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Non-invasive measurement of the physiological stress response of wild rabbits to the odour of a predator

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Summary. Stress has been widely studied in different mammals, but the physiological stress reaction that the odour of a predator could induce in preys has not received much attention. Besides, not all the animals would respond to the same extent to a known stressor.

We developed an experimental procedure with eleven naïve European rabbits (*Oryctolagus cuniculus*) in order to determine the individual physiological response to the olfactory detection of a potential predator. The rabbits were housed singly in small enclosures with a concrete burrow system and food and water were available *ad libitum*. The animals followed a control trial, without odour, and an experimental trial where we confronted the rabbits with fox (*Vulpes vulpes*) odour. Furthermore, another sample of eleven rabbits followed a control procedure subjected to the same housing and handling procedures but without facing the predator odour. In order to assess the physiological response we analysed the concentration of glucocorticoid metabolites in the faeces of the rabbits. Therefore, everyday faecal samples were collected and analysed with an enzyme immunoassay in order to measure the corticosterone metabolites (CM), particularly, those metabolites with a 5α-3β, 11β-diol structure.

After validating the assay for wild rabbits, we found that the simulated presence of a predator (fox odour) in the enclosure resulted in an increase in faecal CM concentrations. However, the stressor did not affect all the animals in the same way. We found a general increase in the individual differences. In particular, males experienced a higher increase than females, though the overall response was similar for both sexes.

To our knowledge this is one of the first attempts to analyse the assessment of the risk of predation by means of non-invasive methods.

Key words. Mammalia – Leporidae – *Oryctolagus cuniculus* – non-invasive methodology – stress response – individual differences – risk of predation

Introduction

Normally animals have to deal with predators during their lifetime and being unsuccessful in this task could mean the total loss of fitness. Therefore, preys have developed some adaptations at different levels (i.e. morphological, behavioural, physiological level) in order to decrease the risk of being preyed (Endler 1991; Lima 1998; Kats & Dill 1998). One of such mechanisms is the recognition of nearby predators by their scent. This allows the prey to avoid the so perilous direct encounters and therefore minimises the risk of being killed.

Generally, the assessment of a risk is translated into a modification of the behaviour of the animal. Behavioural responses of preys to the odour of predators have been widely studied in mammals (Hennessy & Owings 1978; Gorman 1984; Dickman & Doncaster 1984; Caine & Weldon 1989; Jedrzejewski & Jedrzejewska 1990; Ward *et al*. 1997; Burwash *et al*. 1998; Jonsson *et al*. 2000; Blumstein *et al*. 2002; Monclús *et al*. 2005). However, the recognition of a predator is not always associated with a behavioural response and this may lead to misinterpretations of the results attained (Ydenberg & Dill 1986). For instance, in those animals in which the costs of the behavioural response surpass the potential benefits, antipredator behaviours might not be present (Blumstein 2002). A complementary approach could be the measurement of the physiological stress response elicited by the recognition of the predator. Predator odour can be a strong stressor, which should activate the hypothalamic pituitary adrenocortical axis (hereafter HPA) and the sympathetico-adrenomedullary system (von Holst 1998; Matteri *et al.* 2001; Möstl & Palme 2002). This would lead to an increase of glucocorticoid and catecholamine levels in the blood, respectively, which are responsible for mobilization of energy. Nevertheless, individual differences between animals in the stress response have been highlighted in several studies (e.g. Cockrem & Silverin 2002).

There are different approaches to the measurement of glucocorticoids. Invasive methods such as blood sampling require trapping, handling and puncture. However, all these procedures affect the glucocorticoid concentrations in blood within a few minutes. Furthermore, especially in small mammals, serial bleeding is not viable (von Holst 1998; Touma & Palme 2005). On the other hand, the use of non-invasive techniques, such as the analysis of glucocorticoid metabolites in the faeces, is highly desirable, as faecal samples can be collected easily without disturbing the animal. Furthermore, since serial sampling is feasible, it

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could provide information about the individual variation among animals. The technique has been established and validated in several species and the suitability for its use in wild animals has been confirmed (reviewed in Möstl & Palme 2002; Touma & Palme 2005).

