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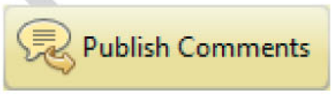

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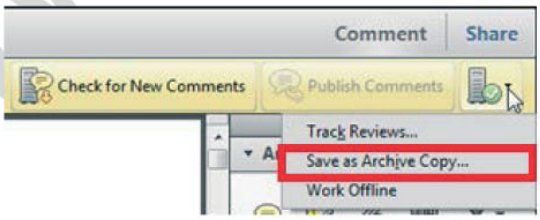

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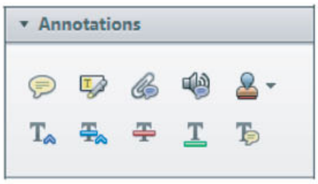

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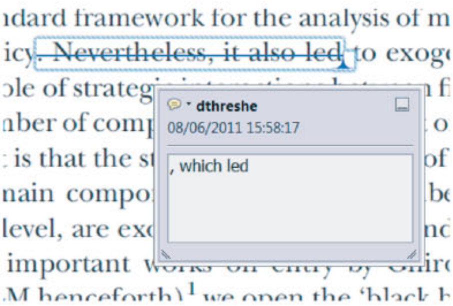

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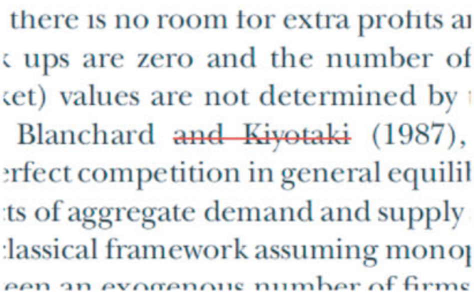

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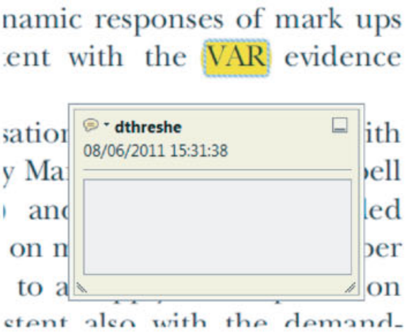

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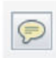

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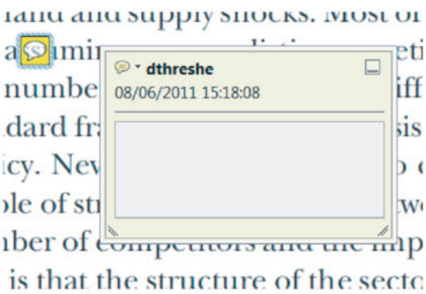

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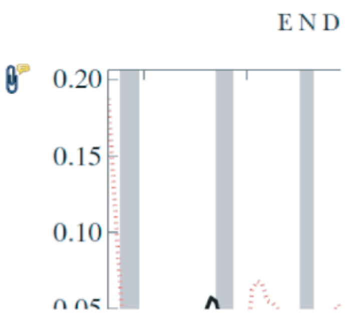

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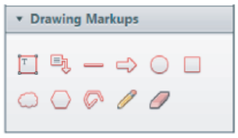

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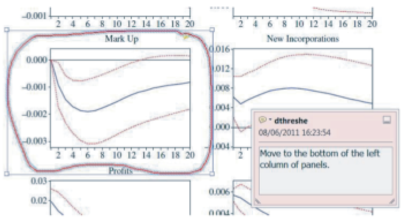

Research Article

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Foraging activity of commensal *Mus musculus* in semi-captivity conditions. Effect of predator odours, previous experience and moonlight

AQ1

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Abstract

BACKGROUND: *Mus musculus* is a pest in urban and rural habitats where it consumes and contaminates food and may transmit diseases to human and domestic animals. Its control by anticoagulants is partially effective because of aversive behaviours and resistance. In this context, we wanted to assess the potential of the use of predator odours as repellents in experimental feeding trials using urine and faeces of domestic cats and faeces of geoffroyi cat, a wild small felid that is one of the main rodent predators in the study area. We also assessed the effect of previous experience and moonlight on foraging activity.

RESULTS: We did not find an aversive response to cat odours in *Mus musculus* individuals. There was a trend to consume food in the same feeding stations over time, and the visit rate was lower in periods with high moonlight than in periods with low moonlight.

