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ARTICLE

Chronic exposure of cat odor enhances aggression, urinary attractiveness and sex pheromones of mice

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Abstract To test whether predator odor exposure negatively affects the behavior of prey, we exposed three groups of male house mice (*Mus musculus*) to the odors of cat (*Felis catus*) urine, rabbit (*Oryctolagus cuniculus*) urine and water (control), respectively, for consecutive 58 days and investigated how the treatments affected the response, aggressiveness, dominance, urinary attractiveness to females and pheromone composition of male mice. Compared to mice exposed to rabbit urine or water, those exposed to cat odor did not show any response habituation to the cat odor and became more aggressive, increased mark urine production and were more attractive to females when the latter were tested with their urine. Furthermore, gas chromatography coupled with mass spectrometry analysis revealed coincident elevations of the well-known male pheromones, *E,E*-α-farnesene, *E*-β-farnesene, *R,R*-dehydro-exo-brevicomin or *S*-2-*sec*-butyl-dihydrothiazole. In addition, rabbit urine exposure increased urinary attractiveness to females and pheromonal levels of the males in comparison with the mice exposed to water. This could be related to olfactory enrichment of heterospecific chemosignals, suggesting that predator odors were more beneficial. In light of these anti-intuitional findings in the chemical interaction between cats and mice, we conclude that predator odor affects prey more profoundly than previously believed and that its impact may not always be negative.

Keywords Aggression · Pheromone · Predator odor · Prey · Sexual attractiveness

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Introduction

Predator odor has been widely documented as a signal that elicits aversive, avoidance and defensive responses and induces fear, anxiety and stress in prey species (e.g. Caine and Weldon 1989; Engelhart and Müller-Schwarze 1995; Burwash et al. 1998; Mason et al. 1994; Kemble and Bolwahnn 1997; Monclús et al. 2005; Takahashi et al. 2005). These behavioral and psychological responses are particularly prominent in rodents, which are low in the food chain and thus have numerous predators in their natural habitats (e.g., Sullivan et al. 1990; Perrot-Sinal et al. 1999; 2000; Herman and Valone 2000). Rodents also rely heavily on olfaction to carry out their daily activities, including feeding, anti-predation response and social interaction. Consequently, rodent models are considered to be among the best of those currently available for studying predator odor and its behavioral, neural, hormonal, psychological, and developmental effects on prey species.

Recent studies of prey response to predator odor have revealed many interesting and insightful aspects of the effects of carnivore odor on rodents. Most predator odors have been documented to exert negative effects on behavior, development, physiological condition and

reproduction (see Apfelbach et al. 2005). For example, cat odor and trimethylthiazoline (TMT, a compound found in fox feces) can elicit behaviors, such as freezing and avoidance, and increase the level of stress hormone in rats (Takahashi et al. 2005). Predator odor also negatively impacts on the physiological condition and developmental process of rodents through changes in the neural and hormonal systems. As a result, long-term stress from exposure to predator odor can inhibit the development of the reproductive system and disrupt normal reproductive cycles in rodents (see Vasilieva et al. 1999; Zhang et al. 2003, 2004; Bian et al. 2005). Our previous findings also revealed that chronic exposure to predator odor reduced aggression, flank marking, and, consequently, social rank in the ratlike hamster (*Tscheskia triton*) and golden hamster (*Mesocricetus auratus*) (Zhang et al. 2003). In particular, the flank gland of the ratlike hamster was atrophied in adult males and hypertrophied in adult females, whereas reproductive organs were suppressed only in subadults by chronic predator exposure (Zhang et al. 2003, 2004).

Hormones often have profound and diffusive effects on animal behavior (see Becker et al. 2002). If predator odor-induced stress affects hormones in prey animals, it is also expected to alter a wider spectrum of behavior than what has been reported to date. Since mammalian pheromone production is controlled by or intimately related to hormones, we should expect that changes in hormones would lead to corresponding alterations in pheromones, which in turn modify social interaction patterns in mammals. In this chain of interrelationships cascading from predator odor to prey behavior, data reported in the literature have already established a solid connection between stress and behavioral or psychological consequences in individual prey animals. However, very little information is currently available on the effect of predator odor-induced stress on pheromonal change and its consequence in social behavior in prey species. As a result, our current understanding of the role of predator odor on prey is largely limited to psychological stress inferred from aversive behavior or fluctuations in the levels of glucocorticoids in prey animals.