The aim of the study was to analyse the individual physiological stress response in adult European rabbits (*Oryctolagus cuniculus*) to the odour of a predator. Apart from differences among individuals, we expected to find sexual differences due to different baseline levels or different metabolic routes (Palme *et al*. 1996; Schatz & Palme 2001; Touma *et al*. 2003). Besides, we had to validate this non-invasive technique for wild rabbits since the assay was firstly developed in mice (Palme 2005; Touma & Palme 2005).

Methods

Animals and housing conditions

The animal experiment was carried out at the Department of Animal Physiology of the University of Bayreuth, Germany. All animals were cared for in accordance with institutional guidelines, and the experiments were announced to the responsible authorities (government of Middle Franconia, Germany, 621-2531.32-1/04). We used eleven (six females and five males) adult European rabbits, which were about eight months old. Another group of eleven animals (two males and nine females) which were 7-8 months old were used to control for the possible responses due to handling and housing conditions (see below for details). All animals were descendants from wild individuals that had been caught at different sites in south Germany in 1984. The animals were raised in social groups in a field enclosure where mammalian predators were excluded by means of two electric fences. During the experiments, the individuals were housed individually in outdoor wire mesh enclosures with sandy soil. Digging was inhibited by a wire mesh layer underneath the sand, and on the top of the enclosure a wire mesh was used to exclude raptors. Each of these enclosures (360 × 460 cm) contained an artificial concrete burrow consisting of a tube (length: 150 cm, diameter: 20 cm) and a chamber with a removable top (diameter: 60 cm). In total, six of these enclosures were available for the experiments. To assure that rabbits detected the odours, the scents were placed next to the food. There were two wooden feeding boxes (30 × 30 × 30 cm) per enclosure. One of the sides was left open to allow the rabbits to enter. Each box contained two feeding dishes. In the inner bowl we placed the odour and in the outer the food pellets. Within each enclosure, the feeding boxes were 3 m apart from each other and from the burrow, forming an equilateral triangle. Water was provided ad libitum and everyday we placed in each box 75 g of rabbit food pellets, which exceeds the daily food requirements of the rabbit (cf. Bini & Xiccato 1998).

Experimental design

Rabbits were left to acclimatise for 20 days within the enclosures. After the habituation period they followed two consecutive trials. The first trial aimed on evaluating basal levels of adrenocortical activity, whereas the aim of the second trial was to evaluate the response to a known stressor, the presence of a simulated predator. Therefore, during the first trial (hereafter non-fox odour trial) no odours were presented but during the second trial (hereafter fox-odour trial) fresh fox faeces were placed at random in one of the two feeding boxes. Due to possible preferences for one of the boxes, the trial was repeated, we shifted the boxes and we averaged the values registered in both trials. In summary, rabbits were subjected to a two-choice experiment, so even if the odour of the fox provoked aversion in the rabbits, they had a further option to feed. The total length of the experiment was 14 days. The non-fox odour trial lasted 9 days, in order to have a reliable measure of the basal levels. The fox-odour trial lasted 5 days.

In order to exclude possible additive effects of the trials, which could result in an increase of the glucocorticoid levels at the end of the experiment, we performed a control with another 11 rabbits. They were housed and handled similarly to the experimental animals but they were not exposed to a predator odour. We expected that rabbits would not show an increase in glucocorticoid metabolites during this procedure in contrast to the experimental animals.

Predator odours

All the fox excrements were collected from captive animals of Hof Zoological Park (Franconia, Germany). The faeces were wrapped individually in aluminium foil and were frozen at –20 ºC until shortly before the experiment took place.