CONCLUSIONS: Predator odours did not seem to be useful as rodent repellents, but maintaining illumination may lower rodent foraging activity. As rodents maintain their feeding sites over time, toxic baits may be more efficiently placed at sites previously known to be used by rodents.

Keywords: *Mus musculus*; pest; aversive behaviour; odours; predators; foraging activity

1 INTRODUCTION

Mus musculus is a worldwide distributed rodent that in many areas has become a pest, causing damage both in urban and rural habitats. Outbreaks of house mice occur irregularly throughout the cereal production areas of Australia,[1] while in many regions of Europe, North America and China, feral populations of house mice do not outbreak and populations inhabit favourable habitats around human dwellings.[2,3]

The control of *M. musculus* is mainly based on the use of anticoagulant baits, especially in grain or food stores,[4] but the effectiveness of the application of anticoagulants may not be maintained in time because of the development of genetically resistant populations.[5,6]

In the Pampean region of Argentina, *M. musculus* is mainly present in poultry farms, while it is scarce in cropfields which are the dominant element of the landscape.[7,8] On farms, it causes losses and contamination of chicken food and it is involved in the transmission of several diseases to humans and chickens. It is present in almost all poultry farms of the area, in spite of the application of anticoagulants.[9] In these systems, the persistence of *M. musculus* populations was explained by compensatory reproduction of surviving individuals, and to the existence of individuals with low susceptibility to anticoagulants.[10]

The problems associated with the use of anticoagulants in rodent control have stimulated the development of alternative methods such as the use of predator odours as reproductive inhibitors,[11,12] repellents or biological sterilants.[13,14] The use of synthetic predator odours as repellents has considerable potential for protection of forest and agricultural crops, and many experiments showed significant avoidance responses to predator odours in several mammal pest species, including hares (*Lepus americanus*), voles (*Microtus* spp.), pocket gophers (*Thomomys talpoides*) and red squirrels (*Tamiasciurus hudsonicus*).[15] Experimental results showed responses both to urine[16,17] and to faecal odours,[15,18] and were related to volatile sulfur compounds that are metabolic derivatives of meat ingestion,[19,20] but avoidance responses were more intensive to complete urine or faecal odours than to fractions of them.[16] In house mice, predator odours cause a similar effect to crowding in reproduction,[21] negatively affecting litter size and development of juveniles.[22] Wild house mice avoid traps smeared with fox faecal odours,[23] even when isolated from foxes for several generations. Laboratory mice from domestic

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strains also show generalised avoidance of odours of their historical predators, in spite of many generations in isolation from such cues to predation risk.[24]

The potential use of odours as repellents is based on the behaviour of prey species that may reduce their probability of being eaten by recognising the odorous evidence of the presence of predators[18] and changing their habitat use or foraging activity according to predation risk. Behaviours that decrease the risk of predation may also be a response to the perception of an increased risk independently of the presence of predators, such as the use of covered habitats or decreased activity in full-moon nights.[25–27]

Avoidance behaviour of rodents may be useful to protect crops or food of domestic animals on breeding farms. It may also be translated in the population dynamics of the pest by decreasing food availability, promoting emigration from treated areas or increasing mortality as a consequence of the attraction of predators by their own odours to treated areas. There may also be behavioural or physiological stress induced by odours.[15]

In this context, the aim of this work was to assess the effect of predator odours on house mouse feeding activity and their potential as repellents. We used odours from the two mammalian predators that are most likely to feed on rodents in the area, the domestic cat (*Felis catus*, mainly in commensal habitats) and the geoffroyi cat (*Leopardus geoffroyi*, in rural habitats). We also assessed the effect of previous experience and moonlight on foraging activity.

The goals of the paper were: (1) to assess the effect of odours of urine of domestic cats fed with rodents on the visit rate of *M. musculus* to feeding stations; (2) to assess the effect of odours of faeces of domestic and geoffroyi cats fed with rodents on the visit rate of *M. musculus* to feeding stations; (3) to assess the effects of previous experience and moonlight on the visit rate of *M. musculus* to feeding stations.

2 MATERIALS AND METHODS

2.1 Experimental animals

We captured *M. musculus* in poultry farms of the Exaltación de la Cruz Department, Buenos Aires Province, Argentina. We used only adult individuals. Animals were kept in laboratory conditions with food and water *ad libitum* until experiments. We did not examine for parasite infections.

