Bigger Doesn't Mean Bolder: Testing the Pace-of-Life Syndrome Hypothesis of Four Wild Rodent Species to Novelty and Predation Risk

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Research

Abstract

Background: Rodents, a globally distributed and diverse taxonomic group, have been the subjects of countless studies emulating risky situations. In controlled laboratory experiments the majority of focus has been on captive-bred rodents, whereas far less attention has been paid to their wild counterparts. Understanding how wild species respond to novel situations with associated risk can provide valuable information toward the pace-of-life syndrome hypothesis; if their behaviors are associated with a fast-slow continuum of life history. Additionally, whether wild populations of rodents embody adaptive capacity and behavioral repertoires, illustrated by habituation and variation in behavioral traits, respectively.

Results: In this comparative study, we examined multiple behavioral responses of three native rodent species *Mus caroli*, *Apodemus agrarius*, *Rattus losea*, and one invasive, *Rattus exulans*, exposed to an unfamiliar microenvironment and novel cue from an allopatric predator, the leopard cat (*Prionailurus bengalensis*). All animals were captured and tested in a laboratory setting in Hualien County, Eastern Taiwan and subject to two consecutive nights of experimental trials. Behavioral responses to a novel situation during the first trial differed between species following the predictions of the pace-of-life syndrome; smaller species investing more time in non-defensive behaviors compared to the larger species. More specifically, the smaller species *M. caroli* and *A. agrarius* allocated more time to exploration and foraging, whereas the larger rat species *R. exulans* and *R. losea* spent more time motionless or concealing. During the second trial, leopard cat cues did not elicit antipredator behaviors, but rather, rodents were found to have opposing responses with increased non-defensive behaviors, specifically foraging efforts.

Conclusions: Our results suggest that these four species do largely adhere to the pace-of-life syndrome with the two smaller mice species demonstrating increased boldness in a novel context compared to the larger rat species. Also, the wild populations of rodents in Eastern Taiwan may be naïve to leopard cats. Finally, the rodents in our study demonstrated habituation to the microenvironment, indicating they possess adaptive capacity.

Background

Rodents are common prey to a suite of predators, and in order to keep pace in an evolutionary arms race they have been equipped with antipredator responses [1, 2]. Rodents have highly developed chemosensory systems and are adapted to discriminate and react accordingly to predator cues [3, 4]. Notwithstanding, antipredator responses come at a cost, and can have consequences for immune function, development and reproduction [5, 6]. Predator cues elevate risk for prey and can instigate defensive behaviors including increased vigilance, avoidance of areas, hiding, motionless and decreased activity [7–9]. Furthermore, according to the 'predator sensitive foraging hypothesis' the risk of predators

will constrain prey foraging activity and efficiency due to an increase in defensive behaviors, such as vigilance and motionless [10, 11].

It has long been studied that dissimilarities in life history can be associated with physiological traits, like metabolic rate, or morphological traits, like body size [12, 13]. In mammals, small species embodying fast-paced life histories tend to favor current reproduction over survival since they are shorter lived, as opposed to larger slow-paced strategists with longer lifespans prioritizing survival over reproduction – thereby exemplifying the fast-slow continuum [12, 14]. According to the pace-of-life syndrome (POLS) hypothesis, species with fast life histories may also be more likely to express behaviors for increased boldness, exploration and foraging for resources, even at risk to their survival [15–17]. Additionally, species with a slower pace-of-life are predicted to exercise more caution in response to risk [18, 19]. Therefore, a comparative study investigating the behavioral responses of several species to risky contexts could provide a means of testing the conceptual framework of the POLS.

In addition to inter-specific behavioral differences owing to variation in life history traits, dissimilarities in risk-taking behavior may also be expected due to sexual selection and inter-sexual disparity [20, 21]. Since the reproductive success of males may be more variable than females, the former sex may demonstrate more boldness, be more proactive in exploration of novel situations and more likely to take risks to acquire resources [22, 23].

An extensive number of studies have manipulated predation risk with the use of auditory, visual and/ or olfactory cues of predators [24–26]. Predation risk studies often focus on a single prey species [7, 27], therefore a comparative investigation of multiple sympatric prey species of varying life-history traits could provide further insight, including validating the POLS hypothesis. Sources of predator olfactory cues generally include urine, feces, fur and skin [27, 28]. The manipulation of predation risk has been executed in both laboratory and field experimental trials, and in both settings studies have reported mixed results [7, 29]. The effectiveness of predator odors remains inconclusive, with some studies observing significant effects of odors eliciting defensive behaviors and others seeing no effect [27, 30, 31]. Explanations for the inconsistencies in prey responses include species traits, individual personality and differences, physiological state, and fear conditioning and habituation [29, 32].

Both field and lab experiments have their advantages. For example, field experiments can be less obtrusive and more ecologically pertinent, whereas laboratory studies provide the ability to control for extraneous or unwanted factors, as well as the simulation of 'micro-environments' and observation of behaviors at a very fine-scale. In laboratory experiments, rodents are often the test animals. Rats and mice have long been used as the subjects of neurological, behavioral and physiological studies testing responses to risk and stress [29, 33, 34]. These risk-related experiments typically involve laboratory-bred strains of rodents tested in a maze or arena and exposed to a stimulus, i.e. novel object, predator odor. Many studies performed on captive-reared rodents have found positive effects of predator odors; acting as deterrents [27, 34]. However, wild rodents may not have the same behavioral responses, especially

since they have higher genetic variation promoting greater diversity of morphological and behavioral traits [35, 36].

In addition to predation risk, in vitro experiments provide opportunities to measure responses to novel environments and/ or objects - testing for neophobia [37, 38]. These tests have the ability to uncover variation between individuals and consistency in behaviors; whether individuals exhibit behavioral types [39], such as boldness, shyness or aggressiveness. Behavioral types have direct implications for fitness, since they can govern habitat use, social interactions, dispersal and responses to risk [40, 41]. Although studies have found intra-individual consistencies and inter-individual variation for behaviors and habituation, indicating behavioral types [32, 41], they have largely focused on one species. A comparative approach examining fine-scale behavioral responses of multiple species to novelty remains relatively unexplored.

In Taiwan, a mammalian predator of rodents is the leopard cat (*Prionailurus bengalensis*) (Kerr 1972). Leopard cats, the sole-remaining native cat, are classified as endangered and protected under Taiwan's Wildlife Conservation Act. This wild felid currently occupies a fraction of its once island-wide distribution [42], which is limited to a few regions in the western part of Taiwan. Rodents contrarily are very widespread in Taiwan and inhabit areas where leopard cats are absent at relatively high densities [43]. These rodents include both native and exotic species. In areas where they live sympatrically with leopard cats, they are a major constituent of the cat's diet [44]. In eastern Taiwan where leopard cats can no longer be found, the murine rodents vary in body size and associated life history traits [45, 46]; the larger rat species can be more than ten times the size of the smaller mice species. Additionally, the smaller mice species have shorter life spans compared to the larger murid rodents, as well as differences in fecundity and number of reproductive periods [14, 47, 48]. Therefore, despite occupying similar habitat, the various murid species in the region may embody variation in their pace-of-life following a slow to fast continuum [14, 49], and may exhibit different strategies regarding exploration, acquisition of resources, and assessing risk. Furthermore, these differences in strategies may also be reflected in their behaviors; smaller species demonstrating more boldness in response to risky situations compared to the larger species – adhering to the POLS [17, 49].