In this study, we used the best known predator–prey interaction system between cats and mice and designed a series of experiments to explore how long-term (8 weeks) exposure to 5 μl cat urine presented with capillaries would affect mouse individual and social behavior. Specifically, we tested the hypothesis that predator odor induces stress in prey by testing the predictions that exposure to cat odor increases aversive behavior and lowers female preference for males. Furthermore, we attempted to connect female preference to corresponding changes in aggressive behavior and pheromone constituents in males stressed by cat odor.

Materials and methods

Subjects

Forty-eight sex-naïve male ICR mice (purchased at 8 weeks of age from Harlan Sprague-Dawley, Indianapolis, IN) were used in our study. They were individually kept in polypropylene cages (27 × 12 × 17 cm) at 21 ± 0.2°C and 50–70% relative humidity at the Indiana University Animal Facility for 4 weeks before being used in the experiments. A 12:12-h (light:dark) reverse light cycle regime was used with the light cycle going on at 22:00 hours. Purina Mouse Chow and water were supplied ad libitum. The bedding material (sawdust) was changed weekly.

At the beginning of the experiment, the mice were randomly assigned to one of three groups, each with 16 individuals. These were housed in three separate rooms for testing the effects of exposure to cat urine, rabbit urine and water (control), respectively. The mice of the three groups did not differ in body weight at the beginning of the experiment (water-group 39.29 ± 3.32, rabbit-urine group 39.1 ± 3.51, cat-urine group 39.21 ± 3.76; one-way ANOVA $F = 0.011$, $P = 0.989$).

An additional 21 ICR females, purchased at the age of 16 weeks, were kept under the same conditions, but separate from the males. The females were used as male odor recipients in experiments after 2 months of acclimation. Only females on the estrous day of their estrous cycle (as determined by vaginal smear) were used for the binary choice test.

The animal handling procedure complied with the institutional guidelines of Indiana University for animal use and care. If the males were injured in the staged dyadic encounters, the tests were terminated and the mice would receive immediate medical care.

Urine collection

Cat (*Felis catus*) urine for use as a predator odor was collected by a veterinarian from two castrated males (aged 7 years and raised on commercial chow). We collected rabbit (*Oryctolagus cuniculus*) urine as a non-predator novel odor from four adult males (New Zealand white strain, raised on Rabbit Chow 5326 Laboratory Diet) individually housed in the animal unit of the Department of Psychology, Indiana University under the 12:12-h (light:-dark) light regime. Urine was collected by placing each cat or rabbit individually in a clean cage with a grid floor and setting a clean collecting pan (with plastic films) underneath. After the animals had urinated into the collecting pan, the urine was immediately collected into vials and placed in a freezer for storage at –20°C until analysis.

Potentially contaminated urine, such as that deposited with or next to feces, was rejected. We pooled urine samples from conspecific individuals and used these for treating the experimental subjects.

Urine samples used for testing their attractiveness to females and determining the pheromone composition were collected from male mice on the days 51–55 of odor exposure. The samples were collected from 12:00 to 17:00 hours during the dark phase of the light cycle in modified mouse metabolic cages, each of which was equally partitioned into five compartments with opaque Plexiglas separators to prevent male urine donors from fighting. We placed five males into each of the five compartments and let urine from the metabolic cages drip into the collecting tube that was immersed in dry ice. Urine from each mouse was collected once a day, and the collection period lasted 2.5 h. Urine samples of the same group were later pooled and stored at –20°C until being used for the chemical analysis and behavioral test. Tap water was used as the control.

Novel odor exposure

To prepare the odor samples to be presented to test subjects, we used a micro-syringe to inject 5 μl cat urine, rabbit urine, or water into a glass capillary (ID 1.5 mm, OD 2.0 mm, length 10 cm), which was then sealed with Bio-seal at one end. The samples stayed inside the micropipette in such a way that test subjects could not come into contact with the urine even if they occasionally touched the capillary. We hung the capillary at the side panel of each feeder, above the lid and just beyond the reach of the mice. The snout of the mouse could come no nearer than 1 cm. We renewed the urine in the capillary daily for 58 consecutive days to keep the odor stimulus fresh.

