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Urine marking and urination in *Lemur catta*: a comparison of design features

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The "design features" of a signal are strictly shaped by selective forces since they affect the optimality of the signal form. In *Lemur catta* urine deposition can be combined with the following tail configurations: (1) tail held up in an evident display (Urine Marking, UM); (2) tail slightly raised to avoid its impregnation with urine (Urinating, UR). It has recently been demonstrated that only UM has marking functions and the visual tail display is only one of the features facilitating detection of the signal by the receiver. Other features help senders to increase the probability of signal detection (e.g. site of deposition and association with other scent depositions). In this paper, we ranked using a multivariate general linear model and logistic regression the relative importance of such features in shaping the two kinds of depositions. Furthermore, we demonstrated that both UM and UR have constant depositional features probably in order to improve the detectability of the urine marking and the animals' safety during urine excretion.

Introduction

The "design features" are a property of a signal. These features, rigorously shaped by selective forces, affect the optimality of the signal form (Bradbury & Veherencamp 1998). Indeed, the magnitude of the sender costs depends on the signal modalities that can render depositions more likely to be perceived by receivers in the most economic manner (Magnahagen 1991, Bradbury & Veherencamp 1998). Several studies have been carried out to identify general design rules that combine the feature requirement of signals according to their function. The following two methods have often been used to recognize general rules: (i) comparing similarities among functionally equivalent signals, and (ii) searching for differences in features among functionally different signals (reviewed in Bradbury & Veherencamp 1998). These studies generally compare signals of different species or different signals of the same species.

In a recent paper, Palagi *et al.* (2005) demonstrated that *Lemur catta* deposits urine with two tail configurations: in the first one (urine marking), urine deposition is combined with an evident display of the tail, which is held up; in the second one (urinating) the tail is only slightly raised. This study revealed that urine marking, with respect to urinating (a) elicits major olfactory responses in receivers, (b) has different deposition features (lower quantity, seasonality, association with genital marking, and releasing in particular sites), and (c) is induced by the presence of foreign individuals. Palagi *et al.* (2005) concluded that urine marking is a complex signal with multimodal and multiple characteristics, directed both to group members and to neighbouring groups. Complex signals combining visual and chemical cues are predicted to be frequent in species which — as *Lemur catta* — live in tropical areas. As high temperature and humidity strongly decrease the durability of scent deposition (Alberts 1992), visual cues could help receivers in a quicker detection of the scent (Hebets & Papaj 2005).

A problem in investigating complex signals is related to the difficulty in separating the components. Additionally, the "unique stimulus hypothesis" predicts that a compound stimulus is capable of eliciting a completely different response from that of individual components (Rescorla 1973). Consequently, by studying the isolated components of a complex signal we miss their synergic function (Rowe 1999). Due to the presence of the two different kinds of urine depositions (combined or not with a visual cue), *Lemur catta* offers the possibility to directly compare, within the same species, the design features of a complex signal (urine marking) and of the simple urine excretion (without any visual display and apparent communicative function) and receiver's response.

Palagi *et al.* (2005) demonstrated by univariate analyses that urine marking presents many depositional features typical of a complex signal, whereas urinating seems to be less strictly designed showing neither differences in deposition sites (core area *vs.* overlapping area) nor an increase in the presence of unfamiliar conspecifics. However, univariate analyses do not permit a direct comparison of the various features.

Here, we applied different statistical approaches (multivariate General Linear Model and Logistic Regression) to a new behavioural data set in order to address the following questions: (i) What are the most characteristic features of urine marking as opposed to a simple urine excretion? (ii) Is urine marking strictly selected and designed with less variable depositional features as compared with those of urinating?

Material and methods

In 2004 and 2005 we collected data on two captive groups of *Lemur catta* (10 individuals) housed in the Pistoia Zoo (Tuscany, Italy). All the individuals under study were adult (older than 18 months) and they were in good health. The two groups utilized the same outside grassy enclosure (about 100 m^2) in alternation from four to six hours per day and they were always in olfactory and visual contact through the doors separating the outdoor and indoor facilities.

We used the all-occurrences sampling (Altmann 1974) for standard data scoring. According to Palagi *et al.* (2005) we discriminated urine marking (UM) from urinating (UR) by the presence of the tail display. During the observations we scored the occurrence of four depositional features for each depositional event (Palagi *et al.* 2005): association with genital marking occurring within 10 seconds from deposition, quantity of urine released (few drops or streams), and elevation where urine was deposited (on the ground or on the branches); finally, we considered depositions occurring within 1 m of the door or food area in order to obtain this standardized variable.

We applied the General Linear Model (GLM) analysis by using the four depositional features as dependent variables and the display of the tail (UM or UR) as binary independent variable. We used the P value and F statistic to rank the importance of the four features in characterizing the two kinds of urine deposition. Moreover, as more than one deposition from the same individual entered the analysis, correlations among observations may occur. For this reason, we also included individuals as an independent factor in the GLM analysis.

