Behavioural Processes 157.(2018): 125-132

DOI: https://doi.org/10.1016/j.beproc.2018.09.007

The landscape of fear: why some free-ranging rodents choose repeated live-trapping over predation risk and how it is associated with the physiological stress response

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Abstract

Live trapping is an essential element of field ecological studies. However, the act of trapping provides two types of conditional benefits (food from the bait when hungry, and refuge from a predator when threatened) against one type of drawback (confinement). Our understanding of how animals assess the two benefits against the lone risk determines how we interpret classic field studies in chemical ecology and wildlife management. Here, we studied wood mice responses to these risks and rewards of field trapping by examining experience through recapture and faecal corticosterone metabolites (FCM) as a physiological response indicator. Wood mice were live-trapped in two different plots subjected to two distinct phases: phase 1, absence of predator cues, and phase 2, in which traps were treated with red fox faeces. During phase 1, the recapture percentage was lower indicating that mice avoided traps while FCM levels in recaptured mice were higher. On the contrary, during phase 2, despite the total number of captures was lower we found an increase in the recapture percentage and FCM levels did not increase in recaptured mice. Our results suggest that under increased risk perception traps could be likely considered as a suitable shelter and thus, for some individuals the benefits of traps may outweigh their risks. In addition, we discovered that the effects of combining two stressors do not result in the addition of the response originated by each factor separately.

Keywords: *Apodemus sylvaticus*; faecal corticosterone metabolites; predator odour; rodent welfare; neophobia; personality

1. Introduction

In nature, wild animals are exposed to a wide variety of threats which compromise their survival. Among them, predation has posed a crucial trade-off in life-history of prey species by affecting not only their ecology and, hence, population densities, but also shaping their behaviour, physiology and morphology (Hegab et al., 2014; Yin et al., 2011; Zanette et al., 2014). Predation risk can modify, among others, daily activity patterns of individuals, use of space, reproduction, social behaviour, feeding habits and the physiological stress response (Clinchy et al., 2013; Lima, 1998; Monclús et al., 2005, 2006).

For prey species, direct observation or physical contact with predators represents an elevated risk of imminent predation. To avoid such encounters, numerous potential prey use remote cues such as predator odours to assess predation risk in every particular situation (Fendt, 2006; Navarro-Castilla and Barja 2014a, b; Navarro-Castilla et al., 2018). A precise and swift identification of the predator, and the entailed risk associated, will confer substantial selective advantages on prey species (Lima, 1998). As a consequence, animals have developed mechanisms which promote efficient recognition of predators to enhance risk evaluation and ensure survival (Tortosa et al., 2015). Even though many behaviours implicated in predator–prey interactions are acquired on an evolutionary timescale, there is persuasive evidence for individual learning (Berger et al., 2007; Griffin et al., 2000; Tortosa et al., 2015). For instance, prey possess the capacity to recognise new predators (Maloney and McLean, 1995; Mirza and Chivers, 2000; Sih et al., 2010) and to acquire avoidance or evasion responses (Ferrari et al., 2005; Kelley and Magurran, 2003). In this regard, experience is critical in the development of these strategies and the choices made based on risk assessment (Keefe, 1992; Sánchez-González et al., 2017). Individuals that were exposed to predator threats in their early development may perform different responses to risky situations compared to those individuals that are naïve (Bischof and Zedrosser, 2009; Lönnstedt et al., 2012; Wiedenmayer, 2009). The characteristics of the antipredator response elicited by a threat constitute an adaptive trade-off between predator avoidance and satisfying vital needs (Lima and Dill, 1990), and these decisions appear to be modulated by the individual's relative level of expertise as well as its body condition (Bachman, 1993). In this manner, experience with a predator threat, whether olfactory or visual, increases the likelihood of surviving in a natural environment (Lönnstedt et al., 2012). Along with visual and odour cues of a predator, prey species acquire environmental information linked to predation risk. For example, moonlight influences the nightly activity of rodents and the perceived predation risk (Orrock et al*.,* 2004; Wróbel and Bogdziewicz, 2015). This phenomenon can be explained by the fact that moonlight improves predator's vision and hence, prey detectability, promoting less activity on full moon and cloudless sky nights in prey species (Díaz, 1992; Wróbel and Bogdziewicz, 2015; Navarro-Castilla and Barja, 2014b).