The Pacific rat (*Rattus exulans*) is one invasive species that has been expanding its range and invasion front in eastern Taiwan (I. Best, unpublished data). Invasive species that are widely distributed are generally thought to be generalists and ecologically plastic [50]; in order to invade a diverse array of habitats. Furthermore, it has been posited that generalist species are more likely to confer boldness and less likely to express neophobia compared to specialist counterparts [38, 51]. Therefore, an invasive rat may respond differently than native species when exposed to a novel situation.

The present-day distribution of leopard cats and rodents allowed us to test the effects of cues from an allopatric predator on multiple rodent species. Since none of the rodents included in our study had ever encountered leopard cats, we could provide a first-step approach to evaluate whether these antipredator behavioral responses are conserved or lost rendering the rodents naïve. In this study, we conducted

laboratory experimental trials on four wild rodent species in eastern Taiwan and measured their behavioral responses to the novel environment and a novel predator cue (leopard cat odor). Our experimental design also enabled us to investigate whether the rodents would habituate to novel conditions. Therefore, our objectives were to examine whether (1) there would be inter-sexual behavioral differences to the novel environment, (2) inter-specific variation in behavioral responses to the novel environment and leopard cat odor, following the POLS hypothesis, (3) leopard cat odor would elicit defensive behaviors, and (4) rodents became habituated to the experimental trials, irrespective of predator cues.

Results

Test subjects

Our sample from the experimental trials included 68 test subjects: 13 *Mus caroli* (5 male, 8 female; average weight: male = 12. 8 g, female = 12.6 g), 16 *Apodemus agrarius* (7 male, 9 female; average weight: male = 27.7 g, female = 28.2 g), 22 *R. exulans* (15 male, 7 female; average weight : male = 44.4 g, female = 33.1 g), and 17 *Rattus losea* (10 male, 7 female; average weight: male = 120.4 g, female = 109.4 g). We employed a stratified random sampling design to assign a similar number of individuals from each species to either the control group or leopard cat odor group. Each treatment group consisted of 34 rodents (control = 7 *M. caroli*, 8 *A. agrarius*, 11 *R. exulans*, 8 *R. losea*; leopard cat odor = 6, 8, 11, 9, respectively).

Behavioral responses to a novel environment

For a complete list of the means and standard errors of all the response variables, please refer to Supplementary Tables 1 and 2. Our analysis found significant effects for all behavioral responses of species (Table 1, Fig. 1). Furthermore, sex had significant effects for the responses *foraging*, *concealing*, *consumption ratio* and *foraging events*; with significant interactions for *foraging*, *motionless*, *concealing* and *foraging events* (Table 1). The males of all species combined spent more time foraging, had a higher consumption ratio with more frequent foraging events, whereas females spent more time concealing. At the species level, males of *R. losea* invested significantly more time foraging with more frequent foraging events compared to females (both $P < 0.005$). Additionally, females of *R. losea* spent more time concealing in the hide ($P < 0.05$). Despite the absence of significant differences, we observed a trend of the males of each species group allocating slightly more time to foraging; as well as the females of *M. caroli* and *A. agrarius* staying concealed for marginally longer durations (Supplementary Table 1). Females of the species *R. exulans* spent more time motionless compared to males ($P < 0.05$).

Table 1
Behavioral responses of the first trial for the factor species, sex and their interaction. Significant values are displayed in bold.

Response	Factor	Wald χ^2	df	P
Defensive	Species	19.03	3	**< 0.001**
	Sex	1.90	1	0.168
	Species*Sex	4.90	3	0.179
Non-defensive	Species	16.80	3	**< 0.001**
	Sex	2.24	1	0.135
	Species*Sex	5.39	3	0.145
Exploring	Species	38.90	3	**< 0.001**
	Sex	0.62	1	0.433
	Species*Sex	2.26	3	0.521
Foraging	Species	38.55	3	**< 0.001**
	Sex	24.68	1	**< 0.001**
	Species*Sex	30.55	3	**< 0.001**
Motionless	Species	48.77	3	**< 0.001**
	Sex	0.94	1	0.332
	Species*Sex	27.92	3	**< 0.001**
Concealing	Species	57.99	3	**< 0.001**
	Sex	29.28	1	**< 0.001**
	Species*Sex	41.71	3	**< 0.001**
Grooming	Species	32.14	3	**< 0.001**
	Sex	3.50	1	0.061
	Species*Sex	6.86	3	0.076
Consumption ratio	Species	21.20	3	**< 0.001**
	Sex	4.19	1	**< 0.05**
	Species*Sex	5.88	3	0.118
Foraging events	Species	21.24	3	**< 0.001**
	Sex	4.96	1	**< 0.05**

Response	Factor	Wald χ²	df	P
	Species*Sex	12.68	3	**< 0.01**
Jumping	Species	60.59	3	**< 0.001**
	Sex	3.86	1	0.052
	Species*Sex	3.32	3	0.345

There were significant effects of species for the behavioral categories *defensive* and *non-defensive*, but not for sex nor the interaction between species and sex (Table 1, Fig. 1). The two mice species, *M. caroli* and *A. agrarius*, spent more time performing non-defensive behaviors, whereas the two rat species, *R. exulans* and *R. losea*, invested more time in defensive behaviors during the first trial (Fig. 1A).

During the first trial the species *M. caroli* spent the most time exploring with the highest number of jumps, while *A. agrarius* spent the most time foraging (Fig. 1B, Fig. 3D). *R. losea* spent more time motionless and grooming compared to the other species, and *R. exulans* spent the most time concealing (Fig. 2B). With respect to the other foraging behaviors *consumption ratio* and *foraging events*, *A. agrarius* was found to have the highest for both (Fig. 3C, Fig. 4D).

Responses to leopard cat odor

At the rodent community level, we found leopard cat odor to have no significant effect on the behavioral categories *defensive* and *non-defensive*, nor was there an interaction between treatment and trial (Table 2, Fig. 2). There was a significant interaction between species and treatment for the *defensive* behavioral category, but not *non-defensive*. The leopard cat odor treatment group of the species *A. agrarius* spent more time exhibiting defensive behaviors compared to the control group (Fig. 2A). For both behavioral categories there were significant differences between species (Table 2). During the second trial the two mice species *M. caroli* and *A. agrarius* spent less time exhibiting defensive behaviors and more time performing non-defensive behaviors compared to the larger rat species, *R. exulans* and R. *losea* (Defensive: *M. caroli* compared to *R. exulans* and *R. losea*, both *P*< 0.005; *A. agrarius* compared *R. exulans* and *R. losea*, both *P*< 0.001; Non-defensive: *M. caroli* compared to *R. exulans* and *R. losea*, both *P*< 0.005; *A. agrarius* compared *R. exulans* and *R. losea*, both *P*< 0.05).

Table 2

The effects and interactions of trial, treatment and species on the behavioral categories. Significant values are displayed in bold.

Response	Factor	Wald χ^2	df	P
Defensive	Trial	0.06	1	0.800
Treatment	1.99	1	0.159	
Species	51.57	3	**< 0.001**	
Trial*Treatment	0.06	1	0.810	
Trial*Species	4.63	3	0.201	
Treatment*Species	35.70	3	**< 0.001**	
Non-defensive	Trial	0.63	1	0.428
	Treatment	0.27	1	0.603
	Species	19.20	3	**< 0.001**
	Trial*Treatment	0.03	1	0.871
	Trial*Species	3.08	3	0.380
	Treatment*Species	6.74	3	0.081

Table 3
Behavioral responses for the effects and interactions of trial, treatment and species. Significant values are displayed in bold.