Collection and analysis of rabbit faeces

Rabbit pellets were collected daily in the morning during the whole procedure. The sampling was done only once a day in order to prevent further disturbance. As rabbits were housed individually, all the faeces within one enclosure belonged to the resident. The rest of the faeces of that enclosure were removed in order to ensure that the samples collected everyday were excreted during the night before. Immediately after collection, the samples were frozen at –60º C.

We collected the faeces approximately 12 h after the rabbits encountered the odours for the first time, as it is the average time until the excretion peak is registered in rabbits (Piekarz 1963). Due to the high variability expected in the time course of the excretion (Piekarz 1963), we averaged the obtained concentrations of CM per animal and per trial. Each sample was homogenised with mortar and pestle and 0.2 g of each was weighed with the help of a precision balance. The volume of the sample was taken up to 0.5 ml by means of adding water. The metabolites were suspended with 5 ml of methanol (80 %) as described before (Palme and Möstl 1997; Teskey-Gerstl *et al*. 2000). After vortexing for 30 minutes, the samples were centrifuged and a dilution (1:10 with assay buffer) of the supernatant was transferred into a new vial and frozen until analysis. For the analysis of CM in the faeces we used an already established enzyme immunoassay (EIA), measuring metabolites with a 5α-3β, 11β-diol structure. This EIA was developed for laboratory mice *Mus domesticus* (for details see Touma *et al.* 2003; 2004).

Physiological validation of the assay

We validated the assay by means of an ACTH challenge test (Touma & Palme 2005). Rabbits (n_{total} = 16; 10 females and 6 males) were injected intramuscularly with 0.1 g of synthetic ACTH (Synacthen, Novartis, Germany). We used 5 animals from the experimental group and 11 animals from the control group. The validation was done at the beginning of the experiment. Faeces were collected before and on the two following days after ACTH injection (see Fig. 1).

Statistical analysis

For all parametric statistical tests, we ensured that the variables were normally distributed (Shapiro Wilk test) and that variances were homogenous (Levene test). In order to assess the individual variability in the response to a stressor, we calculated the coefficients of variation between animals. For that purpose we used the mean of all the values measured of each animal in each trial.

Results

We could positively validate the assay (repeated-measures ANOVA: $F_{1,15} = 26.529$, $P < 0.001$; Fig. 1). After the injection of ACTH, the values of the faecal CM increased by 174 % (paired *t*-test: $t_{15} = -5.140$, $P < 0.001$). We did not find

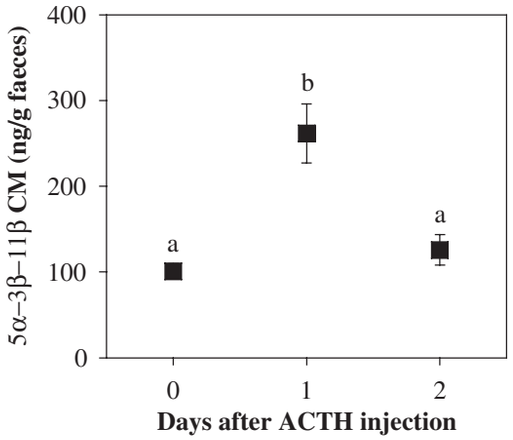

Fig. 1 Concentrations of faecal corticosterone metabolites (5-3,11-diol CM; mean ± SE) after an injection of synthetic ACTH (Synacthen, 0.1 g/ml). Different letters indicate significant ($P < 0.050$) differences according to paired *t*-tests post hoc to a repeated measures ANOVA (see text for statistics)