Quantification of behavior

Habituation of males to the exposed odor

On the days 56–58 of odor exposure, we tested the responses of cat urine-exposed males to cat urine samples, those of rabbit-urine exposed males to rabbit urine samples and those of water-exposed males to rabbit urine and cat urine samples. All tests were carried out from 12:00 to 17:00 hours during the dark phase. Immediately prior to each trial, we transferred a test mouse from its home cage to the test room under dim light. One sample type (5 μl) was injected into and kept in a disposable glass capillary as described above. The sample-containing end of the capillary was presented to mice, while the other end was held by an investigator wearing disposable plastic gloves. The capillary was lowered through the wire lid and the sample presented to the test subject for 3 min. Stopwatches were used to record the potential time (latency) from the first sniffing response to first contact (licking/biting) with the capillaries, accumulative time spent in sniffing within a 1-cm radius of the tip and accumulative time spent licking/biting the end of the capillary.

Binary choice test of the response of females to male urine

To test female preference for males treated with one of the three different odors, we first selected estrous females and moved them individually from their home cages to a separate room. Using an experimental procedure similar to that described above, with the same amount of urine, we simultaneously presented paired urine samples (treated with different odors) to each test female for 3 min after initial sniffing of the mouse at one end of the cage. The two capillaries holding odor samples (approximately 2 cm apart) were lowered through the wire lid. The durations that the females spent sniffing and occasionally licking the end of the capillaries within a 1-cm radius of the tip were measured with two stopwatches (Zhang et al. 2007). A mouse was used only once a day, and data from subjects whose investigating time was less than 1 s were excluded from analysis.

Aggressive behavior

The observed patterns of aggressive behavior included rudely licking and pushing the partner's head and back, biting, chasing and sideway posture (Gray and Hurst 1995; Zhang et al. 2001). To study aggressive behavior, we allowed male mice to stage dyadic encounters in a separate room under dim illumination during the dark cycle on the 59th day of odor exposure. All mice were tested once. Two paired males were weight-matched (within a 2-g difference in weight) and simultaneously placed in a clear mouse cage (dimensions 27 × 12 × 17 cm). The frequency of aggressive behaviors was continuously recorded for 10 min beginning with the first appearance of an aggressive behavior. Such behaviors were recorded by hand on a data sheet with a pre-calibrated time scale in units of 10 s; that is, a behavior pattern that lasted 10 s or less was treated as one unit. If the duration was greater than 10 s but less than 20 s, the behavior was considered to be two units, and so on (Zhang et al. 2001). The time was measured with a stopwatch.

Quantification of pool urine and mark urine

To quantify "pool urine" (namely, regular urine) excreted by mice in cage corners in a pile, indicating subordination, and "mark urine", by which mice vigorously urinate all over their cages in numerous droplets, indicating dominance (Desjardins et al. 1973), we used a micropipette to separately collect the two different kinds of urine from each subject. We pipetted up as much as possible of the two types of urine whenever the mice urinated during the test. Since the volumes were small and differed among the groups, we pooled urine samples together according to treatment group and converted them into percentages in volume to show how much mark urine was produced. This provided us with a descriptive estimate on marking behavior associated with treatment with different odors (Drickamer 1995).

Chemical analysis

The chemical analysis procedures followed those described by Soini et al. (2005) and Zhang et al. (2005). Briefly, we employed a relatively new stir bar sorptive extraction (SBSE) method in the aqueous sorptive extraction (HSSE) mode to sample the volatiles and semivolatiles in the urine. A Finnigan MAT Magnum ion trap gas chromatograph/mass spectrometer (GC-MS) system with a nitrogen-cooled pro-column loop was used for compound identification (Finnigan MAT, San Jose, CA), which was conducted by comparing the compounds' gas chromatographic retention times and corresponding MS spectra with those reported in the literature (Schwende et al. 1986) and verified by authentic analogues. The GC equipment used for the quantitative analysis consisted of an Agilent GC Model 6890 system with the Agilent ChemStation software and an AED Model G2350A (Agilent Technologies, Wilmington, DE). The system had a DB-5 capillary column (length 30 m, internal diameter 0.25 mm, film thickness 0.25 lm; JandW Scientific, Folsom, CA). Peak areas (PAs) were normalized by dividing a respective PA by the PA of the internal standard (ISA) (i.e. PA × 100/ISA). The emission lines for carbon (193 nm) and sulfur (181 nm) were monitored during the AED quantitative analysis.

