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Predator presence affects the reproductive success of prey in outdoor conditions

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Abstract. The reproductive outcomes of laboratory rats (*Rattus norvegicus*) housed at different distances (2, 20 and 80 m) from a predator (*Lynx lynx*) were investigated. Virgin female (n = 120) and male (n = 40) rats of an outbred laboratory population were used for the experiments. Groups of rats (one male and three females) were housed in standard cages in close proximity to the predator. Litter size, sex ratio, number of live pups, number of placental scars and corpora lutea were counted; and pre- and post-implantation losses were calculated for each female. The reproductive success of females, estimated as the number of live pups per female, was significantly higher in both control groups (20 and 80 m) than in both experimental groups (2 and 2 m). Equal numbers of corpora lutea in all groups but different numbers of placental scars between control and experimental groups indicated higher pre-implantation losses in the experimental groups. Post-implantation losses were also higher in both experimental groups. Total losses (calculated as a difference between the number of corpora lutea and live pups) were twice as high in experimental groups. Reproductive success of rats depended on concentration/intensity of predator scents: when concentration/intensity was higher, the number of live pups was less and the total loss was higher.

Introduction

Many mammals utilise olfactory cues to detect potential danger from predators. Avoidance of the predator odours and suppressed feeding behaviour have been described for potential prey species of three main mammalian taxonomic groups: rodents, lagomorphs and ungulates (Muller-Schwarze 1973; Sullivan et al. 1988; Boag and Mlotkiewicz 1994). Other behaviours of prey may also be affected by the presence of a predator or its odours. For example, predator odours derived from predator faeces, urine and gland secretions, and compounds isolated from these sources, suppress feeding behaviour in rodents (Sullivan et al. 1988). On the bases of these studies, predator scents as natural repellents have been used to develop pest management products to protect plants from herbivores. However, behavioural responses of prey species are not restricted to avoidance and changes in feeding behaviour. Prey species under high predation risk may change their activity rhythms to minimise risk. High predation risk may decrease the locomotor activities of prey, change their activity level and spatial distribution or alter their natural rhythm of activity (for example, from nocturnal to diurnal) (Fenn and MacDonald 1995).

Predator odours may also directly affect the reproductive physiology and behaviour of rodents. In nature, predators are one of the most powerful extrinsic factors affecting prey population cycles (Hentonnen et al. 1987; Klemola et al. 1997). We previously showed that oestrous cycles were extended in Norway rats that were exposed to mink (*Mustela vison*) anal sac secretions (Voznessenskaya et al. 1992). Similarly, the duration of oestrous cycles was extended in bank voles (*Clethrionomys glareolus*) exposed to weasel (*Mustela nivalis*) odours (Koskela et al. 1996). Fewer bank voles bred when exposed to weasel odours relative to control voles not exposed to weasel odours (Ylonen 1989; Mappes and Ylonen 1997). In our earlier laboratory studies, we observed reductions in the litter size of Norway rats when they were exposed to predator chemical cues. Reductions in litter size are correlated with resorption of embryos and declines in plasma progesterone (Voznessenskaya et al. 1999, 2000).

The aim of this study was to determine the relationship between reproductive responses of the prey and the proximity and intensity of predator signals.

Materials and methods

The study was performed at the biological station ‘Tchernogolovka’, 50 km north of Moscow in 1998–1999. Eurasian lynx were kept in large enclosures and fed a diet of chicken meat, rats and voles. Four shelters for rats were constructed at different distances (2 m (n = 2), 25 m and

80 m) from the lynx enclosures. Rats from a laboratory outbred population (120 virgin females, 40 males) were used for the experiments. Animals were kept in groups of one male and three females. There were 11 groups of 4 animals at 2 m; 9 groups of 4 animals at 2 m, where the lynx urine was placed on the bedding; and 10 groups of 4 animals at each of 25 m and 80 m. Rats received rat chow and water *ab libitum.*

Each group of rats could not see any lynx but they could smell and detect their auditory signals. In addition, lynx urine was placed directly on the bedding of the rats' cages for one of the groups held 2 m from the lynx. We recorded the duration between pairing of animals and parturition, total number of pups for each litter, number of live pups for each litter, number of corpora lutea and number of placental scars for each female. Pre-implantation loss was recorded as number of corpora lutea versus number of placental scars. Post-implantation loss was counted as number of placental scars versus number of newborn live pups. We included stillborn pups and pups that died within a few hours of birth because of the mothers' mistakes or their birth injuries.

For the statistical analysis, the data for both experimental groups at a distance of 2 m were pooled and compared with the pooled data of the groups held at 25 and 80 m. Student's *t*-test was used to analyse the data with normal distribution and Fisher's test was used for analysis of percentages of pre- and post-natal losses. All indices were calculated for each group.