In order to cope with ever changing environmental demands, animals require a series of physiological and behavioural responses to maintain homeostasis. As a result, animals have developed a wide array of neuroendocrine, morphologic and behavioural adaptations to endure harsh conditions and threats (Willmer et al., 2009; Wingfield et al., 1997). Within this complex array of responses, physiological changes are of pivotal importance, as they increase the energy available for the individual to overcome the environmental stressors (Sapolsky et al., 2000). The physiological stress response is a highly integrated neuroendocrine-systemic process which plays an essential role in the adaptability of animals to changes in the environment (Möstl and Palme, 2002). The response begins with the perception of a stressor, which triggers the activation of the hypothalamic-pituitary-adrenocortical (HPA) axis, stimulating the secretion of glucocorticoids (GC) in the adrenal tissues (Barton et al., 2002; Bonga, 1997). The short-term release of GC is an adaptive response that redirects energy from non-vital activities towards survival (Sapolsky et al., 2000; Wingfield et al., 1998; Wingfield and Romero, 2001). In spite of that fact, chronically elevated GC levels may induce critical deleterious effects, leading to a reduction in the survival rate and fitness (Romero, 2004; Sapolsky et al., 2000; Stewart, 2003). Given this, faecal cortisol/corticosterone metabolites (FCM) have been extensively used as a reliable, suitable and non-invasive measure of GC levels to evaluate the physiological response in vertebrates under stressful circumstances (Barja et al., 2007, 2012; Sheriff et al., 2011; Piñeiro et al., 2012) including small mammals (Fletcher and Boonstra, 2006b; Navarro-Castilla et al., 2014a, b; Navarro-Castilla and Barja, 2014b; Sánchez-González et al., 2018a).

Anthropogenic activities can likewise alter key biological aspects of wildlife species (Barja et al., 2007; Navarro-Castilla et al., 2014b; Casas et al., 2016). Among the vast variety of this kind of threat, field research can be considered as a type of human disturbance having several repercussions on wildlife (e. g. Baker and Johanos, 2002; Moorhouse and Macdonald, 2005; Wilson et al., 2012) including effects on the physiological stress response (Fletcher and Boonstra, 2006a; Harper and Austard, 2001; Place and Kenagy, 2000). Amid field work methodologies, live-trapping has been indispensable in the study of many small mammal species in their natural environment. However, it has been demonstrated to be a stressful event for some species (e.g. Boonstra et al., 2001; Fletcher and Boonstra, 2006a; Harper and Austad, 2001). In addition, it is essential to consider that disturbance effects cannot always be detected by changes in behavioural patterns (Beale and Monaghan, 2004a, b). Previous studies have found evidence of physiological alteration in animals even when they exhibited little or no behavioural reaction or sign of disturbance (Müllner et al., 2004; Ratz and Thompson, 1999). In this manner, to properly understand, assess and minimise disturbance impacts on wildlife populations, the combination of physiological and behavioural measures would be a preferable approach.

Taking all this into consideration, the aim of this study was to analyse the relationship between repeated live-trapping and predation risk on the FCM levels of wood mice (*Apodemus sylvaticus*). In particular, our study explored how previous experience with live-trapping influenced the physiological stress response of wood mice and how predator cues affected this response. Moreover, we examined the link between FCM levels and mice decision making process, attempting to highlight the importance of physiological measures in behavioural research.

Despite the stressful effect of live-trapping for some small mammal species (see references above), we predict lower FCM levels in recaptured mice as a consequence of the harmless previous experience with traps and habituation (Love et al., 2003; Rich and Romero, 2005). Furthermore, we expect that recaptured mice under the influence of predation risk would continue to trigger the physiological stress response. Therefore, we predict higher stress-hormone levels (FCM) in recaptured mice exposed to predator odour compared to the individuals experiencing no predator cues, since imminent predator risk perception could compromise others ongoing physiological and behavioural processes. In addition, we expect diminished captures in traps exposed to predator cues, due to the increase in the perceived predation risk would prompt mice to avoid the area. Finally, because the influence of individual factors (e.g. sex and breeding condition) on capture rate and physiological stress responses has been previously reported in this rodent species (Navarro-Castilla and Barja 2014a, Navarro-Castilla et al. 2014b) both factors were also considered. Due to differences in energetic requirements among these groups, we would expect heightened stress levels and a higher recapture ratio for females and breeding individuals, owing to their increased energetic demands.

2. Materials and methods

2.1 Study area

The study took place in the ‘Monte de Valdelatas’ (Madrid, Spain), a Mediterranean forest situated at an altitude of 650 m a.s.l. The area consists of holm oak forests (*Quercus ilex ballota*) with scrublands, mostly composed by gum rock roses (*Cistus ladanifer*), thyme (*Thymus zygis*) and umbel-flowered sun roses (*Halimium umbellatum*). Predators, such as red fox (*Vulpes Vulpes*) and genet (*Genetta genetta*) can be found in these habitats, the red fox being more abundant (De Miguel et al., 2009; Monclús et al., 2009; Navarro-Castilla and Barja, 2014a).