Statistical analysis

One-way ANOVA was used to test for significance in differences for gain in body weight among the three groups treated with different odors. The Mann–Whitney *U* test was used to test significance in differences for investigative response of individuals after odor treatment. Wilcoxon matched-pairs signed-ranks test was used for the female choice test between urinary pheromones from different groups of males.

All statistical tests were two-tailed and were carried out with SPSS ver. 10 (SPSS, Chicago, IL). For the behavioral response, the level of significance was set at $\alpha = 0.05$ a priori. For the difference in the change in urinary chemical compounds, the level of significance was set at $\alpha = 0.10$ a priori, which has been commonly used in similar studies (e.g. Gassett et al. 1996) for the ease of comparison with parallel studies.

Results

Although all male mice treated with water, rabbit odor or cat odor grew substantially, there was no significant difference among them in body weight at the end of the study (water-group 46.35 ± 5.54, rabbit-urine group 44.67 ± 5.12, cat-urine group 46.34 ± 6.64; one-way ANOVA $F = 0.4348$, $P = 0.6504$).

Compared with those treated with cat urine, males treated with rabbit urine had a shorter potential time and longer contact (licking/bitting) time with rabbit urine in their response to cat urine (Mann–Whitney *U*-test: sniff $U = 99.0$, $P = 0.608$; contact: $U = 56.0$, $P = 0.019$; potential time $U = 39.5$, $P = 0.002$, Fig. 1a). Such differences did not occur between the water-exposed (control) and cat urine-exposed mice in their response to cat urine (sniff $U = 123.0$, $P = 0.851$; contact $U = 102.0$, $P = 0.317$; potential time $U = 128.0$, $P = 1.000$, Fig. 1b). However, the control group had a shorter contact time and longer potential time did the rabbit urine-exposed mice in their response to rabbit urine (sniff $U = 85.0$, $P = 0.262$; contact $U = 62.0$, $P = 0.038$; potential time $U = 49.5$, $P = 0.008$, Fig. 1c). These results indicate that chronic exposure to rabbit (non-predator) odor produced habituation, whereas a similar exposure to cat urine failed to produce such habituation.

In the binary choice test for male urinary pheromones, mice showed no left- and right-preference in 63 trials (Wilcoxon matched-pairs signed-ranks test $Z = 0.9345$, $P = 0.350$). Estrous females spent significantly more time in investigating urine from males that had been exposed to cat odor than investigating urine from males that had been exposed to rabbit urine ($Z = 2.35$, $n = 21$, $P = 0.019$) or males that had been exposed to water ($Z = 2.59$, $n = 21$, $P = 0.010$, Fig. 2). Along the same line, females showed more interest in the urine of males that had been treated with rabbit urine than to urine of males that had been treated with water control ($Z = 2.31$, $N = 21$, $P = 0.021$, Fig. 2).

Cat odor-treated males were more likely to initiate attack (Binomial test $n = 12$, $P = 0.039$) and attacked more frequently ($Z = 2.118$, $n = 12$; $P = 0.034$) than those treated with rabbit urine (Fig. 3). In terms of the production of mark urine in volume (ml), cat urine-treated mice collectively produced the most urine (2.5/3.1 = 80.7%), followed by rabbit urine-treated (1.7/3.4 = 50.0%) and water-treated mice (1.5/5.3 = 28.3%).

As a general tendency, exposure to cat or rabbit odor elevated the relative concentrations of the 11 urinary volatiles. Among the notable were three furans, three ketones, *R,R*-dehydro-*exo*-brevicomin, *S*-2-*sec*-butyl-4, 5-dihydrothiazole and two farnesenses (Table 1). In particular, the levels of the well-known male pheromone compounds, farnesenes, which are attractive to females and indicate dominance (Harvey et al. 1989; Novotny et al. 1990), became significantly higher in cat urine-exposed mice than in rabbit urine- or water-exposed mice. Also, *R,R*-dehydro-*exo*-brevicomin and *S*-2-*sec*-butyl-4,5-dihydrothiazole were enhanced in rabbit-urine exposed mice compared to water-exposed mice (Table 1).

