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ABSTRACT

House mice (*Mus musculus*) pose a threat to the native flora and fauna on islands, and can cause significant damage wherever they have been introduced. Methods used to eradicate invasive rodents, like house mice, at high population densities may not be appropriate for intercepting them at lower densities. A better understanding of the immediate behavior of house mice when first introduced to a novel environment would help managers develop effective biosecurity techniques to protect against new invasions. To address this problem, we conducted a controlled laboratory experiment that simulated an invasion by wild house mice into a novel environment. We quantified and compared the immediate behaviors of wild house mice ($n = 40$) by testing various odors and other attractants, including odors (e.g., foods and conspecific), shelter, water, and a control. There was a significant difference in mouse responses to these treatments ($P \leq 0.0001$). We found that the most common immediate reaction of invading mice was to seek shelter in a den box ($\mu = 47.7$ box entries) rather than responding to the other potential attractants presented. Secondarily, the mice were interested in some food scents, particularly bacon grease ($\mu = 18.3$ box entries), peanut butter ($\mu = 17.0$ box entries), and cheese ($\mu = 14.5$ box entries). The sex of the mouse did not influence their responses to odors and attractants ($P \geq 0.243$), however, we noted that females visited male feces and urine odors ($\mu = 17$ visits) more than males visited female feces and urine odors ($\mu = 11$ visits). Fewest visits were to the empty box ($\mu = 8.0$ box entries) and the water box ($\mu = 5.1$ box entries) Based on our findings, we surmise that a secure den box which included certain food odors might entice and hold mice in a restricted area for a short duration in a novel environment. If done properly, this arrangement could be utilized for early detection and response to newly-invading house mice.

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1. Introduction

Originally from the Middle East and Asia, house mice (*Mus musculus*) are now found worldwide, mainly because of human introductions (Long, 2003). House mice pose a threat to the native flora and fauna of islands (Burbidge and Morris, 2002) and can cause significant damage to agricultural commodities and property (Long, 2003; Timm, 1994). In many situations, house mice have a close commensal relationship with humans because humans incidentally provide food and shelter. However, Witmer and Jojola (2006) revealed that many tropical islands and portions of some continents contain free-ranging house mice that are not reliant on humans. Additionally, despite the small size of house mice, they have been shown to cause significant predation on seabird nestlings, even those much larger in size (e.g., Wanless et al., 2007). Most island seabirds have not evolved in the presence of sympatric

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predators and are very vulnerable to introduced rodents (Moors and Atkinson, 1984). Periodically the populations of mice have irrupted in places such as Australia and Hawaii, causing "plagues" (Long, 2003).

MacKay et al. (2011) explained that intercepting individual rodents is often difficult, but once better developed, intercepting the first arrivals will be more effective at controlling invasive species when compared to reactive measures. Methods used to detect and eradicate invasive rodents at high densities may not be appropriate for intercepting rodents at low densities (Russell et al., 2005), or for removing the last remaining rodents at the end of an eradication effort (MacKay et al., 2007). Dense grids of bait stations may not be effective because many rodents exhibit neophobia (Russell et al., 2005), and bait stations may be inappropriately designed or spaced for invasive rodents (Spurr et al., 2006, 2007). Additionally, invading rodents may roam widely (Russell, 2007), so entry rates rather than encounter rates of bait stations are likely more important. Proactive monitoring should allow quicker and more cost effective targeting of the invading rodents in order to remove them without having to resort to island-wide rodenticide baiting (Broome, 2007). A better understanding of a rodent's immediate behavior when it first arrives in a novel environment (e.g., island) would allow managers to develop effective biosecurity techniques to prevent rodent invasions.

House mice are primarily nocturnal and have a keen sense of smell, taste, and touch (Witmer and Jojola, 2006). They rely on these senses for many important activities during their lives, such as food location, object detection and avoidance, predation avoidance, maintenance of social systems, and reproduction (Kemble and Bolwahnn, 1997; Meehan, 1984; Timm and Salmon, 1988; Witmer and Jojola, 2006). By exploiting those senses, we hope to identify materials that can meet the immediate needs of invasive house mice (i.e., food, water, shelter, and contact with conspecifics or potential mates) so we can draw conclusions on their initial priorities following arrival in a novel environment. We can then extrapolate these findings to assist in designing strategies for detection and quick removal of house mice when they first invade a new environment.