2.2 Experimental enclosures

Twelve metal enclosures of $4 \times 2\ m^2$ were built in a rural area. Metal sheets were buried to a depth of 30 cm to prevent tunnelling escape and were covered with wire mesh to prevent access of birds, sylvan rodents or mammal predators such as dogs (*Canis lupus*), domestic cats (*Felis silvestris*) and oppossums (*Didelphis albiventris*). The enclosures were covered with spontaneous vegetation. An artificial nest was placed in the centre of the enclosure. On each occasion, a 1 m wide buffer around the perimeter was mown to prevent mice escaping by climbing vegetation.

2.3 Source of odours

We collected urine from domestic cats that usually feed on rodents and were trained to urinate over wood shavings. We collected the wood shavings in plastic bags that were refrigerated until experiments. We mixed urine from three adult males and three adult females. Wood shavings were embedded in water, and the extract was used as the source of urine odour (the proportion of water was less than 5% in volume with respect to the wood shavings). Faeces of geoffroyi cats were collected in the field, slightly diluted in water and applied to pieces of cotton wool that were used as sources of odours in the trials. In order to collect fresh faeces, we located cat latrines, removed old faeces and then revisited latrines to collect new faeces. Faeces were refrigerated until experiments. We did not assess the sex of geoffroyi cats. From the same domestic cats that were used as the source of urine odours, faeces were collected from cat litter trays and applied to embedded pieces of cotton wool.

2.4 Feeding stations

We offered millet seeds in plastic bottles (350 mL) with a lateral entrance that allowed the access of rodents. The entrance was surrounded with tape in order to prevent the removal of seeds by ants or other insects. This method was successfully used in previous foraging experiments with rodents.[25]

2.5 Experimental design and data analysis

2.5.1 *Effect of cat urine odour*

Experiment 1. In order to assess the effect of domestic cat urine odour on the feeding activity of *M. musculus*, one rodent was placed in each of 12 enclosures. All individuals were adults, and the sex ratio was 0.5. Along the walls of each enclosure we set six feeding stations (four in the corners and two in the middle) containing 1 g of millet seeds. We recorded food removal or consumption (yes/no) and the presence of rodent faeces for each bottle daily for 1 week. Bottles were cleaned and replenished with millet seeds each day.

After the first week of ~~aclimitisation~~ of rodents to enclosures and after confirming that they consumed the millet seeds, we randomly selected six enclosures to apply domestic cat odours (experimental group), and the other six enclosures were untreated experimental controls. In the treated enclosures, three foraging stations were selected at random, and we sprayed the extract of domestic cat urine at the outside of the bottle. Odour was renewed daily. We used a spray in order to avoid visual signals that might change rodent behaviour.

To assess the effect of odours at the level of enclosure we used a generalised linear model (GLM) where the response variable was the total number of visits to feeding stations considering only the last 4 days of observation (with a maximum value of six feeding stations × 4 days), and the explanatory variables were treatment and the total number of visits in the period before treatment. For analysis of the effect of odours at the level of feeding stations, we used a generalised linear mixed model (GLMM) considering the number of days with seed removal/consumption for each feeding station (visit rate) as the response variable, and the explanatory variables were the enclosure as a random effect and the visit rate previous to the treatment and the application of odour as fixed factors. Visit rate previous to treatment was included in the analysis to assess whether rodents have a trend to use the same sites over time, independent of the treatments. We also included an interaction term between previous visit rate and odour. In all analyses we assumed a binomial distribution with a logit link funtion. All analyses were conducted by the R 3.1 program.[28]

2.5.2 *Effect of odours of faeces of domestic and geoffroyi cat*

Experiment 2. We used the same enclosures and individual rodents as in the first experiment, but placed only four feeding stations at the extremes of the enclosure and at the same distance from the nest, and we registered consumption for 4 days. We decreased the number of feeding stations to enhance the probability that animals would feed at each station, and to ensure that no consumption was related to aversion. This experiment was conducted 1 month after the completion of the prior experiment to ensure that there were no remaining odours in the enclosures.