2.2 Live-trapping and data collection

Mice were captured between February and March 2014. 40 Sherman® live traps were set in two selected plots separated 35 m to be sure that wood mice from each plot belonged to a different population and thus plots constituted independent replicates for mice captures. Furthermore, since we used waterproof paints to identify each mouse, we could verify that the individuals did not cross from one plot to another, hence, we can consider them as two independent clusters. Each plot had 20 traps in a 4 x 5 grid with 7m between all trap locations (Sánchez-González *et al*., 2017; 2018b) to guarantee no differences in vegetation structure across traps surroundings and plots. Live traps were baited with 4 g of toasted corn and they were placed under vegetation to buffer extreme environmental conditions. Moreover, all traps were oriented against the slope to allow correct closing.

Live-trapping was conducted in two consecutive different phases: phase 1 and phase 2, each phase took place during 5 successive days in the same two plots previously described. During phase 1, none of the plots was treated with predator faecal odour, so we could infer the baseline stress-hormone levels (FCM). Next, during the phase 2, both plots were subjected to faecal odour from predator (see detailed information below). There was no gap between both phases, they were consecutive. Total trapping effort was 400 trap-nights (20 traps per grid x 2 plots x 5 nights x 2 phases). Moreover, in order to avoid any potential influence of moonlight on mice's behaviour, trapping sessions for both phases were conducted during days close to a new moon phase, moonlight was on average 10.57% (Min:0%; Max:34%, www.opendata.aemet.es). Additionally, since cloud cover can affect night sky brightness and hence, predation risk, the percentage of sky covered by clouds was taken into account to control for its possible effect (Wróbel and Bogdziewicz, 2015; Sánchez-González et al., 2018b). Cloudiness ranged from 0.10% to 95.40% (50.93% on average, www.opendata.aemet.es).

Each captured individual was identified to species by analysing external morphology. Sex and breeding condition were analysed according to Gurnell and Flowerdew (2006). Sex was determined using the anal-genital distance, which is longer in males than in females. In breeding adult males, the testicles are bigger and usually descend into the scrotal sac, while in breeding adult females a perforated vaginal membrane and prominent nipples in abdomen and thorax can be found. Body weight was measured using a 100-g hand-held scale (PESNET, 100 g), selecting only adults, i.e. those weighing over 20 g (Behnke et al., 1999; Lewis, 1968; Navarro-Castilla and

Barja, 2014a). In addition, we used harmless waterproof paints (Marking stick DFV, www.divasa-farmavic.com) in order to discriminate recaptures. Each individual possessed a unique identification code based on different colour combinations and distinct body parts (paws, inner ear area and tail, where marks were less likely to degrade due to hair loss, Hernández *et al*., 2018). Also, the long-lasting of the marks was confirmed since individuals were recaptured with their marks intact during the whole study. Also, the paint was reapplied to each recaptured individual to ensure the correct individual identification and avoid pseudoreplication. Finally, all captured animals were immediately released at the same place of capture.

2.3 Simulating predation risk by faecal odour

Red fox faeces were used to simulate predation risk since they are one of the most common small mammal predators (Padial et al., 2002; Serafini and Lovari, 1993) and because they have been confirmed to trigger antipredatory responses effectively (Dickman and Doncaster, 1984; Navarro-Castilla and Barja, 2014a,b). Fresh faeces used to make the treatments were gathered from a captive pair of red foxes (one male and one female) from the Cañada Real Open Center (Madrid, Spain). We considered as fresh faeces only those ones with a layer of mucus, an elevated level of hydration and strong odour (Barja et al., 2011; Liu et al., 2006; Martín et al., 2010). These captive foxes were on a carnivorous diet comparable to what they would eat in natural conditions and all fresh faeces samples were frozen at -20 ºC until treatment preparation. Since volatile compounds vary in relation to seasonal or individual factors (Martín et al., 2010; Raymer et al., 1984) all collected faeces were mixed to guarantee homogenization, providing a similar degree of predation risk in all the treated traps, and therefore, avoiding possible result bias. Consequently, each predator treatment consists in 10 g of defrosted and homogenised faecal sample. The faecal material was placed on one side of the trap entrance to avoid blocking the entry for rodents but close enough to act as a potential predation risk cue (i.e. 3 cm approximately). To guarantee odour effectiveness, predator treatment was replaced every day at sunset, in this manner, mice would find fresh fox faeces when they begin their activity peak, i.e. two or four hours after the dusk (Montgomery and Gurnell, 1985). We also controlled the natural presence of wild predator faeces in our study by checking the surrounding area of every trap before data collection, excluding those samples if it was necessary.