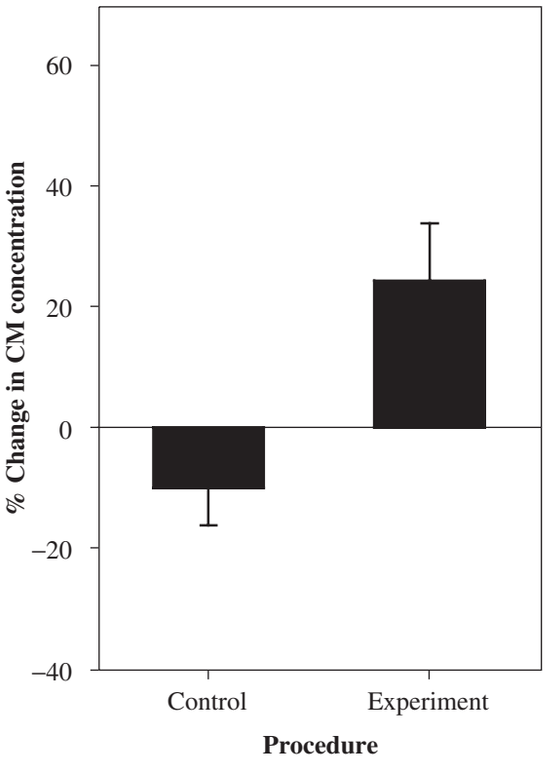

Fig. 2 Comparison of the percentage of change in the faecal CM concentrations (mean ± SE) between the control group and the experimental group. In the experimental group ($n_{individuals} = 11$) fox odour was presented during the second trial but not during the first trial. In the control group ($n_{individuals} = 11$) no fox odour was presented during both trials. See text for statistics

significant differences in the initial increase experienced by males and females (*t*-test: $t_{14.} = 1.555$, $P = 0.173$).

The faecal CM concentrations of the animals of the control group and the experimental group did not differ significantly during the non-fox odour trial (two-way ANOVA: $F_{1,18} = 1.180$, $P = 0.292$). We also did not find statistically significant differences in these initial values between individuals of both sexes ($F_{1,18} = 3.202$, $P = 0.090$). However, the CM values of the males tended to be higher, on average 39.3 % (males: 94.3 ng/g faeces ± 24.0 SD; females: 67.8 ng/g faeces ± 18.7 SD). The interaction between both factors was not significant (group × sex: $F_{1,18} = 1.404$, $P = 0.251$).

After confronting the animals of the experimental group with fox faeces next to one of their two feeding bowls, we detected a strong increase (% change) in the faecal CM concentration. This change differed significantly from the one observed in the control group (*t*-test: $t_{20} = -3.034$, $P = 0.006$; Fig. 2), whereas the males that were exposed to predator odour displayed significantly higher values than females (47.68 % higher) ($Z = -2.646$, $n_{males} = 4$, $n_{females} = 7$, $P = 0.008$). The average values of males and females, respectively, were 126.6 ± 25.0 SD and 68.4 ± 17.6 SD. Nevertheless, these sex differences were not apparent any more with respect to the percentage of change in the experimental group (*t*-test: $t_9 = -1.040$, $P = 0.330$).

We found that during the fox-odour trial two of the animals did not show any increase in their metabolites;. However all the other animals showed a notable increase (> 10 %). In five of these animals, the CM concentrations increased 12 hours after encountering the odour, and in the other four, the increase was apparent 24 h later (36 h since the first encounter). These differences registered in the time course of excretion (12 h or 36 h) were not due to the sex of the animals (Fisher's Exact: $P = 0.524$).

The coefficients of variation (CV) for the experimental group were 29.0 % during the non-fox odour trial and increased to 39.2 %, when fox odour was presented. However, for the control animals the values did not increase between trials, being the CV 27.9 % and 24.7 %, respectively.

Discussion

The measurement of glucocorticoid metabolites in the faeces has been shown to be a useful tool for registering the assessment of the risk of predation in European rabbits. Our results proved that the rabbits were able to recognise a predator by means of its odour and, as a consequence, they exhibited a physiological stress response. However, not all the animals responded to the same extent. We found sex differences when subjected to a stressful situation as well as inter-individual differences in the occurrence of the excretion peaks.