Response	Factor	Wald χ^2		df	P
Exploring	Trial	12.18		1	**< 0.001**
Treatment		0.39	1	0.531	
Species		155.08	3	**< 0.001**	
Trial*Treatment		0.02	1	0.882	
Trial*Species		24.71	3	**< 0.001**	
Treatment*Species		1.63	3	0.653	
Foraging	Trial	4.96		1	**< 0.05**
Treatment		0.10	1	0.756	
Species		42.90	3	**< 0.001**	
Trial*Treatment		1.27	1	0.261	
Trial*Species		11.86	3	**< 0.01**	
Treatment*Species		4.05	3	0.257	
Motionless	Trial	26.07		1	**< 0.001**
Treatment		0.18	1	0.668	
Species		93.87	3	**< 0.001**	
Trial*Treatment		0.16	1	0.691	
Trial*Species		19.06	3	**< 0.001**	
Treatment*Species		17.17	3	**< 0.005**	
Concealing	Trial	3.06		1	0.080
Treatment		4.14	1	**< 0.05**	
Species		31.80	3	**< 0.001**	
Trial*Treatment		0.02	1	0.882	
Trial*Species		7.01	3	0.071	
Treatment*Species		26.26	3	**< 0.001**	
Grooming	Trial	10.73		1	**< 0.005**
Treatment		1.29	1	0.256	

	Species	51.16	3	**< 0.001**
	Trial*Treatment	0.23	1	0.633
	Trial*Species	11.45	3	**< 0.05**
	Treatment*Species	4.71	3	0.194
Consumption ratio	Trial	27.32	1	**< 0.001**
	Treatment	0.05	1	0.818
	Species	90.46	3	**< 0.001**
	Trial*Treatment	0.35	1	0.553
	Trial*Species	8.38	3	**< 0.05**
	Treatment*Species	6.92	3	0.075
Foraging events	Trial	1.32	1	0.251
	Treatment	0.70	1	0.403
	Species	4.66	3	0.199
	Trial*Treatment	0.33	1	0.563
	Trial*Species	26.65	3	**< 0.001**
	Treatment*Species	0.37	3	0.947
Jumping	Trial	0.07	1	0.789
	Treatment	0.05	1	0.825
	Species	67.30	3	**< 0.001**
	Trial*Treatment	0.30	1	0.584
	Trial*Species	0.33	3	0.847
	Treatment*Species	13.19	3	**< 0.005**

Table 4
Behavioral response variables measured from experimental trials

Response	Unit measured	Definition
Exploring	Time (s.)	Locomotive activity, investigation of the arena and objects, climbing
Foraging	Time (s.)	The subject consumed and/ or searched for seeds in the foraging tray
Motionless	Time (s.)	The subject remained stationary (except for breathing); body remained stationary with occasional head scanning
Concealing	Time (s.)	The subject was in the hide (at least 75% of the body was concealed); the head was slightly exposed from the hide
Grooming	Time (s.)	The subject was grooming, e.g. licking or rubbing
Consumption	Weight (g)	The amount of seeds consumed (± 0.1 g). Calculated by subtracting the remaining amount from the initial 5.0 g
Foraging events	No. occurrences	The number of events of foraging of the test subject
Jumping	No. occurrences	The subject actively jumped; all four paws left the base of the arena
Contact	No. occurrences	The subject investigated or had tactile contact with the treatment apparatus, e.g. sniffing or biting

Notes: seconds (s.), number of (no.) occurrences, grams (g). Response variables adapted from [33, 61, 62].

The only response variable leopard cat odor had a significant effect on was *concealing* (Table 3, Fig. 3B). Additionally, there was also a significant interaction between species and treatment for this variable. *A. agrarius* exposed to the predator odor spent more time concealing than their counterparts without exposure. These results may be explained by a consistency in concealing behavior across the two trials for two individuals of *A. agrarius* (1 male, 1 female) that were included in the leopard cat odor treatment group (Supplementary Tables 1 and 2). For the behaviors *motionless* and *jumping* there were significant interactions of species and treatment (Table 3). The control group of the species *R. exulans* spent more time motionless compared to the group exposed to leopard cat odor (Fig. 3A). The number of jumps performed by the control group of *R. losea* was found to be significantly higher than the treatment group (Fig. 3D). These results may not be so much of an effect of the leopard cat odor, but rather intra-specific variation and consistency at the individual level for certain behaviors.

Leopard cat odor did not discourage rodents from making contact with the treatment apparatus (Wald χ^2 = 0.04, *P* = 0.85), nor was there an interaction between treatment type and species for this behavior (Wald χ^2 = 0.55, *P* = 0.91). There were significant differences between species for the behavior *contact* (Wald χ^2

= 7.98, $P < 0.05$). *M. caroli* had the highest number of contacts, irrespective of treatment type (*M. caroli* compared to *A. agrarius*, *R. exulans* and *R. losea*, all $P < 0.05$).

Behavioral responses across trials

In addition to measuring the test animals' responses to a novel environment and predator cue, we analyzed whether their behaviors would significantly change across the trials associated with different conditions. Trial did not have a significant effect on the *defensive* or *non-defensive* behavioral categories (Table 2). For these two behaviors there also was no significant interaction between trial and species. Therefore, the amount of time each species group exhibited *defensive* or *non-defensive* behaviors did not differ significantly between trials. However, trial had a significant effect on the behaviors *exploring*, *foraging*, *motionless* and *grooming* (Table 3). We also found significant interactions of trial and species for *exploring*, *foraging*, *motionless*, *grooming*, *foraging events* and *consumption ratio* (Table 3).

When the results of all species were combined, there was a decrease in time spent exploring, motionless and grooming, and an increase in time spent foraging during the second trial (Fig. 4). The species *A. agrarius* displayed a decrease in time spent exploring on the second night (Fig. 4A). Both *A. agrarius* and *R. exulans* significantly increased the time spent foraging. Also, during the second trial the species *R. exulans* and *M. caroli* reduced the amount of time spent motionless, and *R. exulans* and *R. losea* spent significantly less time grooming (Fig. 3A, Fig. 4). The number of foraging events nearly doubled for *M. caroli* whereas they halved for *A. agrarius* (Fig. 3C). On the second night, *A. agrarius* carried out longer, uninterrupted bouts of foraging. The consumption ratio of the species *M. caroli* and *A. agrarius* also increased (Fig. 4D).

Discussion

In the present study, inter-specific variation was observed for behavioral responses in an experiment testing novelty. On average, the smallest species in our sample, *M. caroli*, spent the most time exhibiting non-defensive behaviors, predominantly comprised of exploring. The other mouse species and second smallest, *A. agrarius*, spent the most time foraging, had the highest consumption ratio and most foraging events during the first trial. Contrarily, the two rat species in our experiments spent considerably more time demonstrating defensive behaviors; *R. exulans* spent the most time hiding and *R. losea* was motionless for the longest cumulative period. One possible explanation for these findings is differences in life history strategies conforming to a fast-slow continuum. Despite the species in our study all being relatively small-bodied animals, they do fit a spectrum of size differentiation, as well as exemplify variation in life history. The larger rat species, included in the present study, have longer lifespans and reach sexual maturity later compared to the two mice species [47, 52]. Our results support our prediction of behavioral differences between species and largely adhere to the POLS hypothesis, demonstrated by the smaller mice species performing a higher proportion of riskier behaviors (exploration and foraging) in a novel situation, in contrast to the larger rat species. The smaller species in our study, *M. caroli* and *A. agrarius*, prioritized fast exploration or acquisition of resources, as oppose to defensive behaviors. Furthermore, not only did *A. agrarius* allocate the most time to foraging, they also consumed the most

proportional to their body weight during the first trial of our experiments. This species favored the acquisition of resources over exploration or cautious behavior in an unfamiliar situation. These results may indicate a trade-off favoring current fitness returns compared to future expectations [16, 18]. Similarly, Vasquez [53] studying foraging behavior of three different Chilean rodent species varying in body size found that under increased risk the largest species was the most cautious.