2.4 Faeces collection and quantification of faecal corticosterone metabolites

Mice's faeces were gathered daily in the morning, avoiding the possible effect of circadian rhythms in excretion patterns (Touma et al., 2003; Touma et al., 2004), and consequently, in FCM measurements. Only fresh faecal samples were collected to prevent the action of environmental conditions and degradation by microorganisms (Barja et al., 2012; Millspaugh and Washburn, 2003; Möstl et al., 2005). Peak faecal corticosterone metabolite (FCM) concentrations appear in the faeces about 10 h after the injection of adrenocorticotropic hormone (ACTH) in wood mice (range: 8–12 h; Navarro-Castilla et al. 2018). In addition, wood mice are captured on average 6 h after trap activation at dusk (range: 5-7 h; Navarro-Castilla et al., 2018). Thus, traps were opened at sunset (ca. 18:00 pm) and reviewed next morning between 10:00-11:30 am to ensure that animals were confined inside traps the time required to see the possible effect of the capture reflected in FCM levels. Furthermore, faeces with urine presence were discarded to prevent a possible cross contamination that could have affected our results (Touma et al., 2003).

Following Navarro-Castilla et al. (2018) methodology for FCM extraction, frozen faecal samples were dried at 90 ºC in a laboratory heater for 3 h. Then, 0.05 g were weighed and mixed with 500 µl of 80 % methanol and 500 µl of phosphate buffer. At that point, samples were vortexed by hand for 15 s and were shaken in a multivortex for 16 h, followed by 15 min of centrifugation at 2500 g. We used a commercial corticosterone enzyme immunoassay (DEMEDITEC Diagnostics GmbH, Kiel, Germany) previously validated for measuring FCM in mice species (Abelson et al., 2016; Navarro-Castilla et al., 2017). Furthermore, this methodology has been previously used and validated (ACTH challenge, parallelism test, intra- and inter-assay coefficients of variation) to monitor FCM levels in the wood mouse (see Navarro-Castilla et al. 2018). FCM levels are expressed as ng/g dry faeces.

2.5 Statistical analysis

First of all, we used a χ^2 test of frequencies to analyse differences in recapture rates between phase 1 and phase 2 in order to establish whether there was a different response to traps in mice related to the presence of predator odour. Differences in FCM levels in mice according to individual and experimental factors were analysed using a repeated measures ANOVA model. FCM levels were used as response variable in the model. Explanatory variables were: treatment (phase 1 / phase 2 with predator faecal odour), sex (male / female), reproductive state (breeding / non-breeding), night brightness (percentage of sky covered by clouds), and the capture (first capture / recapture) as the repeated measure. Although some individuals were caught several times, we used data only from the first capture and first recapture in the model in order to set comparable conditions and to avoid the inclusion of possible sources of noise in the analysis. First capture was defined as the first time an individual was trapped in each one of the phases, thus, first capture is independently applied in each phase. In order to avoid age-related effects (Navarro-Castilla and Barja, 2018), we decided to use data only from adult individuals in our model. FCM data were log-transformed to meet the assumptions of normality, homocedasticity, and sphericity, which were tested by plotting the residuals and with Mauchly sphericity test, respectively (Quinn and Keough, 2002). Analyses were performed in R 3.3.3 (R Core Team, 2017), using 'car' library (Fox and Weisberg, 2011).

3. Results

A total number of 97 wood mouse individuals were captured during this study; no other species was captured. During phase 1, the total number of captures was 60 and 27% (N=16) of the mice were recaptured. During phase 2, the total number of captures significantly decreased to 37 ($\chi^2_{1, 97} = 5.454$, P = 0.020) while recapture percentage increased to 51% (N=19) (Figure 1), which entails a significant increment in the recapture rate ($\chi^2_{1, 97} = 6.047$, P = 0.014).