Radial arm mazes have typically been used in operant conditioning studies to test the spatial memory abilities of laboratory animals (Barnett et al., 1978; Ilersich et al., 1988; Van Haaren et al., 1987). These mazes can also be used to test for preferences between different olfactory cues and other stimuli, or to identify potential attractants or repellents. We examined the immediate behaviors of wild house mice in new environments, under controlled conditions. We placed wild-caught mice into an eight-armed radial arm maze (Med Associates, Inc., Georgia, VT, USA), that represented a novel environment, and monitored which odors or other types of attractants or objects the mice initially focused on. By examining the selections that wild-caught house mice made in the maze, we made inferences about the preferences of the wild mice in a novel environment. We hypothesized that mice arriving on an island (via shipping cargo, shipwreck, or on floating debris) might seek one or more of the following items: food, fresh water, a location reasonably safe from potential predators, or a mate. We chose a variety of materials to test this hypothesis and assumed that one or more preferred items would be identified. Furthermore, the identification of attractive food rewards may help refining laboratory studies on mice, where positive reinforcement can be used to train mice.

2. Materials and methods

We captured 40 wild house mice from two dairy farms in Fort Collins, CO, USA using Sherman live traps (H.B. Sherman Traps, Tallahassee, FL, USA) baited with peanut butter and oatmeal, and cotton balls for insulation. Traps were set in the late afternoon and were checked the following morning. The captured mice were transported to the USDA National Wildlife Research Center (NWRC), Fort Collins, CO, USA where they were quarantined for 2 weeks prior to the initiation of the study. All mice were maintained in individual 29 cm × 18 cm × 13 cm shoebox cages with wire mesh lids and provided with a dry rodent chow (Formulab 5008, PMI Nutrition International, Inc., Brentwood, TN, USA), slices of apple, water, bedding material and a cardboard den tube. Each cage contained corn cob floor covering and the bedding material was cotton balls. The animal room was maintained at 21 °C, 40% relative humidity, and a 12 h/12 h light–dark cycle (7:00–19:00 h lights on). Animals were captured, transported, and maintained in compliance with the United States' Animal Welfare Act under the IACUC-approved study protocol QA-1628 The study mice were randomly assigned to four groups of 10 mice (five males and five females). Each group was randomly assigned to a trial (see Table 1). To ensure the mice would be likely interested in finding food during the trials, we removed food from the holding cages approximately 12 h before each mouse was tested; i.e., they were lightly fasted as approved by the IACUC. This was to reflect the condition likely to occur with mice arriving at an island via a shipwreck or on floating debris which is how many island invasions are thought to occur.

The radial arm maze consisted of an octagonal central hub that was 30 cm high and 30 cm in diameter. When opened, the eight drop doors allowed access to the arms. Each arm was 46 cm long, 9 cm wide and 15 cm high. There was a small entry box at the end of each arm; each box was 5 cm wide, 5 cm deep and 6.5 cm high. The floor of the box consisted of a small wire mesh under which was a slide-on box in which a food or odor item could be added. The mouse did not have direct access to this material (i.e., could smell the item, but not consume it). One entry box had a water bottle inserted from which the mouse could drink. At the end of one arm, instead of a small entry box, there was a plastic dome-shaped den box 10 cm in diameter and 8 cm high. This den box had a floor covering of burlap. The maze was equipped with three infrared sensors. Two were located in each arm a short distance (5 cm and 9 cm) from the hub door. These detected (depending which was triggered first) when a mouse entered an arm from the hub or when it left the arm to return to the hub. The third sensor was located at the entry box opening and detected when a mouse investigated the box at the end of an arm. We assigned different odors and other attractants to the boxes on the end of each arm of the maze. Specifically,

Table 1
Test materials used inside the arms of a radial arm maze with 10 house mice (five male and five female) for each of four trials.

Arm	Trial 1	Trial 2	Trial 3	Trial 4
1	Cheese[a]	Peanut butter[b]	Brussels sprouts	Apple
2	Rodent chow[c]	Fatty acid scent[d]	Tuna fish[e]	Dog chow[f]
3	Water	Water	Water	Water
4	Urine and feces	Urine and feces	Urine and feces	Urine and feces
5	Empty	Empty	Empty	Empty
6	Diphacinone pellets[g]	Brodifacoum pellets[h]	Anise[i]	Bacon grease
7	Almond extract[j]	Lemon extract[j]	Melon extract[k]	Banana
8	Den box	Den box	Den box	Den box