The response variables foraging, foraging events, consumption ratio and concealing were found to differ significantly between sexes. At the rodent community level (all species combined), males spent more time foraging with more foraging bouts compared to females for their first trial. Since male rodents generally have less parental investment and are promiscuous, it can be expected that there will be sex-related differences for trade-offs between risk and reward [20, 54]. Therefore, males may have a higher propensity to expose themselves to risk in return for a reward [21]; in the case of the present study, risk of exposure in an unfamiliar environment and a reward of access to food. Furthermore, since males are territorial and will often compete over resources [54], such as food, the opportunity to freely forage (as was the case in our trials) without competition may have prevailed over the perceived risks. Male rodents are generally larger than females [52, 54], therefore, they may also have a higher food intake potential [55], as was observed in the present study. Overall, the defensive behavior concealing was higher for females, which indicates that in response to a novel, unfamiliar situation females exercised more caution. Adult, sexually mature females may show a preference for defensive behaviors in a novel context since the risks may outweigh rewards as they incur higher costs for parental care [54]. Our results are consistent with other studies examining behavioral responses to high risk situations [21, 25], with female rodents exhibiting a higher proportion of defensive behaviors, such as hiding, compared to males. Even though our results do not demonstrate significant differences between sexes for each species group for the behaviors foraging and concealing, we still observed trends. With respect to time spent foraging, the males of each species group had, at least, somewhat longer durations. Additionally, we detected a trend for females favoring slightly more time concealing for three of the four species in our study: *M. caroli*, *A. agrarius* and *R. losea*.

The presence of leopard cat cues during the second trial did not have effects on the defensive and non-defensive behavioral categories. There was, however, a significant interaction between species and treatment for the defensive behavioral category. Moreover, the only individual behavior that was influenced by predator odor was concealing, which is a defensive behavior. This result can most likely be explained by a consistency in concealing behavior for individuals of the *A. agrarius* species; they spent similar amounts of time hiding for both trials. Individuals of *A. agrarius* that were randomly assigned to the leopard cat odor treatment group also were more inclined to hide. We also found a significant interaction between treatment and species for the behavior motionless. In this case, individuals of *R. exulans* in the control group spent more time motionless during the second trial compared to those in the predator odor group. Therefore, once again this finding can most likely be attributed to intra-individual constancy for this defensive behavior; certain individuals displaying a higher affinity for remaining still. Repeatability of behaviors over time and even across varying situations has been observed in similar experiments [41, 56, 57], and can even outweigh the effects of predator odors [32].

The predator odor failing to elicit aversive behaviors in the present study conforms with many other studies that have exposed rodent species from wild populations to predator cues both in lab [25, 32, 58] and field [31, 59, 60] contexts. Furthermore, the majority of studies that have found significant effects of predator odors performed their experiments on captive-bred rodents [21, 27, 61, 62]. The domestication process of captive rodents may lead to an inhibition of behavioral variation and adaptability [35, 63], resulting in more pronounced responses to foreign odorous stimuli. There is a growing consensus stipulating that for wild prey populations predator odors alone may not evoke strong antipredator responses [31, 49, 64], but in turn, a combination of factors, including physiology, type of perceived risk, and habituation [29]. Indirect risk factors, such as illumination and vegetation cover, have been found to play larger roles in governing rodent foraging behavior compared to direct predator cues, such as odor [64, 65].

Since leopard cats have been absent in Eastern Taiwan for several decades, and therefore numerous generations of the local rodent species, it is possible these respective rodents have lost the ability to discriminate the odor. Additionally, other small carnivores in eastern Taiwan that are capable of predating on rodents, such as the lesser civet (*Viverricula indica*) and feral cats (*Felis catus*), occur at low densities (I. Best, unpublished data) or rodents are not a main prey item for them [66, 67]. Antipredator responses are very costly [68] and if a given trait no longer serves a purpose it is likely that it will be selected against and lost [69]. Furthermore, according to the naiveté hypothesis prey are not expected to discriminate and respond accordingly to novel predators due to no previous encounters [70]. In Australia, the invasion of cane toads (*Rhinella marina*) prompted the relocation of native Northern quolls (*Dasyurus hallucatus*) to predator-free islands, and they have lived in these conditions for multiple generations [58]. Jolly et al. [58] compared responses of quolls from both the predator-free island population and mainland Australia to native predator cues. Opposite to the mainland quolls, the island population showed no aversion to the predator odors. For the current study, despite the possibility that rodents inhabiting leopard cat-free regions are naïve to the predator and are unable to recognize their odors, further research testing rodents in areas where leopard cats are present is necessary to affirm this prediction. Additional studies could also be conducted to test the responses of these populations of wild rodents to other mammalian carnivores that do occur in the region, considering that the predation pressure is likely weak.

Given the lack of predator odor effects on rodent behavior, we were able to examine behavioral responses across trials. Even though trial did not have a significant effect on the behavioral categories (defensive and non-defensive), specific responses representative of behavioral plasticity and habituation [29, 41] did change. Two out of the four species showed significant increases in amount of time foraging, and *M. caroli* did spend more time foraging despite the difference not being significant. *M. caroli* and *R. exulans* also significantly decreased the amount of time spent motionless during the second trial. Therefore, the three species, *M. caroli, A. agrarius* and *R. exulans*, demonstrated a trade-off in defensive behaviors, as well as exploration, for access to food resources. Even though exploring can be constituted as a non-defensive behavior conferring boldness, individuals are still able to keep some level of vigilance [16, 49] whereas with foraging, vigilance is sacrificed to a much higher degree [71]. Our results provide further support that wild populations of rodent species can have behavioral plasticity, as habituation can be

linked to phenotypic plasticity [41]. In the case of the present study, the increase in foraging activities and exploitation of the food patch can reflect learning and also be a measure for information processing [72]. We find it unlikely that the increases in foraging behaviors observed were stress-induced or a product of our experimental procedure. Animals were food deprived for the same amount of time on both days of testing, and were provided with ample food upon return to their housing cage after completing the first trial. Moreover, high levels of acute stress on rodents may actually inhibit food intake and prompt defensive behaviors [73, 74]. The variation between individuals that was observed in our experiments could also indicate not only behavioral plasticity, but also large behavioral repertoires [75]. In a study conducted by Holmes et al. [76], wild mice in plus-maze experiments were found to demonstrate a greater selection of behaviors compared to captive strains. A broad behavioral repertoire could also have implications for fitness under a changing environment – increased human activity and disturbance. A species with a wider behavioral range (boldness-shyness) may be more resilient to disturbances [38, 77].