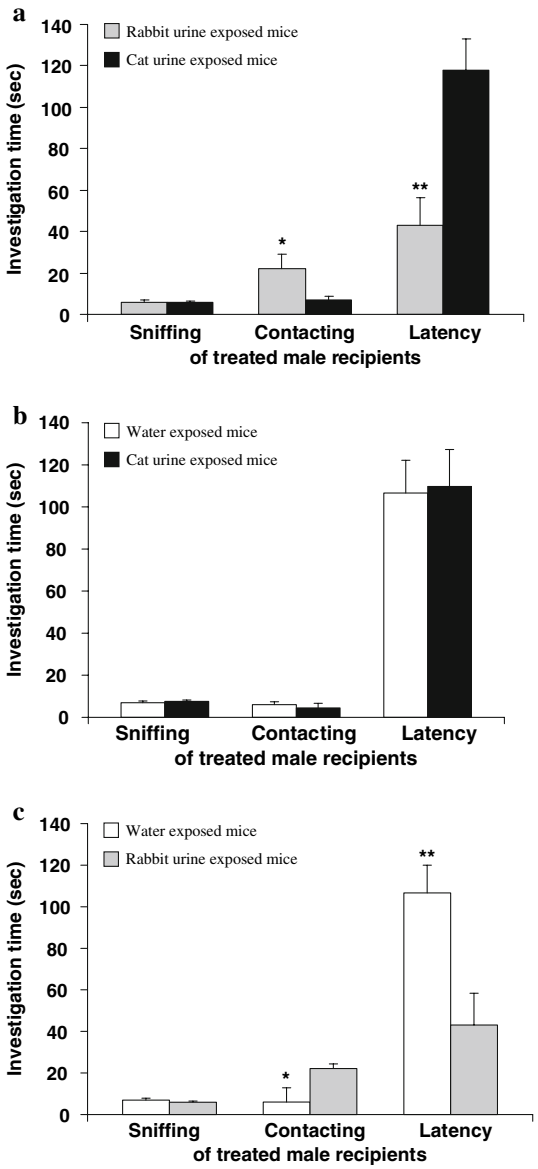

Fig. 1 Comparison of the time (mean ± SE, in seconds) spent by male mice exposed to rabbit urine in investigating rabbit urine and mice exposed to cat urine in investigating cat urine (**a**), spent by male mice exposed to water or cat urine in investigating cat urine (**b**) spent by male mice exposed to water or rabbit urine in investigating rabbit urine (**c**). $^{*}P < 0.05$, $^{**}P < 0.01$ (Mann–Whitney *U*-test)

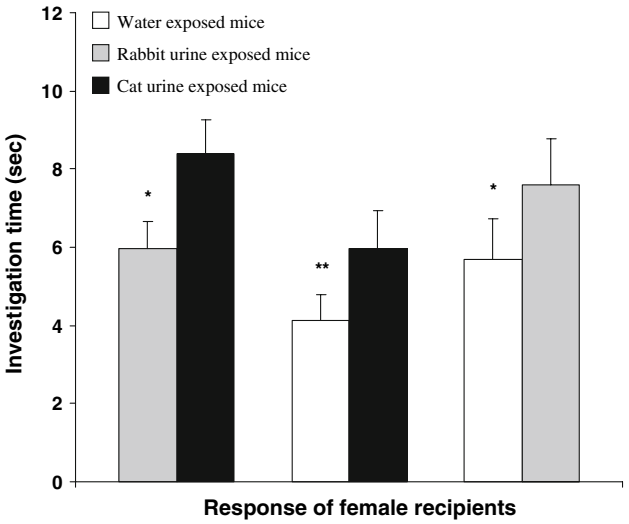

Fig. 2 Comparison of response (mean ± SE, in seconds) of female mice to the urine from two of male mice exposed to cat urine, rabbit urine or water. $^{*}P < 0.05$, $^{**}P < 0.01$ (Wilcoxon matched-pairs signed-ranks test)

Fig. 3 Aggressive interaction between male mice exposed to cat urine and rabbit urine. $^{*}P < 0.05$ (Wilcoxon matched-pairs signed-ranks test)