Overall, the analysis of the stress response showed that recaptured individuals showed lower stress-hormone levels (24079 mean ± 4953 SE) than those captured the first time (412669 mean ± 384942 SE) (F1,29 = 5.52, P = 0.026, N=97). In addition, captured individuals exposed to predator faecal odour (N=37) exhibited higher stress-hormone levels (828535 mean ± 794279 SE) than those captured during phase 1 without the predator odour (22371 mean ± 5413 SE) (F1,29 = 5.41, P = 0.027, N=60) (Table 1). However, FCM levels were more precisely explained by the significant interaction between capture and treatment (F 1,29 = 7.83, P = 0.009; Table 1): during phase 1 (no predator odour), recaptured individuals exhibited higher FCM levels (30670 mean ± 7816 SE) than individuals captured for the first time (9196 mean ± 3612 SE) (β = -2.12

± 0.79; p = 0.0125, N=16). Conversely, this was not the case for individuals recaptured during phase 2 (N=19), FCM levels were in fact marginally higher in first captured mice (2021120 mean ± 1963543 SE) (β = -1.42 ± 0.73; p = 0.061) than in recaptured ones (326969 mean ± 311255) (Figure 2). Additionally, reproductive mice (N=27) showed higher stress levels (1143712 mean ± 965093) than non-reproductive ones (22874 mean ± 4339) (F 1,29 = 8.45, P = 0.007, N=70) (Figure 3). No other factor or interactions were significant in the model. The statistical model is summarized in Table 1. A more detailed description about sample sizes can be found in table A of supplementary material section.

4. Discussion

In our study, physiological stress measures have demonstrated to be of crucial importance, allowing us to detect changes in the behavioural learning process and revealing the magnitude of the live-trapping and predation risk effects. Our results have revealed that the exposure to predator odour triggered the physiological stress response in the wood mice as a consequence of perceived imminent predation risk, although repeated live-trapping seems to dilute the predator´s effect. Therefore, red fox faecal chemical signals are used by wood mice as a cue for risk assessment as previous studies have attested (Navarro-Castilla and Barja, 2014a, b; Sánchez-González et al., 2017). Moreover, as we expected, predator faecal cues decreased the total number of captures. Consequently, as previous studies have also highlighted (Navarro-Castilla and Barja, 2014a), some mice tend to avoid risky environments.

Contrary to our initial prediction, instead of diluting the potential stressor effect due to the previous non-harmful experience inside traps, recapture was found in fact to increase mice FCM levels. However, this was the case only for the phase 1 (i.e. mice not exposed to predator odour). Previous experience with trapping seems to intensify the physiological stress response in recaptured mice. Some studies have reported a failure to habituate to trapping stress for small mammal species (Lapointe et al., 2015; Hämäläinen et al., 2014). Nevertheless, our findings go further by revealing a possible sensitization process, being individuals more sensitive to live-trapping if they have already gone through that ordeal, as they are aware of the following hours of confinement. In this respect, comparing our recapture ratio result between both phases (phase 1: 27%; phase 2: 51%) we found evidence of mice showing increased trap avoidance when they were not under predation risk. Alternatively, it would be reasonable to think that mice's ability to learn from harmless but unusual experiences would be a process that takes more time and repetitions to correctly assess its potential danger and repercussions. Since antipredator strategies involve some associated costs (Preisser et al., 2005), these responses cannot persist indefinitely, especially when they are unnecessary. Hence, it could be plausible that repeated trapping sessions over time leads to a reduction in the physiological stress response. If mice have effortless access to food without suffering any damage they might eventually learn that the cues associated with such encounter would not be as dangerous as they considered them the first time. To confirm such theories, further research would be necessary.

Regarding the physiological stress response of mice exposed to predator odour, we found that it was not affected by recapture. In this case, despite we expected increased FCM levels in recaptured mice as the result of the combination of both stressors (predation risk and being confined for the second time), this interaction did not show a synergistic effect. As results have shown, FCM levels were similar in recaptured mice, with or without predator odour, hence, repeated live-trapping could be considered as an equally powerful stressor as predation risk is. Furthermore, this result could indicate that once a stressor is operating, the presence of another factor does not proportionally increase the amount of FCMs, perhaps because the physiological response is triggered only just once independently of the number of causing factors that were present. Another possible explanation could be that predation risk was the predominant stressor masking the effect of the recapture in the treatment phase. According to this, mice under imminent predation risk reach maximum levels of FCM and the repeated confinement loses importance upon the possible occurrence of a predator attack.

On the other hand, it could be also possible that when predation risk is operating, mice consider traps as a safe shelter instead of a dangerous space, restraining the expected synergistic increase in FCM levels. This hypothesis found empirical support once we analysed recaptures during each phase of the study. Previous studies in the wood mice have shown a recapture ratio above 30% (Navarro-Castilla and Barja, 2014b; Sánchez-González et al., 2017), while in our case was slightly lower (27%) in phase 1 and significantly higher in phase 2 (51%). This suggests that when predator odour is present, some mice actively searched for shelter, considering traps as a suitable refuge. It seems that when perceived predation risk is high, the benefits of the traps overbalance the fear to confinement. However, since total number of captures decreased in phase 2, we believe that mice energy requirements and personality may be driving these results (Quinn and Cresswell, 2005; Dosmann and Mateo, 2014; Yuen et al., 2016). Thus, some individuals avoided predator cues, and this would be the reason for the diminished total captures in phase 2, while other individuals could consider traps as a refuge and/or had different energetic demands, increasing the recapture ratio. Alternatively, previous experience and the predator inspection phenomenon (Parsons et al, 2018) could have also influenced mice behavior contributing to the increased recapture ration during phase 2. .