The largest species included in our study, *R. losea*, had contrasting responses compared to the other species during the second trial. Namely, the species failed to exhibit significant increases in any of the non-defensive behaviors. These results may indicate different rates of habituation between the species. On average, *R. losea* ranged from three to ten times larger in size than the other species. With the predictions of the POLS, *R. losea* would be expected to be the most cautious species in our study, therefore, it could also be possible that this species would habituate to novelty at a slower pace. Larger species with slower life history traits have a tendency to be more cautious with stronger neophobia responses [16, 38, 49], therefore habituation to a novel situation with associated risk maybe slower compared to smaller species.

The invasive species, *R. exulans*, somewhat surprisingly spent the most time concealing during the first trial. However, the second trial for this species comprised a drastic reduction staying motionless with an increase in foraging. The average amount of time spent hiding was also lower, though the difference between the two trials was not significant. These results demonstrate the plasticity and habituation potential of the rat, which may be characteristic of an invasive species [39, 78, 79]. Additionally, the initial caution the species exercised could also be somewhat indicative of their strategy for occupying novel environments – not overly bold to a degree of recklessness. The species could benefit from processing information and assessing risk about the new environment from a safe refuge in addition to exploration [80, 81]. To better understand the habituation potential and rate of invasive species, further studies adopting a comparative approach involving multiple invasive and native species will be necessary.

Interestingly, in tandem with the range expansion of *R. exulans* in Eastern Taiwan, *A. agrarius* has been experiencing population declines [82; I. Best, unpublished data]. In the present study, we observed *A. agrarius* to be the most voracious foragers exposing themselves to risk for the longest periods of time. The lack of defensive behaviors to the simulated cues of risk in our experiments (novel environment and objects) may suggest that they have an increased vulnerability to predators, biological enemies and other disturbances in the wild.

Conclusions

Most POLS studies to date have largely focused on behavioral covariation among individuals or populations of a single species [49, 83, 84], therefore our study provides further insight for the POLS framework exemplified by inter-specific behavioral variation in accordance with a fast-slow continuum. In a novel microenvironment, the smaller, "faster" species of mice displayed behaviors conferring boldness, whereas the larger, "slower" rat species exercised more caution. Our findings also suggest that these four species of rodents in eastern Taiwan may be naïve to leopard cat cues, indicating that antipredator behaviors may be learned from experience. However, further research is required to uncover this assumption. Finally, despite the addition of a predator odor and novel objects, we observed a trend for an increase in non-defensive behaviors across all species – representing habituation and behavioral plasticity. In the context of regions undergoing landscape changes facilitated by increased human activity and development, as is the case in Hualien County in eastern Taiwan, the survival and success of wild rodents may be dependent on broad behavioral repertoires.

Methods

Study area

We conducted our study in Hualien County located in Eastern Taiwan. Our experiments took place at National Dong Hwa University, Shoufeng Township, Hualien County (23.90 °N, 121.54 °E). In low-elevation areas of Hualien a variety of habitats supports rodents including the Ryukyu mouse (*Mus caroli*), striped field mouse (*Apodemus agrarius*), lesser ricefield rat (*Rattus losea*), greater bandicoot rat (*Bandicota indica*), as well as the introduced species the house mouse (*Mus musculus*) and Pacific rat (*Rattus exulans*). These murine rodents are often hosts to chigger mites and hard ticks that can transmit scrub typhus and spotted fever group rickettsiae, respectively [46, 85]. Therefore, since the aforementioned rodents play a role in the survival of ectoparasites, and hence pathogen prevalence, understanding how rodents respond to novel environments in close proximity to humans could have implications for disease risk.

Leopard cats have been absent in Hualien for multiple decades, but there are historical records of their occurrence in the region [42]. We selected this area for our study due to the abundance of multiple rodent species and the absence of the predator the leopard cat. This allowed us to test leopard cat odors as a novel predator cue, which accounted for a secondary level of novelty in our experiments. Moreover, performing our study in this area enabled us to assess whether the native rodents are naïve to leopard cat odors and subsequently lack anti-predator behavioral responses.

Animal collection and maintenance

Animals were live-trapped using a combination of Sherman (26.5 × 10 × 8.5 cm) and mesh (27 × 16 × 13 cm) traps set in transects at 10-m intervals. The larger mesh traps were used to capture the larger species *R. losea*. We deployed the traps at sites in fields of the agricultural areas of northern Hualien

County. Since an objective of this study was to include individuals from multiple rodent species, we sampled different habitat types. All sites were a minimum distance of 500 m apart and only sampled once to ensure that we did not trap the same individual more than once. Wang & Wang [86] reported that large rodent species, such as *R. losea*, rarely move more than 500 meters. Traps were baited with sweet potato covered in peanut butter and set in the late afternoon and rechecked first thing the next morning.

Our target species included two mice species, *M. caroli* and *A. agrarius*, and two rat species, *R. exulans* and *R. losea*. The inclusion of these species was due to higher trapping success and for inter-specific representation of rodent communities exhibiting variation in morphological and life history traits. Additionally, since *R. exulans* is an invasive species [82], we wanted to determine if there were any associated behavioral differences from the other native species. Shrews and non-target species that we trapped were released immediately. Furthermore, only adults of each species group were included in our experimental trials. Upon capture, target species that met our criteria were examined to determine sex and reproductive status. Reproductive maturity was concluded if testes were descended in the scrotal region for males, and the presence of vaginal perforation and/ or swollen nipples for females. To avoid potential sources of behavioral bias, if females were considered pregnant they were excluded from the trial. We also measured body weight (± 0.1 g), body length (snout to anus, mm) and tail length (anus to tail tip, mm). Animals were kept for a maximum period of 48-hours after which they were released at the same site they were captured. We kept rodents in a designated housing room in mesh cages (27 × 16 × 13 cm); with one rodent housed per cage and no more than ten test animals were kept at a given time. Rodents were provided with water and food *ad libitum*. Additionally, cages contained shredded paper for bedding, a cardboard tube for hiding, and we placed a cover over all cages for additional privacy and to maintain separation. The housing room was maintained at 24 ± 1 °C with natural lighting. Only one researcher entered the housing room to provide water, food and to collect rodents for the trials; this was to minimize disturbance.

Predator odor

Leopard cat body odor and fecal samples were collected from captive individuals at Taipei Zoo and Pingtung Rescue Center for Endangered Wild Animals. Body odors were obtained by placing clean towels sterilized by an Autoclave in the sleeping areas of that cats' enclosures for a period of roughly 30 days. This duration was to allow for the towel to be sufficiently permeated with the leopard cat's odor. Upon receiving the towels, they were cut into smaller segments (15 × 15 cm), which has proven to be an effective size at eliciting antipredator behavioral responses in prey species [34, 87]. The segments were then placed in airtight, re-sealable plastic bags and stored in a -20 °C freezer until later use. Clean, latex gloves were worn at all times when handling the towels. Fecal samples were also collected from the same donor individuals that provided the body odor samples. Upon request of collection, fresh feces were collected daily, placed in airtight, re-sealable plastic bags and stored in a freezer at -20 °C. Samples were stored in a freezer for a maximum period of two months before use. On the day of experimental trials, fecal samples of the same donor individual were thawed and pooled together. The feces were then crushed and diluted with distilled water to create a mixture with a ratio of 1 part feces (g) and 1 part

distilled water (mL). This ratio has been commonly used in other predator odor experiments [27, 88]. We used body odor and fecal samples in concert for our leopard cat odor treatment. Corresponding body odor and fecal samples of the same donor individual were always paired together. We did not consider the combination of both odor types to be an exaggeration of leopard cat cues, since our aim was to simulate high predation risk. Furthermore, predators, such as felids, often leave multiple scent types at areas they visit [89–91]. Moreover, the use of 'natural' olfactory cues, such as fecal or body odor samples, has been found to be more effective in simulating predation risk and evoking defensive responses in prey compared to single, synthesized volatile chemicals, such as the commercially-available trimethylthiazoline (TMT) [90, 92].