Results and discussion

Predator presence did not affect the percentage of females breeding (86.7–97%) in the two groups held within 2 m of a lynx. The addition of the lynx urine on the bedding of the rat cage did not decrease the reproductive success of females in comparison to the other group situated within 2 m of the enclosure. No significant differences in numbers of females giving birth were found for the experimental groups within 2 m of the lynx in comparison to the control groups (25 and 80 m). However, the average litter size was slightly less (about 7.4%) and the average number of live pups was significantly less in both experimental groups than in the control groups (Table 1). Estimated post-implantation losses (Fisher test, $T = 6.26$, $p < 0.001$) and pre-implantation losses (percent of non-implanted eggs) (Fisher test, $T = 2.44$, $p < 0.05$) were higher in the experimental groups than in the control groups. The average number of corpora lutea per female was similar for the experimental and control groups (Student *t*-test, $T = 1{,}10$, not significant). Analysis of the number of successfully implanted eggs (placental scars) showed that control females had significantly more scars than other females (*t*-test, $T = 11.43$, $p < 0.001$; 9.1% less in experimental groups). Total losses (calculated as number of live pups versus number of ovulated eggs) were almost twice as high in the experimental groups where almost two thirds of the ovulated eggs died at different stages of preg-

Table 1. Influence of distance from predator presence on reproduction of rats (mean ± standard deviation; numbers given in brackets = number of animals; * = $p < 0.05$, *** = $p < 0.001$)

Reproductive parameter	Distance from predator odour and sound			
	Experimental groups		Control groups	
	2 m	2 m + urine on bedding	25 m	80 m
Pregnant females (%)	97.0 (33)	96.3 (27)	93.3 (30)	86.7 (30)
Time interval (pairing–parturition) (days)	25.5 ± 2.9 (28)*	25.5 ± 2.4 (23)	25.0 ± 4.2 (27)	24.9 ± 4.5 (25)
Litter size (*n*)	8.9 ± 3.1 (29)*	8.5 ± 2.7 (24)***	9.4 ± 3.1 (28)	9.4 ± 2.8 (25)
	8.7 ± 2.9 (53)***		9.4 ± 3.0 (53)	
Live pups (*n*)	5.4 ± 4.0 (29)***	6.9 ± 3.8 (24)***	8.4 ± 3.7 (28)	8.7 ± 3.3 (25)
	6.1 ± 4.0 (53)***		8.5 ± 3.5 (53)	
Placental scars (*n*)	9.9 ± 3.7 (31)***	10.1 ± 2.9 (25)***	10.8 ± 3.6 (28)	11.2 ± 2.4 (26)
	10.0 ± 3.3 (56)***		11.0 ± 3.1 (54)	
Number of corpora lutea	12.9 ± 2.2 (15)	13.6 ± 4.4 (12)	12.5 ± 2.8 (8)	13.2 ± 2.2 (10)
	13.2 ± 3.3 (27)		12.9 ± 2.4 (18)	
Estimated pre-implantation losses (%)	23.8 (193)	29.4 (163)*	19.0 (100)	16.7 (132)
	26.4 (356)*		17.7 (232)	
Estimated post-implantation losses (%)	47.6 (288)***	33.8 (237)*	22.4 (303)	25.2 (290)
	41.3 (525)***		23.8 (593)	
Estimated total losses (%)	69.0 (171)***	51.3 (158)**	33.0 (100)	34.2 (117)
	60.5 (329)***		33.6 (217)	

nancy (eggs did not implant, embryos resorbed at different stages, pups died during or after parturition). Among the control females, significantly fewer ovulated eggs (less than one-third) were lost (Fisher's test, $T = 6.15$; $p < 0.001$).

Thus, pre- and post-implantation losses were higher for the experimental groups. It is possible that losses during both of these stages of pregnancy may be an important reproductive strategy for the prey in the presence of predator.

Litter size decreased significantly in rats exposed to domestic cat odours in the laboratory with a high percentage of embryos resorbed after implantation (Voznessenskaya and Naidenko 1999; Voznessenskaya et al. 1999). The resorption rate was probably due to a low level of progesterone in the blood plasma of rats exposed to cat urine (Voznessenskaya et al. 1999, 2000). This study in outdoor conditions with natural light and temperature provides an opportunity to estimate prey reproductive success with respect to intensity and proximity of predator signals. Some of the pups that died soon after birth had morphological deformities, which could have been due to partial resorption at the late stages of pregnancy.

In this study, female rats in close proximity to lynx had higher pre-implantation losses than control groups held at greater distances. Total losses in experimental groups were twice as high as in control groups. The presence of the predator affected pre-implantation losses, though not as much as the effects on post-implantation losses. Although the predator odour decreased reproductive success of Norway rat females (Voznessenskaya et al. 1999; Voznessenskaya and Naidenko 1999) the addition of lynx urine on the bedding of rats' cages did not increase the effect. Possibly the optimal reproductive strategy for rats under high predation risk might be to decrease reproductive output but not to stop reproduction.

The reproductive output of female rats measured as the number of live pups depended on intensity of lynx signals. Close proximity to the predator affected significantly the reproductive success of each female prey but it did not change the percentage of females reproducing as was described for voles (Ylonen 1989).

Conclusion

The concentration of lynx olfactory signals and/or the intensity of auditory signals significantly influenced the reproductive success of rats. Average litter size and number of live pups were lower in experimental groups. Prenatal mortality before and after implantation was lower in both control groups. Approximately two of three ovulated eggs failed during the pregnancy in experimental females, twice as high as in control females. The decrease in litter size and number of live pups in the presence of the predator might represent an adaptive response of female rats to the high intensities of predator signals.

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