We also found that reproductive status influences FCM levels in the wood mouse, being higher in breeding individuals as previous studies have highlighted (Navarro-Castilla et al., 2014b; Sánchez-González et al., 2017). This result can be explained by the vast increase in energetic demands that female mice experience during the breeding period and the increase in the number and magnitude of agonistic interactions due to intraspecific competition (Malo et al., 2013; Montgomery et al., 1997). Overall, breeding males become territorial and a dominance hierarchy is established, while females have to protect their progeny (Montgomery and Gurnell, 1985; Wolton, 1985). In all of these cases, the increment in FCM levels could be probably linked to an intensification of the aggressive response, aimed to ensure their inversion in biological fitness (Frid and Dill, 2002).

To the best of our knowledge, the present study is the first to examine the combined effects of predation risk and recapture on the physiological stress response. Through this novel approach we found that possibly due to personality and energetic demands differences, the benefits of traps surpass the costs of being confined for some mice when predation cues are present, while others still considered it as a risky environment and tend to avoid it. In addition, we have discovered that the effects of combining two stressors (i.e. repeated confinement and predation risk cues) do not result in the addition of the response elicited by these factors individually. In other words, we found that once a stressor is present, the inclusion of another stressful factor does not exacerbate the physiological stress response. To conclude, live-trapping can be considered as an influential factor affecting wood mouse physiological stress response. Consequently, the potential effects of repeated trapping methods should be taken into account in the experimental design of future studies.

Acknowledgements

The authors would like to thank the Comunidad Autónoma of Madrid (Spain) for providing the permits required to conduct this study. We are grateful to Cañada Real Open Centre, especially to José España, for supplying the red fox faeces needed to carry out the experiments. Finally, special thanks to Juan Malo and Cristina Mata for providing us the trapping equipment.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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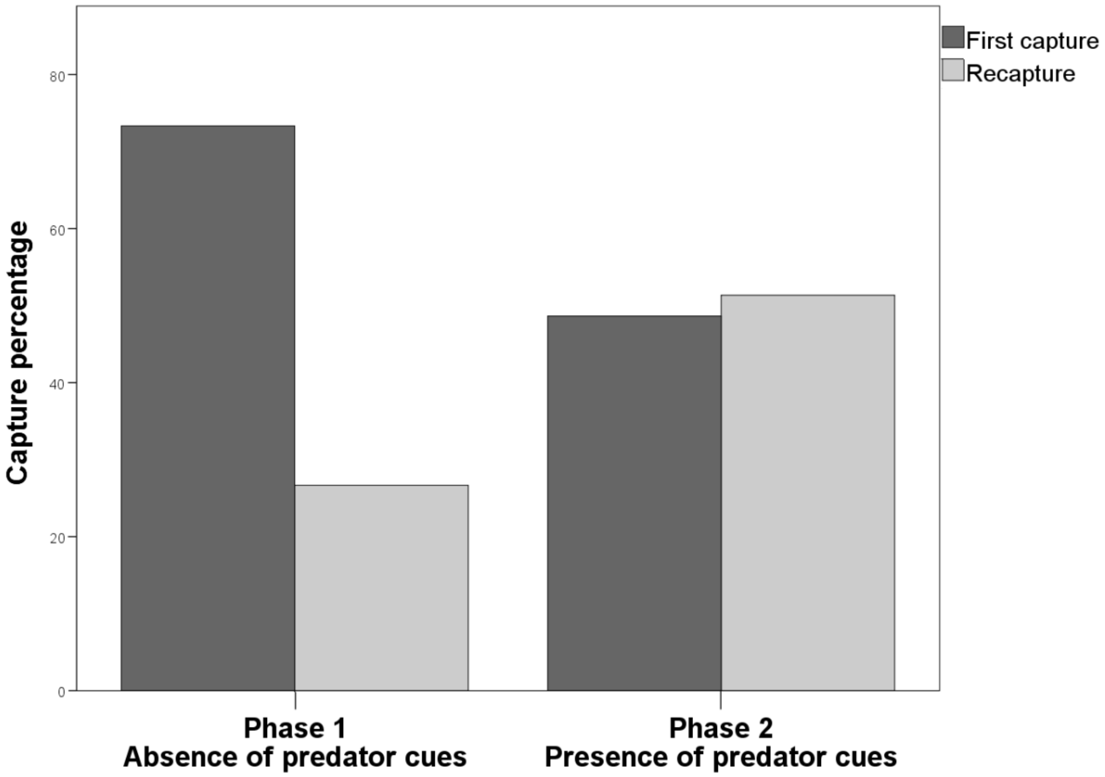