Experimental apparatus

Trials were conducted in an open-area test arena (165 cm long X 80 cm wide X 70 cm deep; Fig. 1), which consisted of an opaque, rectangular-shaped box made of plastic material that was non-permeable and easy to clean. The size of the arena was to allow for sufficient exploration and to prevent escape. The arena was divided into three-sections using a non-odorous tape that was clearly visible under low light; in Sect. 1 a PVC tri-entry tube (referred to as the hide; 50 mm diameter) was placed in the center to allow concealing. We thought it was important to include a hide, as evasion and/ or hiding are common defensive behavioral responses of wild rodents when facing risk [54, 93]. In section 3 at the opposite end of arena we placed a foraging tray and the treatment apparatus (present only during the treatment trial) (Fig. 5). The foraging trays (17.3 × 12.1 × 3.8 cm) contained 5.0 g of millet seed mixed thoroughly in 75 g of extra fine sand. Through our preliminary tests and pilot study, we were able to determine millet seed as an appropriate food source.

We affixed a WI-FI enabled surveillance camera (D-Link DCS-936L; D-Link, Taipei, Taiwan) equipped with infrared capabilities to the upper edge of the interior wall above Sect. 3 (Fig. 5) and positioned the camera to fit the treatment apparatus, foraging tray and hide in the field of view. This camera also provided us with live streaming of all trials. We also used a camcorder (HausBell HDV-302S; USCLOUND Trade Inc., California, USA) with infrared attached to a tripod and positioned to have the interior of the arena in the field of view. The combination of the two cameras ensured there were no blind spots and the whole interior of the arena was fully captured.

The apparatus for the leopard cat odor treatment consisted of a body odor towel segment placed on a tray (22 × 17 × 3 cm) with 5 g of the fecal solution on a petri dish positioned on top. The non-odor control treatment comprised a clean towel segment sprayed with distilled water placed on a tray with an empty petri dish on top. These apparatus are hereafter referred to as treatment apparatus.

Trial procedures

Our experimental trials took place from September to November 2018 and January to June 2019. All trials were conducted between 18:00 and 23:00, starting after dusk, in a testing room with the lights turned off to reflect natural light conditions and account for the rodents' active period. Test subjects were food deprived for at least 10 hours before each trial, since an objective of this study was to examine

foraging behavior. All test animals were tested for two consecutive nights. The purpose of the first trial (first night for each animal) was to test the rodents' responses to a novel environment (test arena), therefore the treatment apparatus was excluded. During the second trial on the successive night, which included the treatment apparatus, the main aim was to assess the rodents' responses to the predator odor. The order for animals to be tested was randomly selected and kept the same upon the second night to allow for 24 hours between each animal's trials. Test animals were transferred from to the testing room in their cages by the same researcher for each of their trials. The cages were placed in Sect. 1 (Fig. 5) of the test arena and their cage door was left open. Once it was confirmed that the rodent had left their cage and entered the arena, cages were removed, cameras were activated and the researcher exited the testing room. Trials were able to be viewed from a separate room via a live stream of the surveillance camera, in addition to being video recorded. The duration of all trials was 35 minutes, which included a 5 minute introductory period, followed by a brief disturbance from a researcher (placement of treatment apparatus in the arena), then the remaining 30 minutes. We selected this length for our trials since our aim was to measure immediate responses to a novel environment and predator cue. Similar trial durations have been employed in lab-based predator odor experiments that have tested on rodents [27, 34, 61, 62]. During the first trial for each animal, since the treatment apparatus was absent the disturbance in this trial was to mimic the procedure of placing the treatment apparatus in the arena during the second trial. During the second trial, the treatment apparatus was placed in Sect. 3 of the arena adjacent to the foraging tray (Fig. 5). Upon completion of each trial, animals were returned to their cages and housing room. The remaining food content in the foraging trays were sieved and weighed using an electronic scale (± 0.1 g) before replacing the seeds and sand. We thoroughly cleaned the test arena and apparatus using 75% ethanol and allowed at least 30 minutes for any lingering odors in the testing room to dissipate before starting the next trial.

Behavioral response analysis

The videos of all trials were analyzed offline and in-depth. The behaviors we scored were *exploring*, *foraging*, *motionless*, *concealing*, *grooming*, *consumption*, *foraging events*, *jumping* and *contact* (Please refer to Table 4 for detailed definitions of each behavioral response).

For each behavior to be considered and scored it would have to last for at least 3 seconds. We included the 'head out' behavior as part of *concealing* because it was not commonly observed amongst the test subjects. Vigilant rearing was also not observed in our trials. Based on our preliminary trials, the test subjects did not display any preference for the different sections of the arena, so the time spent in different sections was not included. We further divided the duration-based behaviors into two categories *defensive* and *non-defensive* defined as exhibiting *motionless* and *concealing*, and *exploring*, *foraging* and *grooming*, respectively. Exploration, foraging and grooming are commonly classified as non-defensive behaviors for rodents, whereas motionless and concealing are considered defensive responses to risk [31, 94, 95]. We defined these behavioral categories in order to test our POLS prediction; a set of behaviors to assess general responses to risk. *Contact* was only scored during the second trial because the treatment apparatus was absent in the arena for the first trial. *Consumption* was expected to vary

across species in our experiment due to the inter-specific size disparity. To account for this, we calculated a *consumption ratio* defined as the amount of food eaten proportional to the animal's body weight and expressed as a percentage. We measured *foraging events* to be used in concert with time foraging and *consumption ratio* to examine foraging efficiency of test animals; whether rodents have long and few foraging bouts or short and frequent.

Statistical analysis

Since our response variables did not meet the assumptions of normality we employed generalized linear models (GLM) and generalized estimating equation (GEE) models encompassing various link functions. Because our response variables could be classified as continuous or count data (e.g. number of seconds in a trial, number of occurrences in a trial) we employed models with functions that best fit the distribution of our data. To take into account potential seasonal influences on rodent behavior, we initially included a seasonality variable in our models; defined as the difference in days between a baseline date (July 1st 2018) and the date of the trials. This seasonality variable had no significant effects on any of our behavioral responses, so we excluded it from all successive models to not exhaust too many degrees of freedom. Additionally, because species already takes into account differences in life history and morphological traits, such as size, we did not include body weight as a factor in our models.

To test responses to a novel environment (first trial only), for all the duration-based response variables, with the exception of *exploring* and *non-defensive* behaviors, we ran a GLM incorporating a negative binomial log-link function with a fixed offset value equal to 2100 (total amount of time in seconds in a trial). In these models, the predictors were fixed factors species and sex, as well as their interaction. The response variables *exploring*, *non-defensive* and *consumption ratio* were analyzed using a GLM fit with a gamma with log-link function; with species and sex set as the fixed factors. A GLM with a negative binomial log-link function was used for the response variables *foraging events* and *jumping*, with the same fixed factors.