[a] Easy Cheese (cheddar flavor), Kraft Foods Global, Inc., Northfield, IL, USA.
[b] Albertson's Creamy Peanut Butter, Albertsons, Inc., Boise, ID, USA.
[c] Lab Diet 5008, PMI Nutrition International LLC, Brentwood, MO, USA.
[d] Pocatello Supply Depot, Pocatello, ID, USA.
[e] Albertson's Tuna in Water, Albertsons, Inc., Boise, ID, USA.
[f] Formulab Diet 5008, PMI Nutrition International LLC, Brentwood, MO, USA.
[g] Ramik Green®, HACCO, Inc., Madison, WI, USA.
[h] CI-25® Rodenticide, Bell Laboratories, Inc., Madison, WI, USA.
[i] Sigma–Aldrich, Inc., St. Louis, MO, USA.
[j] McCormick & CO., Inc., Hunt Valley, MO, USA.
[k] Peak Can & Supplies, Denver, CO, USA.

we randomly assigned odors from animal or plant foods or extracts and rodenticides baits (consisting primarily of grains and mineral oil, but also with proprietary attractants such as sweeteners) to four arms (see arms one, two, six, and seven; Table 1). The remaining four arms were randomly assigned to one of each of the following, for every trial: conspecific urine and feces of opposite sex, a water bottle, a den box with a burlap cloth, and a control (empty box). All odorous substances were placed on a piece of filter paper (Whatman International, Maidstone, England) inside a small plastic weighing dish (VWR Scientific, Batavia, IL, USA), and then placed in each of the odor boxes below the entry boxes. Urine and feces were collected from live house mice. Females on trial were always exposed to the urine and feces of males, and males were always exposed to female urine and feces.

As part of the experimental trials, a randomly selected house mouse was placed in the central hub of the radial arm maze under dark room conditions because wild mice are most active during the dark. After 1 min of acclimation time, all eight doors to the arms opened and the mouse was free to explore the maze for 15 min. This was called an individual mouse run. Using the manufacturer's software, we were able to decipher: (1) how many minutes the mouse spent in each arm of the maze, (2) how many times the mouse entered each arm, and (3) how many times the mouse investigated each box at the end of each arm. After each individual mouse run we carefully cleaned the entire maze with an odorless, non-toxic cleanser (Skilcraft® Clean, Lighthouse of Houston, Houston, TX, USA) and waited until the maze was completely dry so that, presumably, no unspecified odors remained for the next mouse tested or at least all arms started out in the same clean condition. The process was repeated until all 10 mice in that trial had completed an individual mouse run.

We combined the potential attractants into seven treatments categories, including; plant food or extracts, animal foods, rodenticides, urine and feces, water, den box, and the control (empty entry box). Plant foods were comprised of almond extract, anise extract, raw apple, raw banana, raw Brussels sprouts, lemon extract, melon extract, peanut butter, and dry dog food treatments. Animal foods were comprised of bacon grease, cheese, and tuna fish treatments. We chose both plant and animal materials because wild house mice are omnivorous in their feeding habits. Rodenticides were comprised of the brodifacoum and diphacinone pellet treatments (both of which are registered by the US Environmental Protection Agency for the eradication of invasive rodents on islands). The rodent chow and fatty acid scent treatments were a mixture of plant and animals food odors, and were considered individually. However, these treatments were not visited often, thus were excluded to simplify further analyses.

2.1. Statistical analyses

To compare the attractiveness of the different treatments to naïve mice, each arm of the radial arm maze was considered as an experimental unit during each individual mouse run. We recorded three different responses for the arms, including: (1) the number of times a mouse entered the arm, (2) the number of times a mouse entered the box at the end of the arm, and the amount of time a mouse spent in the arm. We pooled the results of all four trials for analysis. We used linear mixed effects models using package lme4 (v1.1-5) in program R (v2.15.1; R Development Core Team) to examine for differences in (1) the mean number of arm entries, (2) the mean number of box entries, (3) the mean amount of time spent in an arm, and (4) differences between males and females to the treatment categories. The null hypothesis was that mice would visit all treatments categories the same amount, and regardless of sex. We accounted for variation in trials, sex of mice, and individual mice using nested random effects. This also accounted for pseudoreplication of each mouse being exposed to eight simultaneous treatments (i.e., eight arms of the maze). We used package lmerTest (v2.0-6) to

Table 2
Treatment means by category for male and female house mice in a radial arm maze.