By means of our double validation (ACTH challenge test and the experiment itself) and our standardised set up we could prove that the EIA we used, which was firstly established in mice (Touma *et al*. 2003), is adequate for its use in wild rabbits.

With our experimental set up we could corroborate the results attained before (Monclús *et al*. 2005). When encountering the predator odour, the rabbits experienced an increase in their CM, which could be assigned to their assessment of the risk of predation. Under stress, the

activation of the HPA axis, together with the activation of the sympathetico-adrenomedullary system, contributes to the mobilization of energy necessary to cope with the stressful situation (Boissy 1995; von Holst 1998; Holberton & Able 2000; Buchanan 2000; Creel 2001). In spite of the importance of this mechanism in the stress response, and given the fact that behavioural responses are not always displayed (Blumstein 2002; but see Calder & Gorman 1991), there are only a few studies focusing on the physiological responses to the odour of a predator (Vernet-Maury *et al*. 1984; Lima 1998). However, in any situation one would expect to find a physiological response, as different stressors lead to the activation of the same axis. It has been shown that in species where the rate of encounter with predators is low, animals display a physiological response, which is not translated into a modification of behaviour (Eilam *et al*. 1999).

The measurement of the physiological response by means of non-invasive methods, allowed us to take many samples from each individual so we could assess the high degree of individual variation in the release of corticosterone in response to a uniform stressor. Cockrem & Silverin (2002) found that in great tits (*Parus major*), the increase of plasma corticosterone levels after handling differed between the birds, but was quite conservative within individuals. It is well known that animals cope with stressors in different ways, which could explain the variability observed (Benus *et al*. 1987; Sapolsky 1990; Wingfield *et al*. 1995; Campbell *et al*. 2003). One possible factor affecting those differences could be the sex of the animals (Warner 1981). In our study, males showed higher values than females. In contrast, Boonstra and co-workers (2001) found in arctic ground squirrels (*Spermophilus parryii*) a stronger reaction in females than in males.

Sexual differences in the physiological stress response have been reported in other species (Touma and Palme 2005) and they are supposed to be partly due to differences in the metabolism of glucocorticoids in males and females (Palme *et al*. 1996; Schatz & Palme 2001; Touma *et al*. 2003). Accordingly, we (Monclús *et al*. 2005) did not find differences between males and females in the corticosterone challenge values in serum, supporting the idea of the different metabolic pathways. However, even if the males had higher values, both males and females showed a similar reaction to the stressor, which could indicate that the differences registered in the absolute values were mainly due to differences in the initial levels.

As expected, the rabbits showed a high variability in the time course of faecal excretion. Piekarz (1963) found that in domestic rabbits, which were mainly nocturnal, as in our case (9 out of 11 were exclusively nocturnal), peak excretion occurred on average 12 h after ingestion. However, due to the high individual variability, they oscillated from 5 to 20 h. The fact that some of the rabbits experienced an increase in the CM later than expected could suggest that the differences were due to the variability in the excretion peaks. Moreover, there are several factors that influence retention times, e.g. coprophagy, age, activity, pregnancy, ambient temperature (Piekarz 1963, Warner 1981). As the measurement of faeces CM strongly relies on the time course of excretion, all these factors should be taken into account.

To our knowledge, this is one of the first attempts to trace the physiological stress response elicited by the odour of a predator by means of non-invasive techniques. The measurement of faecal glucocorticoid metabolites is becoming an essential tool in many disciplines, such as animal welfare and conservation biology as it avoids trapping and handling. EIA's have been validated in many different species (reviewed in Möstl & Palme 2002; Möstl *et al*. 2005; Palme 2005, Touma & Palme 2005). However there are still some issues which need improvement, specially when working with free ranging species where sex, rank and reproductive status cannot be achieved so easily (Huber *et al*. 2003; Touma & Palme 2005). Further research should be done in order to study the responses in more complex situations, where social interactions and different trade-offs could modulate the responses.

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