We measured rodent responses to leopard cat odor using a GEE (with the exception of *contact*) with test animal ID as the subject variable and trial as the within-subject variable. GEEs with negative binomial log-link functions were performed for each duration-based response incorporating an offset equal to 2100 and setting trial (first and second), treatment (leopard cat odor or control), and species as the fixed factors. The variable trial was included in our models as a factor because in addition to testing the effects of a predator odor, we sought to asses any differences in behaviors between the first and second trials. We included two-way interactions between our fixed factors in our models, but not a three-way interaction. We excluded a three-way interaction because it did not coincide with our research objectives and to save degrees of freedom. The variable sex was excluded from these models since animal ID was already included, which factored in sex as well as the other unique characteristics of an individual animal. Additionally, testing the effect of sex was not an objective of ours for the second trial, so in order to save degrees of freedom the variable sex was omitted from this part of the analysis. The same model parameters were used for the responses *foraging events* and *jumping*, but with an offset omitted. *Consumption ratio* was tested using a GEE with a gamma log-link function including the aforementioned

fixed factors. In all the GEE models performed we used an AR(1) correlation matrix structure. For the response *contact* we ran a GLM with a negative binomial log-link function and included treatment and species as fixed factors, since this variable was only measured during the second trial. The previously mentioned GEE analyses also allowed us to test for changes in behavior between the first and second trial (i.e. different levels of novelty) at both the community and species level. Post hoc analyses were performed to test for differences between subgroups of our fixed factors using estimated marginal means with a pairwise contrast incorporating a least significant difference. For all of our statistical analyses significance was considered at α = 0.05. All statistical analyses were performed with SPSS *v.25.0* (IBM, Armonk, USA).

Abbreviations

Pace-of-life syndrome
POLS
Generalized linear model
GLM
Generalized estimating equation
GEE

Declarations

Ethics approval and consent to participate

All components of this study were approved by National Taiwan Normal University Animal Care and Use Advisory Committee (Permit # NTNU-106047). All researchers involved in this study abided to the legal requirements of animal handling and welfare in Taiwan. Furthermore, none of the animals included in the experimental procedures are classified as threatened in Taiwan.

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets used and/or analyzed during the current study will be deposited in open database once the manuscript is accepted or is requested by reviewers during the reviewing process .

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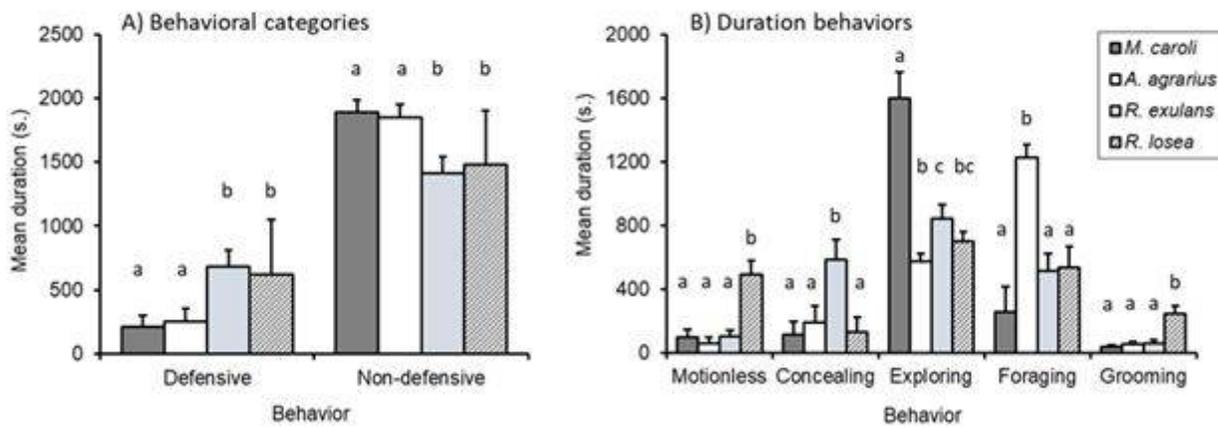
Figures

Figure 1

Mean duration (out of 2100 seconds) of behavioral responses between species during the first trial; A) Defensive and non-defensive categories, B) All duration-based behaviors. Error bars represent standard error of the mean. Differences in letters above each response variable indicate significant differences between species groups.
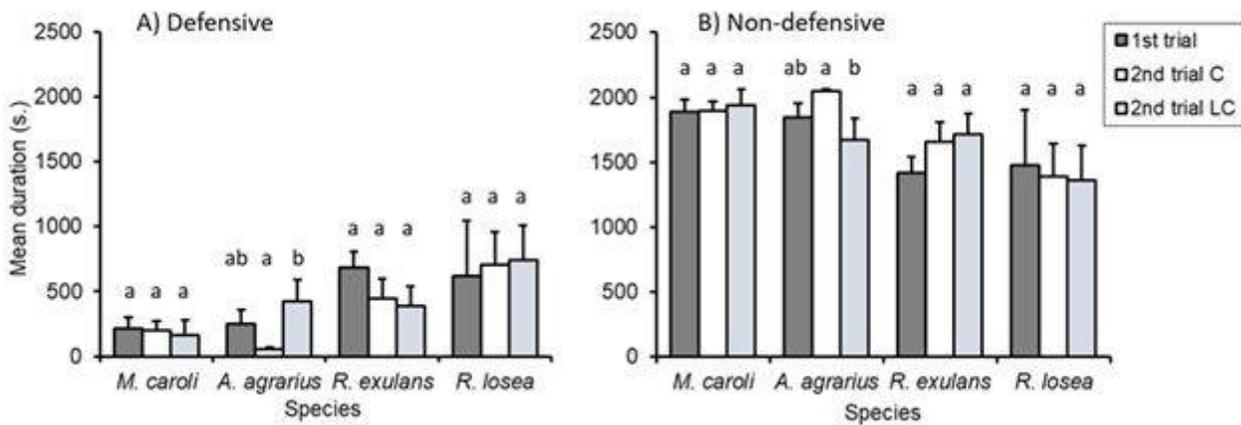