We studied a total of 12 animals (each in a different enclosure): six of them were assigned to geoffroyi cat odour, and the other six to domestic cat odour. Treatments were applied in both cases by placing cotton wool with slightly diluted faeces inside a PVC tube (diameter 3 cm, length 10 cm) to protect them from rain. Odour was applied near (approximately 3 cm away from) two randomly selected feeding stations in each enclosure, and near the other two we placed a PVC tube containing cotton wool with tap water. Visit rate was estimated as in the first experiment.

The effect of faeces odours of both species of cats on the visit rate (response variable) was assessed by a GLMM in which we included the enclosure as a random factor and treatment of the enclosure (domestic or geoffroyi cat), odour (odour/no odour at the level of the feeding station) and the interaction between treatment and odour as fixed factors. We compared the results of the GLMM with those of the simpler GLM, and because of the similarity of coefficients we selected the latter analysis to compare alternative models using the Akaike information criterion (AIC). Taking into account the low sample size, we used the AIC_c or $QAIC_c$, depending on the value of the dispersion parameter.[29] We estimated average estimators from models that had $\Delta < 4$. All analyses were conducted with the R 3.1 program.[28]

Experiment 3. According to observations during the first phase of the study, we decided to conduct a new experiment (experiment 3) to assess the effect of geoffroyi cat faeces and moonlight with increased sample size. We tested 21 new adult animals (30% of males, according to captures). As in the previous experiments, visit rate was the response variable (ranging from 0 to 4), and the categorical explanatory variables were odour/no odour and lunar phase (with two levels: ±5 days from the new moon and ±5 days from the full moon, considering only clear nights). Different animals were used for each phase. Visit rate before the treatment was included as a quantitative variable. As in the previous experiment, we used both a GLMM and a GLM, and finally used a GLM and $QAIC_c$.[29] We estimated average estimators from models that had a $\Delta < 4$.[29] All analyses were conducted with the R 3.1 program.[28]

Table 1. Effect of the application of domestic cat urine odour at the level of enclosure (GLM) and feeding stations (GLMM) on house mouse visit rate. At both levels, explanatory variables were the treatment (odour or no odour) and the number of visits to feeding stations before the treatment (previous). The number of observations corresponds to the number of enclosures or feeding stations where food consumption/removal was observed at least once in both pre- and post-treatment periods. At the level of feeding stations, enclosures were random explanatory variables

	Intercept	Treatment (odour)	Previous	Treatment × previous
Enclosure level (GLM)				
Estimate	−0.5406	−0.1139	0.0373	
Z-value	−1.1650	−0.4530	1.1920	
P	0.2440	0.6510	0.2330	
Number of observations: 11	dp = 1.12			
Feeding station level (GLMM)				
Fixed effects				
Estimate	−0.7371	−0.1209	0.2380	0.0681
Z-value	−1.1200	−0.1250	0.8970	0.8500
P	0.2630	0.9010	0.3700	0.8530
Random effect: enclosures (6)	Variance = 0.0356	SD = 0.2316		
Number of observations: 34				

Table 2. Effect of odour of faeces of domestic and geoffroyi cats on house mouse visit rate to food stations. GLM explanatory variables were treatment of the enclosure (domestic or geoffroyi odour) and application of odour at the level of feeding station (odour, no odour). The number of observations corresponds to the number of feeding stations that were visited at least once

	Estimate	*Z*-value	*P*
Intercept	0.9694	2.7380	0.00619
Geoffroyi cat odour	−0.2385	−0.4880	0.6286
Odour	−0.5640	−1.1770	0.2392
Treatment × odour	0.0337	0.0510	0.9597
Number of observations: 40			

3 RESULTS

3.1 Effect of domestic cat urine odour

The effect of domestic cat urine odour and the previous number of visits did not have a significant effect at both the enclosure and feeding station scales (Table 1).

3.2 Effect of odours of faeces of domestic and geoffroyi cats

There was no significant effect of treatment at the enclosure level (treated with geoffroyi or domestic cat faeces odours) or at the feeding station level (with or without odour) (Tables 2 to 4).