Figure 1. Percentage of first capture and recaptured mice during each phase of the study (Phase 1: absence of predator odour; Phase 2: presence of predator odour).

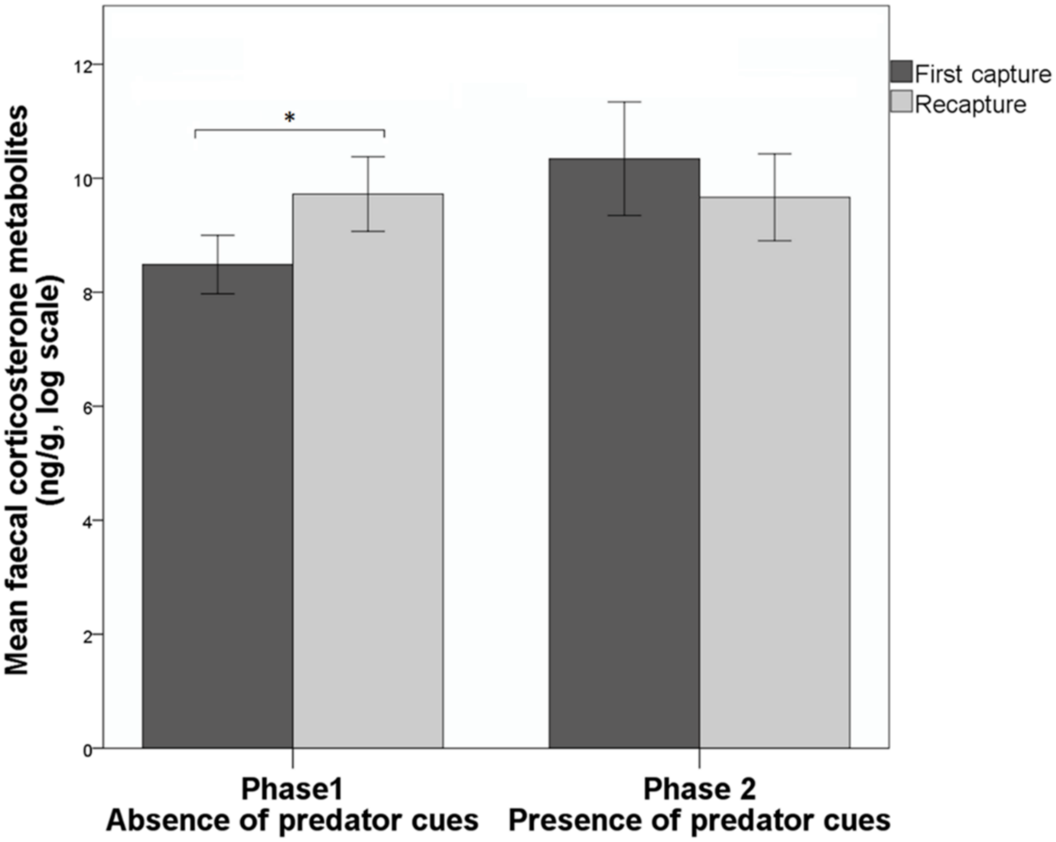

Figure 2. Faecal corticosterone metabolite levels (mean ± SE, log transformed) of individuals exposed and non-exposed to predator odour during the first capture and the recapture. $^*p < 0.05$