Figure 2

Mean duration (out of 2100 seconds) of A) defensive and B) non-defensive behavioral categories compared between species, treatment group and trial. 1st trial comprises both treatment groups. '2nd trial C' refers to the control group during the second trial. '2nd trial LC' refers to the leopard cat odor group during the second trial. Error bars represent standard error of the mean. Differences in letters above each species indicates significant differences between subgroups: 1st trial, 2nd trial C, 2nd trial LC.
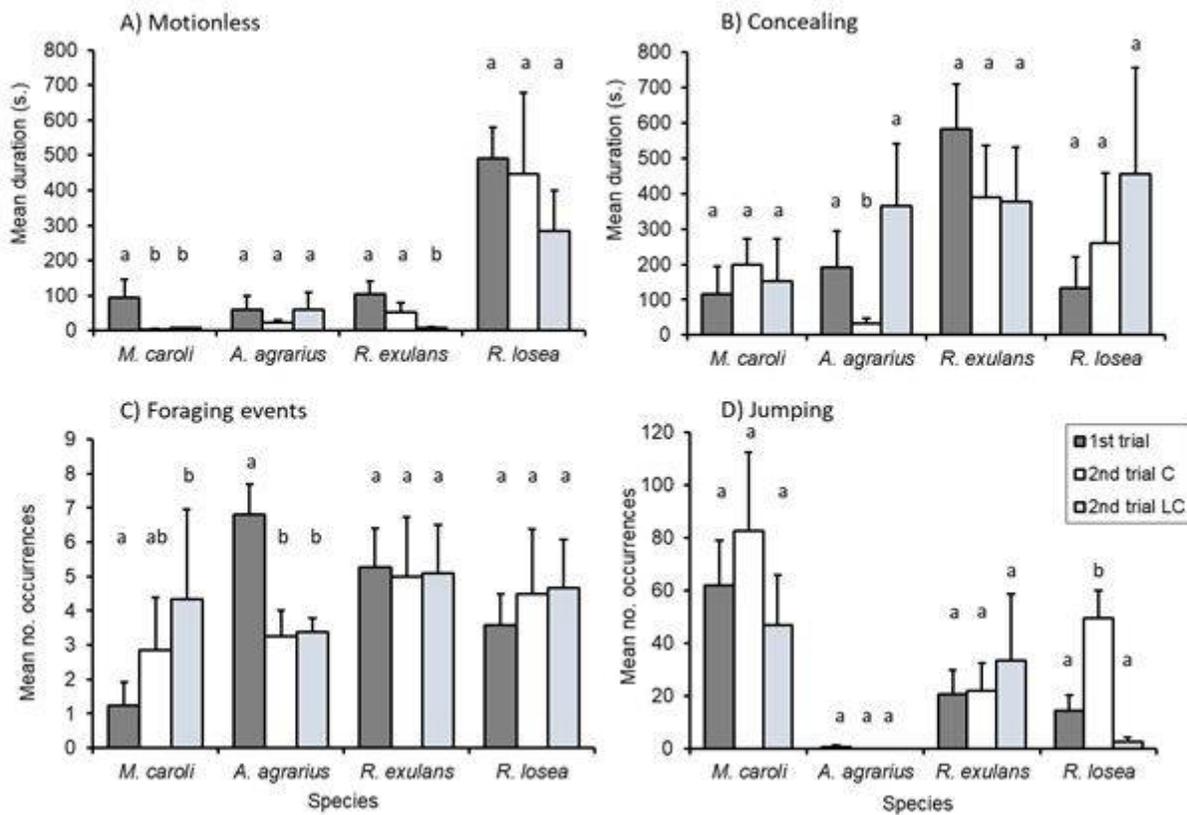
Figure 3

Mean duration (out of 2100 seconds) of A) Motionless, and B) Concealing; mean number of occurrences of C) Foraging events, and D) Jumping. Each response variable is compared between species and treatment groups, with 1st trial as a reference. 1st trial comprises both treatment groups. '2nd trial C' refers to the control group during the second trial. '2nd trial LC' refers to the leopard cat odor treatment group during the second trial. Error bars represent standard error of the mean. Differences in letters above each species indicates significant differences between subgroups: 1st trial, 2nd trial C, 2nd trial LC.
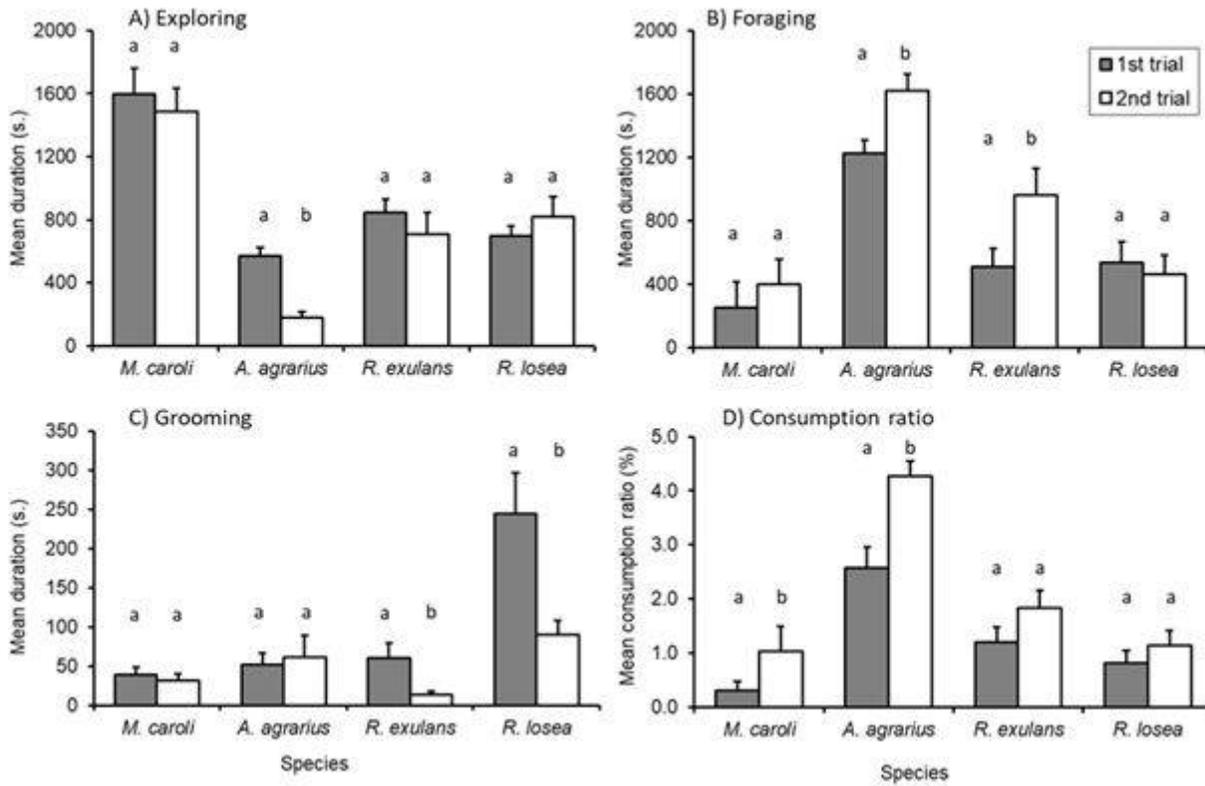
Figure 4

Mean duration (out of 2100 seconds) of behaviors A) Exploring, B) Foraging, C) Grooming, and D) mean consumption ratio. Each response variable is compared between species and trial. Error bars represent standard error of the mean. Differences in letters above each species indicates significant differences between 1st trial and 2nd trial for that species.
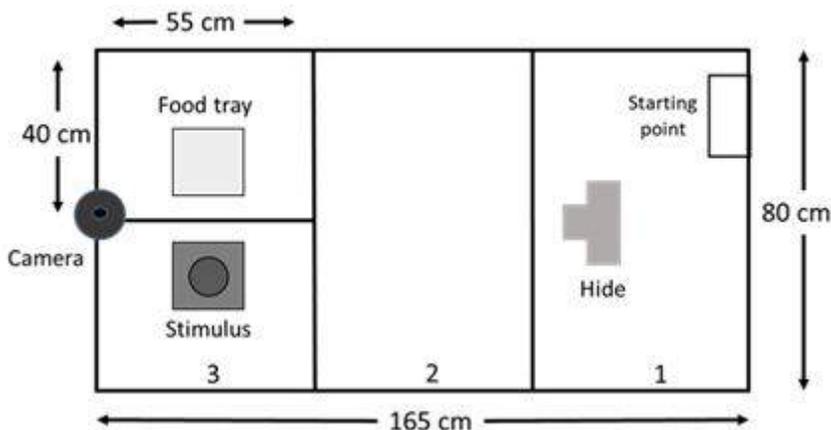

Figure 5

Schematic of the base of the test arena in the trials. The divisions of the different sections are marked with solid black lines. The numbers correspond to the specified section. Section 3 included both the area with the food tray and stimulus. Stimulus refers to treatment apparatus.

Supplementary Files

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- SupplementaryTables.docx