We performed LogRA using the four features as covariates, whilst the dependent variable was the display of the tail distinctive of UM and UR. The covariates were entered into the model after selection by the forward stepwise method. We used the percentage of correctly classified cases in LogRA to evaluate whether UM depositions have more strictly designed features as compared with UR ones. To test this assumption we analysed with the G-test the results obtained by LogRA; in order to do that we compared the number of correct- and mis-classified UMs with

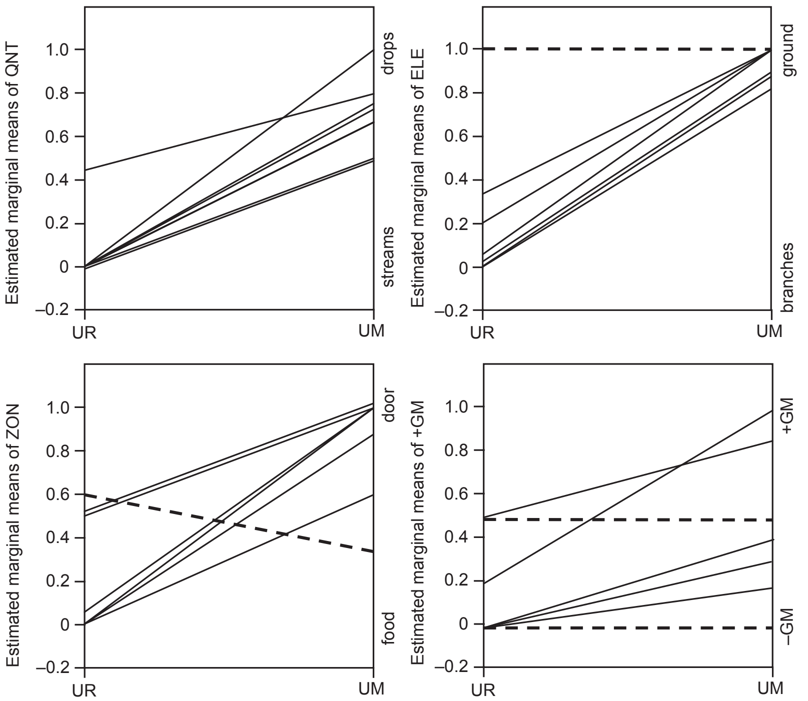

Fig. 1. Graphs of the interaction of the tail patterns (urine marking, UM and urinate, UR) and the seven individuals (lines) in urine depositional features. Dashed lines represent individuals that behaved against the trend.

URs in a 2 × 2 contingency table (observed, predicted; UM, UR). We used SPSS 9 for all statistical analyses.

Results

A total of 126 urine depositions (79 UM and 47 UR) were recorded. As three animals did not perform at least two depositions per pattern, we eliminated them from the analyses obtaining 99 depositions (55 UM and 44 UR) belonging to seven individuals. GLM revealed that all the four variables differed between UM and UR, but the most striking difference is the site where urine was deposited. Indeed, the elevation (on the ground for UM, and on the branches for UR, $F = 89.37$, $P < 0.001$) and the zone (door zone for UM, food zone for UR, $F = 59.17$, $P < 0.001$) appeared to be the most significant features characterizing the two kinds of depositions. UM depositions were performed on the ground and in the door zone in 83.64% of the cases, whereas UR depositions performed on branches within the food zone were observed in 79.55% of the cases.

There was a significant interaction effect between the two tail patterns (UM and UR) and the subjects in respect to the elevation ($F = 5.77$, $P < 0.001$) and zone of urine deposition ($F = 4.47$, $P = 0.001$). However, examining the graphs of the interaction for the four features separately, it is evident that most animals behaved in a similar manner with the exception of one or two individuals only (Fig. 1).

LogRA resulted in an overall correct discrimination of 89.9% of the cases. Moreover, we observed that LogRA assigned the 89.1% of UM (49 out of 55) and the 90.1% of UR (40 out of 44) to their correct group (*G*-test: $G = 0.085$, $P = 0.770$) demonstrating a similar strict characterization for both UM and UR (Fig. 2). Only three of the four features — elevation ($B = –3.253$), quantity ($B = –1.919$), and the zone of the cage ($B = –1.618$) — entered the model after stepwise selection (for further statistical values *see* Table 1). Also in this case, elevation is the most important variable distinguishing the two depositional patterns as revealed by the *B* values.

Discussion

The evaluation of costs and benefits of signalling is mostly very difficult to assess in captive groups, where predation and inter-group conflicts do not occur. However, it can be predicted that the conspicuous display of an evident body part such as the tail of *Lemur catta* could result in an increase of predation and attack risks.