Table 1 Quantitative differences in urinary volatiles among male mice exposed to different odors

Gas chromatographic peak no.	Retention time (min)	Compounds	Cat urine-exposed male mice	Rabbit urine-exposed male mice	Water-exposed male mice
1	5.78	5,5-Dimethyl-2-ethyl-4,5-dihydrofuran	1497.6 ± 162.3^{ab}	1258.3 ± 178.6^{a}	1079.2 ± 210.0^{b}
2	9.08	*Z*-5,5-Dimethyl-2-ethylidenetetrahydrofuran	442.0 ± 39.51^{b}	378.7 ± 54.86^{c}	306.7 ± 50.55^{bc}
3	9.80	2-Heptanone	76.60 ± 18.45^{ab}	106.5 ± 7.630^{ac}	44.20 ± 10.93^{bc}
4	10.13	5-Hepten-2-one	135.5 ± 62.73^{b}	107.8 ± 10.30^{c}	72.40 ± 18.70^{bc}
5	10.97	*E*-5,5-dimethyl-2-ethylidenetetrahydrofuran	124.9 ± 13.87^{b}	107.8 ± 16.62^{c}	79.70 ± 10.64^{bc}
6	15.07	6-Methyl-5-hepten-3-one	173.3 ± 62.65^{b}	110.2 ± 26.48	86.80 ± 62.17^{b}
7	20.63	*R,R*-Dehydro-*exo*-brevicomin	427.2 ± 14.87^{ab}	558.7 ± 60.06^{ac}	365.4 ± 50.40^{bc}
8(s)[a]	24.65	*S*-2-*sec*-Butyl-4,5-dihydrothiazole	183.9 ± 17.30	196.6 ± 6.750^{c}	162.7 ± 33.34^{c}
9	49.23	*E*-beta-Farnesene	27.72 ± 15.36^{b}	16.13 ± 1.440	9.830 ± 4.330^{b}
10	50.10	7-Tridecanone (IS)	100.0 ± 0.000	100.0 ± 0.00	100.0 ± 0.000
11	51.61	*E,E*-alpha-Farnesene	3.580 ± 2.560^{a}	0.000 ± 0.000^{a}	2.360 ± 2.750

The means in a row followed by the same superscript letters (a–c) are significant at the 0.1 level, using Kruskal–Wallis *H* and the post hoc Mann–Whitney *U* test

[a] The letter "s" in parenthesis indicates that the gas chromatographic (GC) peak area values are from the sulfur line; all others are from the carbon line of GC-AED procedure. An area value of less than 100 were taken as zero

Discussion

In general agreement with previous studies, our data also shows that exposure to cat odor did not affect the body weight of adult male mice (Zhang et al. 2003, 2004). It is likely that predator odor exposure only affects the growth of immature rodents (Vasilieva et al. 1999; Zhang et al. 2004).

However, adult mice could distinguish cat odor from rabbit odor, as indicated by significant differences in potential time and contact responses (Fig. 1a). This result certainly supports the prediction that cat odor increases aversive behavior in mice. Interestingly, our subjects failed to show any habituation to cat odor when this behavior was compared with the responses of the rabbit urine-exposed males to rabbit urine and those of the water-exposed males to the cat urine (Fig. 1a, b). We would normally expect animals to habituate to a novel stimulus when it is presented repeatedly because the value of the information contained in the stimulus diminishes with time, as demonstrated by our mice's response to rabbit odor. While non-habituation to predator odor is a generally believed premise, the efficacy of repellents is often significantly reduced over time, as has been shown in tests using predator odors as repellents for rodent control in nature (Müller-Schwarze 1995). Non-habituation to repeated presentations of a stimulus may demonstrate the vital importance of the stimulus to the recipients. One such case is found in beavers when they respond to conspecific anal gland secretions, which contain the biologically important information on genetic identity (Sun and Müller-Schwarze 1999). By the same token, the observed non-habituation in our study may also indicate the vital role played by predator odor for mice to recognize the risk of predation.