In experiment 3 the visit rate of house mice was positively related to the presence of geoffroyi cat faeces odour and to the visit rate prior to the treatment period and negatively to moonlight (Table 5), as suggested by the best GLM model ($w_i = 0.503$) (Table 6). Averaging from the three models for which $\Delta < 4$,[29] previous visit rate was the variable with the highest relative importance, followed by odour and moonlight (Table 7). Analysing sex-specific visit rates, we found a positive effect of previous visit rate (coefficient = 0.6509, $P = 0.0000$ for females and coefficient = 0.5191, $P = 0.0073$ for males), a marginally positive significant effect of odour (coefficient = 0.5690, $P = 0.0646$ for females and coefficient = 0.8803, $P = 0.052$ for males) and a significant negative effect of moonlight on visit rate of females (coefficient = −1.2743, $P = 0.0000$). For males we did not include moonlight in the model because of the low sample size.

4 DISCUSSION AND CONCLUSIONS

There was no evidence for predator odours to reduce the visit rate of *M. musculus* to feeding stations. However, we found that animals tended to use the same group of feeding stations and decreased their activity in full-moon nights. Our results contrast with previous work, which found that both wild and laboratory strains of house mouse avoid predator odours.[23,24] The findings are consistent

AQ7 **Table 3.** Model selection table for GLM, explaining variation in the visit rate of house mice to food stations exposed to domestic and geoffroyi cat faeces odour. Model selection was based on the $QAIC_c$ because the dispersion parameter was 2.26. Models are listed in order of importance (w_i). Δ is the difference in the value of $QAIC_c$ of the model with respect to the best model (in this case, model 1)

AQ8

Model	Intercept	Treatment (T)	Odour (O)	Interaction (T × O)	df	QAICc	Δ	w_i
1	0.5645				1	68.3	0	0.466
3	0.8473		+		2	69.4	1.12	0.266
2	0.6745	+			2	70.4	2.15	0.159
4	0.9599	+	+		3	71.7	3.4	0.085
8	0.9694	+	+	+	4	74.3	6.02	0.023

with results from a variety of other small mammal species, which show that indirect cues of predation risk such as moonlight or cloudiness can be more important than direct cues of predator odours.[26,27,30,31] A study conducted on geoffroyi cat diet in the area[32] showed that *M. musculus* is rarely consumed, suggesting that this cat does not represent a serious predation risk to this rodent species, and domestic cats are not common on farms. In the study area, *M. musculus* probably does not have an innate response to odours of these cat species. Aerial predators, on the other hand, may have influenced *M. musculus* evolution, and their effect is maintained in commensal populations, because there is a significant negative relation between visit rate and moonlight. The temporal trend to repeat foraging at sites where mice have foraged previously may have been an effect of indirect cues, suggesting that animals learn to consider some feeding stations as safer or more profitable than others.

In our study, *M. musculus* feeding behaviour was barely related to direct cues of predation risk. This may have been related to a life history at high risk of mortality from anticoagulant rodenticides, which may decrease the effect of other selection pressures. Changes in avoidance behaviour according to the probability of survival were observed in *R. fuscipes*, *M. cervinipes* and *M. oeconomus*, where adults with low probability of survival until a new breeding season maximised their breeding opportunities and did not avoid predator odours, while young animals recognised and avoided predator odours, thereby avoiding predation and surviving to reproduce.[15] In our study, individuals were adults and subject to mortality by toxic baits, and consequently they could maximise breeding and not discriminate among feeding sources. Another characteristic of rodents that may have affected the results of the experiment was sex.[33] However, analyses conducted separately for both sexes showed similar results, and consequently we believe that rodent sex was not affecting the response.

The apparent attraction of geoffroyi cat faeces odour for *M. musculus* individuals was an unexpected result, because many authors found no effect of predator odours, and positive effects have not been reported so far. There are many studies, however, that show that rodents infected with *Toxoplasma gondii* change their behaviour, increasing the chances for the parasite to reach its feline definitive host.[34,35] We did not have any data on infection with *T. gondii* in *M. musculus* in the study area, so this remains an open question for future work, but at other sites *T. gondii* prevalence in house mice was higher than 60%.[35] Domestic chickens are also frequently infected with *T. gondii*,[35] enhancing the probability of finding infected mice in poultry farms.

An alternative explanation for the lack of predator aversion may be the low sample size, or that the source of odours was not a good signal, because the loss of components that are responsible for the behavioural response may have affected the results. We used faeces collected in the field, and although we first cleaned the cat latrines in order to collect fresh faeces, they remained in outside conditions for up to 12 h. With respect to urine, the extraction with water from wood shavings may have reduced the concentration of some substances that are responsible for the behavioural response.[36] Urine used for the experiment came from both male and female cats. An evaluation of the effect of cat sex would have been a valuable addition to this study, because testosterone increases urinary free felinine excretion in cats,[37,38] and results may have been different, depending on cat sex.