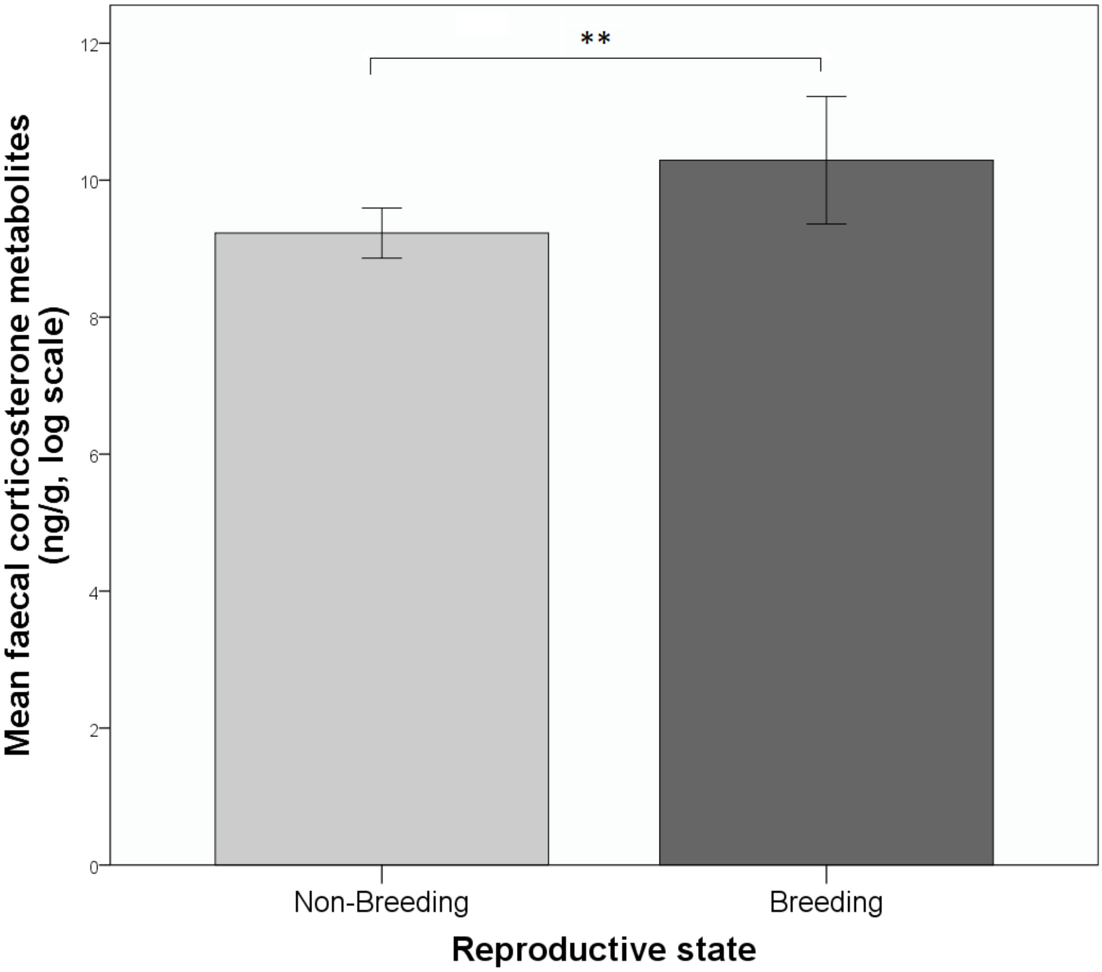

Figure 3. Comparison between faecal corticosterone metabolite levels of reproductive and non-reproductive individuals (mean ± SE, log transformed). **$p < 0.01$

Table 1.

Results of the repeated measures ANOVA model analysing faecal corticosterone metabolites in mice depending on environmental and individual factors.

Variable	**Partial eta^2**	**SS**	**F**	**df**	***P***
Intercept	0.89101	175.14	82.51	1.29	< 0.001***
Capture (first capture / recapture)	0.1054	15.44	5.52	1.29	0.026*
Treatment (phase 1 / phase 2)	0.15715	11.48	5.41	1.29	0.027*
Sex (male / female)	0.001	0.06	0.03	1.29	0.866
Reproductive state (breeding / non-breeding)	0.22573	17.95	8.45	1.29	0.007**
Night brightness (cloud cover)	0.02828	1.79	0.42	2.29	0.660
Capture * Treatment	0.21263	21.88	7.83	1.29	0.009**
Capture * Sex	0.03845	3.24	1.16	1.29	0.290
Capture * Reproductive state	0.00037	0.03	0.01	1.29	0.918
Capture * Night brightness	0.10517	9.52	1.70	2.29	0.200

Supplementary material.

Table A. Descriptive table for the data collected including predictor variables (sex, reproductive state and recapture) depending on the phase (phase 1: absence of predator odour and phase 2: presence of predator odour).

	Non-breeding		**Breeding**			
	Males	Females	Males	Females	**Grand Total**	**Recaptures**
Grand total	**30**	**40**	**18**	**9**	**97**	35
Phase 1	19	24	9	8	60	16
Phase 2	11	16	9	1	37	19
Recaptures	**10**	**13**	**8**	**4**	**35**	
Phase 1	5	5	3	3	16	
Phase 2	5	8	5	1	19	