdoor enclosure, which represents the overlapping area for P1 and P2 groups.

Statistical analysis

The peak areas of the FID gas chromatograms of each sample were processed and analyzed using Varian Star GC Workstation 6.0. Each peak was identified on the basis of the relative retention time in the 35 analyses; peak areas were transformed into percentages for each sample. All peaks with a percentage area less than 0.01% of the total compound content (considering all the samples) were excluded from the analyses because of unreliable quantification at such low relative amounts, as suggested by Smith et al. (Smith et al., 2001).

We performed Discriminant Analysis (DA) on 28 samples collected from five donors in different years (from 2003 to 2006) and periods (mating and birth seasons) to determine whether the samples from each animal could be distinguished according to their chemical composition. We performed Principal Component Analysis (PCA) to reduce the number of variables into a smaller number of uncorrelated principal components. We extracted 13 factors with eigenvalues greater than 1, which together explained 100% of the total variance. As no peak showed communalities of <0.8, we did not remove any peak from the PCA. The 13 principal components were used as independent variables for the DA. Wilks' lambda and the number of cases assigned to their original group were used as indexes of correct DA.

We used the Wilcoxon matched-pairs signed-rank test to evaluate differences in time spent investigating during scent tests (blank paper *vs* genital secretion), habituation/discrimination tests (habituated *vs* non-habituated scent) and functional tests (familiar *vs* unfamiliar scent). We used exact tests as suggested by Mundry and Fischer (Mundry and Fischer, 1998).

We used randomization tests when males and females were tested separately. All analyses were two-tailed, and the level of significance was set at 5%.

Results

Chemical analyses (Experiment 1)

The analysis of the clean filter paper revealed 15 peaks (probably a mix of linear hydrocarbons) that were removed from the analysis. A total of 50 peaks (absent in the clean paper) reached 0.01% peak area in the GC/FID analyses of the genital secretions of the five subjects.

DA performed on the 28 samples using the 13 PCs obtained by PCA extracted four functions explaining 100% of variance and correctly assigned 100% of cases to their own group (Fig. 1). In particular, on the basis of function 1 (explained variance 50.1%, Wilks' lambda=0.003, P<0.001) and function

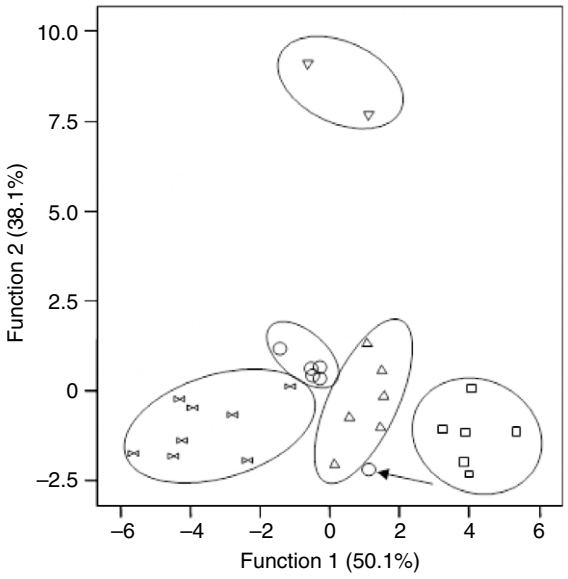

Fig. 1. Canonical discriminant functions. Discriminant Analysis of 28 samples of genital secretions from five *Lemur catta* females on the basis of the proportions of the peaks identified using GC/FID. The percentages of the variance explained by each of the two main functions are given in parentheses. The arrow indicates the only sample incorrectly assigned to its own subject on the basis of the two first functions.