We used visit rate as a measure of feeding station use, but did not quantify the amount of food consumed. It may be possible that *M. musculus* does not show a yes/no response to predator odours but changes the time spent at each feeding station according to perceived predation risk. Many works showed that giving-up densities (the rate of food return remaining when an animal quits a patch) are higher in exposed relative to sheltered habitats.[25,27] However, *P. leucopus* showed similar patterns of seed removal and tray visitation according to indirect (cloudiness) and direct (predator odours) evidence of predation risk, and to thermal conditions, suggesting that much of the foraging cost may be associated with travel to

AQ9 **Table 4.** Model averaging for the estimation of coefficients for the effect of domestic and geoffroyi faeces on house mouse visit rate to food stations. We considered models with Δ < 4

	Estimate	2.5%	97.5%	Relative variable importance
Intercept	0.6939	0.1762	1.2115	
Odour	−0.1960	−1.2192	0.1285	0.36
Treatment (geoffroyi)	−0.0545	−0.8872	0.4513	0.25

Table 5. Effect of previous experience, moonlight and geoffroyi cat faeces odour on house mouse visit rate to food stations. Fixed explanatory variables were odour/no odour, lunar phase and visit rate before the treatment (previous). Enclosures were the random explanatory variables. The number of observations corresponds to the number of feeding stations that were visited at least once over the experiment

Fixed effects	Estimate	*Z*-value	*P*
Intercept	−1.436	−4.655	0.000
Previous	0.557	5.488	0.000
High moonlight	−0.684	−2.135	0.033
Odour	0.703	2.797	0.005
Random effect: enclosures (21)	Variance = 0.201	SD = 0.448	
Number of observations: 84			

Table 6. GLM explaining the variation in the visit rate of house mice to food stations in the presence of geoffroyi cat faeces. The model selection table was constructed according to the $QAIC_c$ because the dispersion parameter was 1.7. Models are listed in order of importance (w_i). Δ is the difference in the value of $QAIC_c$ of the model with respect to the best model (model 8)

Model	Intercept	Previous	Moonlight	Odour	df	$QAIC_c$	Δ	w_i
8	−1.415	0.553	+	+	4	156.5	0.00	0.503
6	−1.752	0.587		+	3	158.2	1.63	0.222
4	−1.094	0.564	+		3	158.5	1.98	0.187
2	−1.427	0.595			2	160.0	3.48	0.088
7	−0.464		+	+	3	176.3	19.76	0.000
3	−0.910		+		2	180.1	23.58	0.000
5	−0.830			+	2	181.9	25.32	0.000
1 (null)	−0.460				1	85.5	28.97	0.000

Table 7. Model averaging for the estimation of coefficients for the effect of previous visit rate, moonlight and geoffroyi cat odour on house mouse visit rate to food stations. We considered models with Δ < 4

	Estimate	2.5%	97.5%	Relative variable importance
Intercept	−1.431	−2.079	−0.783	
Previous	0.566	0.376	0.756	1.0
High moonlight	−0.637	−1.129	−0.139	0.69
Odour	0.654	0.163	0.146	0.72

and from foraging trays.[27] We preferred to assess the effect of predation risk on visit rate rather than consumption because rodent visits affect poultry food by consumption, contamination and disease transmission.[9]

From the management point of view, the observed trend of *M. musculus* individuals to reuse the sites of consumption may be useful to the design of rodenticide applications. There should be evaluation of foraging sites prior to bait application and application of rodenticides at sites where consumption by mice is concentrated. The effect of moonlight may also be taken into account for the design of control measures. It would be more profitable to apply rodenticides on dark nights or without artificial illumination. On the other hand, if the goal is to prevent mice from consuming chicken feed or other domestic animals' food without the application of rodenticides, artificial illumination would reduce the foraging activity of mice, as was reported by local farmers (Diez F, private communication). With respect to predator odours, it would be useful to conduct more studies with more reliable sources of odours, such as the collection of urine by manual pressure of the bladder or from cats housed in metabolic cages,[35,37] and the collection of fresh faeces from captive cats. This may also allow assessment of the effect of cat sex on the response of rodents to odours.

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