The most surprising result was that male mice that had been exposed to cat odor became more attractive to female mice than those that had been exposed to rabbit odor or water. In face of this seemingly anti-intuitive result, we have to reject our prediction that females would reduce their preference for males that are stressed by the presence of predators. This result, however, becomes reasonable after we observed that the aggressive behavior of male mice increased, rather than decreased, after being exposed to cat odor. Male–male aggression is positively related to dominance, namely, cat odor-exposed mice became socially dominant (Francis 1988). This consideration was further supported by the fact that these mice more frequently produced mark urine than males treated with rabbit urine or water. It has been demonstrated that the frequency of mark urine can be used as an indicator to distinguish between dominant and subordinate individuals in mice populations (Desjardins et al. 1973; Drickamer

1995). This finding is clearly opposed to our previous founding in ratlike and golden hamsters exposed to a overdose of Siberian weasels (*Mustela sibirica*) odor (Zhang et al. 2003).

A plausible explanation for why females were attracted to the urine of males that had been exposed to cat odor is that cat odor-induced aggression may represent a stronger male that is able to survive high predation pressure. Moreover, males exposed to cat odor had some of their urinary volatiles enhanced, which might indicate the ability of male conspecifics to survive in the presence of predators. This argument is in consensus with the indicator hypothesis (see Andersson 1994; Arnqvist and Rowe 2005) developed from the well-known handicap hypothesis (Zahavi 1975) in sexual selection via female choice. In any case, our results represent an exception where predator odor may not always negatively affect the fitness of prey. In natural situations, prey species have to share habitats with sympatric predators and encounter predator odors regularly. Frequent exposure to predator odor is thus inevitable. One would expect that prey animals would therefore adapt to the frequent presence of predator odor, which is also necessary to maintain a normal level of aggression in mice. Removal of a predator odor would then result in the loss of a vital stimulus in the environment. An appropriate level of aggression appears to be an important indicator of the psychological health of captive mice, and mice in an enriched environment often show a higher level of aggression (McGregor and Ayling 1990; Haemisch et al. 1994). One implication from our results is that the presence of predator odor should not always be treated as a stressor. On the contrary, it is a necessary and wholesome component of prey animals' natural environment and should be incorporated into enrichment practice in captivity. Novel odors, including predator and non-predator animal odors (rabbit odor is not equal to plain water in this sense!), are often highly effective in terms of olfactory enrichment, and their use is recommended in conjunction with other enrichment strategies (Mandairon et al. 2006).

In pursuit of the question of how female mice exercise their choice, we found that the corresponding changes in urinary volatiles provide a proximate cause of how females are able to differentiate males that have been exposed to different odors. Among the 11 major compounds studied, most increased in the cat urine- and rabbit urine-exposed males (Table 1). Some of the volatiles have been confirmed to have pheromonal activity (e.g. Jemiolo et al. 1985, 1991). In particular, 2-*sec*-butyl-4,5-dihydrothiazole and dehydro-*exo*-brevicomin can work synergistically to attract females (Jemiolo et al. 1985). Interestingly, in this study, both compounds increased in male mice that had been exposed to rabbit urine; as a result, these males became more attractive to females than water-exposed male mice. Similarly, mice treated with cat urine had higher levels of farnesenes and, consequently, were more attractive to females than males treated with rabbit urine or water (Jemiolo et al. 1991). To date, there is been no published evidence showing that other urinary volatiles can also modify male attractiveness (Novotny et al. 1999). In addition, although treatments with both predator and non-predator odor increased the attractiveness of male urine, these odors differ in terms of the chemical composition of their urinary volatiles. Since 2-*sec*-butyl-4,5-dihydrothiazole and dehydro-*exo*-brevicomin originate from metabolic urine whereas farnesenes originate from preputial glands and are excreted with urine, it would appear that predator odor may mainly affect preputial glands secretion while non-predator mammal odor influenced urinary compounds.

Since most of the documented positive results on the effects of predators or their odors on rodents have been reported to be stressors that suppress rodent behavior, physiology and reproduction, our study is particularly interesting in that it provides potent evidence of sex attractiveness, pheromonal levels and dominance as beneficial effects. In particular, we have established a plausible link between female preference and pheromonal changes in male urine induced by predator and non-predator odors. Alternatively, our results can be related to olfactory enrichment, similar to the results of Roy et al. (2001) which revealed that chronic cat odor exposure imparts beneficial impacts on the mice, in that we have especially shown that heterospecific odors of different ecological relationships have different effects in terms of olfactory enrichment.

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