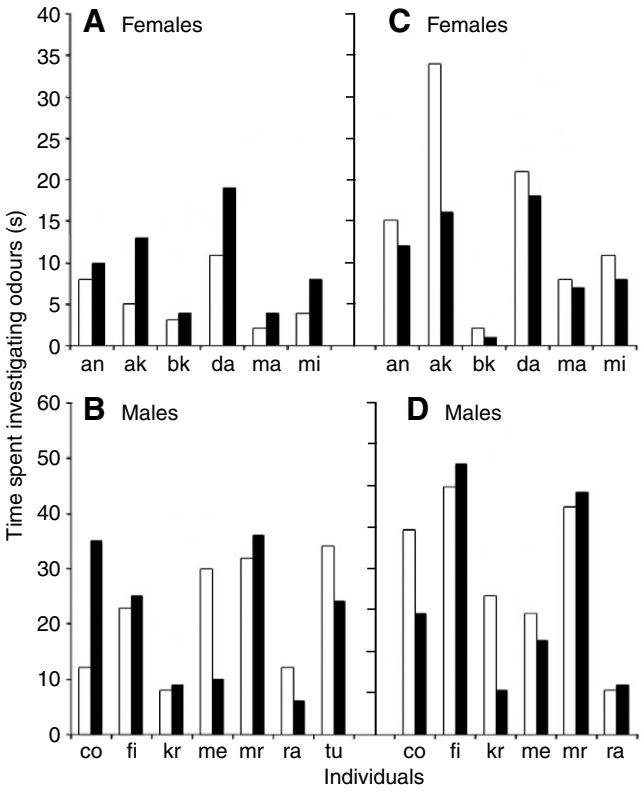

Fig. 2. Olfactory investigation performed by males and females on (A,B) group-mate (open bars) and unfamiliar (filled bars) odours (Experiment 3a) and on (C,D) familiar-competitor (open bars) and unfamiliar (filled bars) odours (Experiment 3b).

2 only (explained variance 38.1%, Wilks' lambda=0.030, P=0.003) we obtained a good separation of the samples belonging to the five females (Fig. 1).

Scent discrimination (Experiment 2)

After four habituation trials, lemurs decreased their olfactory response to the habituated scent (1st *vs* 4th trial; Exact Wilcoxon signed-ranks test, T=0, ties=0, N=10, P=0.002) and, in the last trial, they preferentially investigated the non-habituated scent compared with the habituated one (Exact Wilcoxon signed-ranks test, T=0, ties=0, N=10, P=0.002).

Individual recognition by scent (Experiment 3)

As a whole, P1 and P2 lemurs showed no preference towards unfamiliar genital markings compared with group-mate ones (Exact Wilcoxon signed-ranks test, T=29, ties=0, N=12, P=0.458). Moreover, subjects from both groups did not prefer to investigate the familiar odour belonging to the competing female (P1 female for P2 group; P2 female for P1 group; Exact Wilcoxon signed-ranks test, T=15.5, ties=0, N=12, P=0.068). However, when males and females were tested separately in Experiment 3a, the analysis revealed that all the females preferred unfamiliar odours to familiar ones (randomization paired test, t=4.32, N=5, P<0.001; Fig. 2A) while males did not show any preference (randomization paired test, t=–0.42, N=7, P=0.702; Fig. 2B). Conversely, in Experiment 3b, all the females preferentially investigated the familiar-competitor odours compared with the unfamiliar ones (randomization paired test, t=–3.47, N=6, P<0.001; Fig. 2C) and males showed no preference again (randomization paired test, t=1.372, N=6, P=0.244).

Discussion

By chemical analyses, we demonstrated that female genital secretions possess unique signatures that are maintained through seasons and years. Moreover, males and females perceive such differences. Although only females showed the action component of recognition, thus demonstrating their ability in individual recognition of other female scents, the absence of the action component based on territorial functional response by males to female secretions does not univocally indicate a male inability to identify females by their scents.

Olfactory behaviour plays a fundamental role in territorial defence (Gould and Overdorff, 2002); owners extensively mark their territories (mainly at boundaries) and spend a lot of time seeking and investigating conspecific depositions [e.g. *Eulemur mongoz* (Curtis and Zaramody, 1999), *L. catta* (Jolly, 1966; Mertl-Millhollen, 1986; Mertl-Millhollen, 2006; Kappeler, 1998), *Propithecus* spp. (Lewis, 2005; Pochron et al., 2005a; Pochron et al., 2005b)]. Generally, an odour belonging to a novel unfamiliar individual (a potential competitor) elicits more intense olfactory responses compared with a scent belonging to a group mate (Ramsay and Giller, 1996; Palagi et al., 2005). The clear response of *L. catta* females during Experiment 3 can be explained by their strong intrasexual competition over resources and by their strong activity in territorial defence, as might be expected in a female-dominant species. Scordato and Drea also found that the strongest response during olfactory trials was that of females towards genital odour from female 'intruders' (Scordato and Drea, 2007). Both in wild and semi-free-ranging ring-tailed lemurs, during intertroop agonistic interactions, females of opposing groups often run toward each other and genital mark concurrently (Nakamichi and Koyama, 1997; Nunn and Deaner, 2004; Mertl-Millhollen, 2006). Moreover, Mertl-Millhollen (Mertl-Millhollen, 2006) observed that when females travelled out of their defended range, they significantly increased their rate of sniffing behaviour. In this view, the capability to recognize the individual ownership, other than to simply perceive the spatial and temporal pattern of scent depositions, may provide considerable advantages both to the sender and the receiver, especially when animals can remember and use information from previous encounters to moderate future responses (Gosling, 1982; Bradbury and Vehrencamp, 1998; Hurst and Beynon, 2004). In particular, Gosling proposed the Scent Matching Hypothesis, which predicts that territory marking provides an olfactory association between the resident and the defended area that allows intruders to identify the resident when they meet and thus reduce the frequency of escalating agonistic encounters (Gosling, 1982).