The design of urine marking (UM) seems to follow some rules of economics in deposition and, at the same time, of displaying the marking costs themselves. Using GLM and LogRA we were able to measure not only what signal features differ between UM and UR (as already reported in our previous paper, Palagi *et al.* 2005) but also to rank such features in order to determine which are the most important ones in discriminating the two depositions. Our GLM results indicate that the location of the signaller (on the ground *vs.* high branches, and in the overlapping- *vs.* the core-area) is the most important factor in distinguishing UM from UR. The few drops of urine usually deposited by urine marking could be lost or dispersed by wind when released from elevated sites such as trees; in addition, lemurs need to deposit urine on the ground to permit the receivers to associate the tail display with scent location. Receiver's motivation to investigate a signal can be improved also by the signaller itself. The evolutionary theory suggests that costly signals are generally honest advertising of the signaller's quality. On the other hand, low cost signals might be prone to cheating and the receiver might be expected to be sceptical in investigating them (Zahavi & Zahavi 1997, Daeg & Scott 1999). Marking at the ground level and the association with the evident tail display probably increase the risk of being discovered by predators and being attacked by the receiver, thus suggesting that this signal is likely to be honest (*sensu* Zahavi & Zahavi 1997). Moreover, UM was performed preferentially in the overlapping zone, thus suggesting both a reduction of the costs linked to the marking of wider areas and a further increase in sender costs as a risk of aggressions by receivers. Conversely, UR was mainly performed on branches and in the core area.

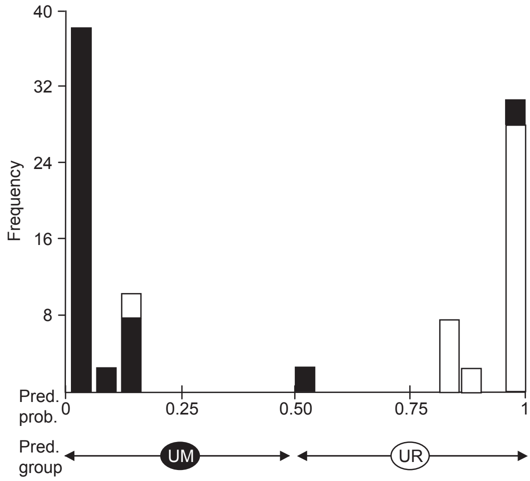

Fig. 2. Frequency of predicted probability (Pred. prob.) and predicted group membership (Pred. group) of the 99 depositions. Black bars represent urine marking (UM), white bars represent urinate (UR).

Table 1. Logistic regression results. Regression coefficients (*B*) and their standard errors (S.E.), Wald statistic, and significance levels of the three variables entered in the model.

Variable	*B*	S.E.	Wald	*P*
QNT	–1.919	0.774	6.149	0.013
ALT	–3.253	0.873	13.898	< 0.001
ZON	–1.618	0.823	3.899	0.049

Finally, LogRA allowed us to measure the strictness of the overall design features of the two kinds of deposition. We found that LogRA correctly classified almost all UM and UR depositions on the basis of three variables. This finding suggests that UM is performed according to severe rules in order to maximize the receiver's response, whereas UR (deposited on branches within the core area) is strictly selected in order to maximize the "safety conditions".

The outcome of these shaped features is a strong reaction of receivers in exploring UM, which is investigated more frequently than UR suggesting a real sender benefit due to tail-up display (Palagi *et al.* 2005). Clearly, the costs of depositing urine holding up the tail are not quantifiable in captivity; our findings, however, may provide a platform for further research in the field to definitely assess this topic.

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References

Alberts, A. C. 1992: Constraints on the design of chemical communication systems in terrestrial vertebrates. — *Am. Nat*. 139(Suppl.): 62–89.

Altman, J. 1974: Observational study of behaviour: sampling methods. — *Behaviour* 49: 227–267.

Bradbury, J. K. & Veherencamp, S. L. 1998: *Principles of animal communication*. — Sinauer Associates, Sunderland.

Daeg, J. M. & Scott, G. W. 1999: Conventional signals in avian agonistic displays: integrating theory, data and different levels of analysis. — *J. Theor. Biol*. 196: 155–162.

Hebets, A. & Papaj, D. R. 2005: Complex signal function: developing a framework of testable hypotheses. — *Behav. Ecol. Sociobiol*. 57: 197–214.

Magnahagen, C. 1991: Predation risk as a cost of reproduction. — *Trends. Ecol. Evol*. 6: 183–186.

Palagi, E., Dapporto, L. & Borgognini-Tarli, S. 2005: The neglected scent: on the marking function of urine in *Lemur catta*. — *Behav. Ecol. Sociobiol*. 58: 432–445.

Rescorla, R. A. 1973: Evidence for “unique stimulus” account of configural conditioning. — *J. Comp. Physiol. Psychol*. 85: 331–338.

Rowe, C. 1999: Receiver psychology and the evolution of multicomponent signals. — *Anim. Behav*. 58: 921–931.

Zahavi, A. & Zahavi, A. 1997: *The handicap principle*. — Oxford University Press, New York.