Demonstrating the action component (the last component of recognition systems) requires (1) a hypothesis about the function of the signal and (2) a functional experiment designed on the basis of such a hypothesis (Fig. 3). The occurrence of the action component not only demonstrates definitively the occurrence of the recognition but also confirms the hypothesis

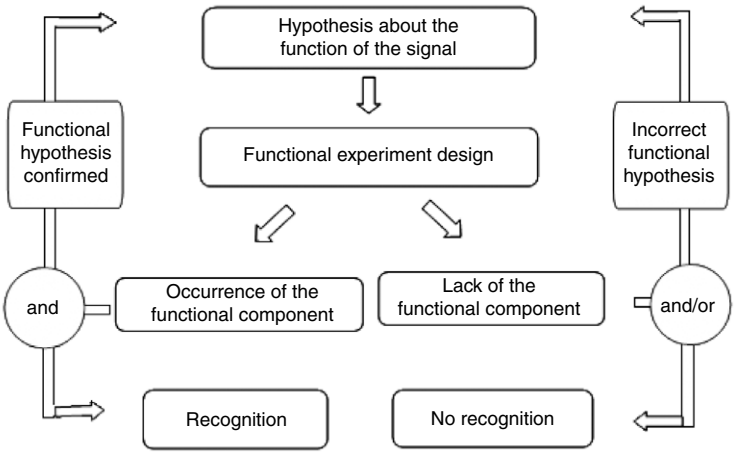

Fig. 3. Scheme summarizing the procedure to design functional experiments and indicating the possible interpretations of the results.

about the function of the signal as well. Conversely, the failure of the experiment does not necessarily imply the lack of the recognition skill, since it may be due to a wrong functional hypothesis (Fig. 3).

During our trials, males were more active than females in olfactory investigation, spending more time in sniffing and licking the scent depositions than did females (Fig. 2). As these sex differences are generally consistent with previous observations of olfactory investigation and scent marking in the wild (Gould and Overdorff, 2002) and in semi-free-ranging ring-tailed lemurs (Kappeler, 1998) it is unlikely that our testing environment significantly altered the natural response pattern. The absence of a territorial functional response by ring-tailed males to female secretions in Experiment 3 may be explained by male-peculiar life histories and reproductive events such as mating and male dispersal. Unlike females, the response of male ring-tailed lemurs is consistent with patterns of olfactory signalling in other mammals (Thiessen and Rice, 1976; Johnston, 2003); males are mainly attentive to the physiological state of potential female mates independently from their familiarity [this evidence is supported also by Heymann (Heymann, 1998) and Scordato and Drea (Scordato and Drea, 2007)], probably because alien females are considered not as competitors but as possible sexual partners. This hypothesis matches the observation in the field, where it has been demonstrated that fights between males and females are rare (4% of the aggressions between groups) (Nakamichi and Koyama, 1997). Moreover, in the wild, male transfer is well documented and females were observed to mate not only with group males or transfer males but also with 'temporary visitors' from adjacent groups (Jolly, 1966; Sauther, 1991; Sussman, 1992). Similarly, Gould (Gould, 1997) documented male migration between November and January, and these foreign males were later able to mate with females, even though they were usually the last to do so (Sussman, 1992). Therefore, in the wild, genital marking by females may also serve to advertise to extra-troop males, thus increasing mate choice opportunities. Since it has been demonstrated that female secretions contain information on their reproductive status (Hayes et al., 2004; Scordato and Drea, 2007), migrating males could use such female scent-marking to gauge into which groups to attempt to immigrate. However, this follow-up on female odours is useless in a multi-female group when a male is not able to recognize the owner of the scent deposition. From this perspective, it is hard to think that, within a species, females are able to individually recognize both males and females, but males are able to individually recognize only males. In a more parsimonious hypothesis we suggest that males did not show the action component toward female genital odours as the territorial defence functional hypothesis is not suitable for resident males toward alien females, which are considered as potential partners more than territorial competitors.

In conclusion, in designing a functional bioassay, a scientist should carefully consider the social and biological characteristics of the species under study in order to avoid type II errors. In *L. catta*, both sexes are probably able to identify females by their unique odour signatures. The absence of preference showed by males towards unfamiliar and familiar-competitor females (Experiment 3) may be due to the sexual dimorphism in territorial defence and/or a high motivation for males in investigating both group-mate and alien females. Both factors could have made the functional bioassay ineffective. Further observational and experimental studies are required to elucidate the role of odour cues in intra- and extra-group dynamics.

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