Treatment	n	Arm entries		Box entries		Time (min)	
		Mean	SE	Mean	SE	Mean	SE
Den box	40	11.7	0.65	47.7	2.73	3.0	0.11
Urine and feces	40	6.5	0.47	14.2	1.23	1.2	0.08
Empty	40	6.0	0.39	8.0	0.90	0.8	0.06
Water	40	6.0	0.42	5.1	1.62	0.7	0.05
Hub	40	NA[a]	NA	NA	NA	4.0	0.12
Animal foods	40	7.5	0.37	14.5	1.08	1.3	0.10
Cheese	10	8.8	0.77	14.5	1.73	1.7	0.18
Bacon grease	10	8.3	0.76	18.3	1.27	1.7	0.18
Tuna fish	10	6.5	0.73	14.4	2.81	1.1	0.14
Dog chow	10	6.2	0.36	10.9	2.12	0.9	0.14
Plant foods	80	8.0	0.34	12.6	0.85	1.4	0.09
Almond extract	10	9.3	0.94	10.6	1.38	1.6	0.18
Peanut butter	10	9.0	0.68	17.0	4.31	2.2	0.47
Fresh banana	10	8.7	1.05	13.9	2.40	1.5	0.17
Lemon extract	10	7.8	1.40	9.8	1.88	1.0	0.19
Anise scent	10	7.7	0.98	11.2	2.03	1.2	0.12
Fresh apple	10	7.5	0.93	11.0	2.29	1.4	0.21
Melon extract	10	7.2	0.84	10.4	1.57	0.9	0.10
Brussels sprouts	10	6.5	0.76	16.7	1.73	1.6	0.16
Rodenticide baits	20	7.0	0.71	12.7	1.92	1.2	0.12
Brodifacoum pellets	10	7.8	1.14	12.4	1.77	1.3	0.14
Diphacinone pellets	10	6.3	0.87	13.0	3.52	1.0	0.18
Non-categorized[b]							
Rodent chow	10	6.6	0.69	12.7	3.38	1.0	0.22
Fatty acid scent	10	6.4	0.95	8.3	2.17	0.8	0.12

[a] NA, not applicable.
[b] Rodent chow and fatty acid scent were not deemed appropriate to combine into any category because they were a mixture of plant and animal material.

calculate *F* statistics and *P*-values based on Satterthwaite approximation for denominator degrees of freedom. We considered differences among treatments and sexes to be significant at the $P \leq 0.05$ level. We examined distribution of our response data and the model residuals to ensure we met the assumptions of linear models.

3. Results

Overall, we examined the responses from the combined four trials of 10 mice (five male and five female) each exposed to eight simultaneous treatments ($n = 320$) in the radial arm maze (Table 2). We found the mean number of arm entries across trials was not different for those treatments categorized as plant foods ($F_{7,33} = 0.97$, $P = 0.467$), animal foods ($F_{3,7} = 3.62$, $P = 0.072$), or rodenticides baits ($F_{1,17} = 1.09$, $P = 0.311$). Therefore, we surmised that combining the individual treatment types into treatment categories did not confound our results. Based on the distribution of our data and model residuals, we surmised that our analysis met the assumptions of linear models.

We found that the number of arm entries ($F_{6,248} = 23.67$, $P = <0.0001$), box entries ($F_{6,248} = 80.98$, $P = <0.0001$), and time spent in each arm ($F_{6,248} = 61.72$, $P = <0.0001$) were not equal among the treatment categories (Table 3). The estimated variances of the random effects for the three models were $\leq$2.49, indicating there was little variance associated with trials, sex, and mice while accounting for the fixed effects in each model. The mice visited the arms of the den box more often the other treatment arms (Fig. 1). The mice also visited the den box more often than the other treatment boxes (Fig. 2). Lastly, the mice spent substantially more time in the den box arm than all other treatment arms (Fig. 3). The mice visited the plant foods, animal foods, rodenticides, and urine/feces treatments in similar amounts (Figs. 1–3). The most commonly visited treatments after the den box were cheese, bacon grease, almond

Table 3
Test of effects for house mice in a radial arm maze.

Effect	Arm entries			Box entries			Time (min)		
	DF[a]	*F* value	*P*	DF[*]	*F* value	*P*	DF[a]	*F* value	*P*
Trt	6,248	23.67	<0.0001	6,248	80.98	<0.0001	6,248	61.72	<0.0001
Sex	1,3	2.10	0.243	1,3	0.55	0.513	1,3	0.001	0.983
Trt × sex	6,248	0.92	0.482	6,248	1.96	0.071	6,248	1.88	0.085

[a] Degrees of freedom reported as: between-groups degrees of freedom (numerator), within-groups degrees of freedom (denominator).

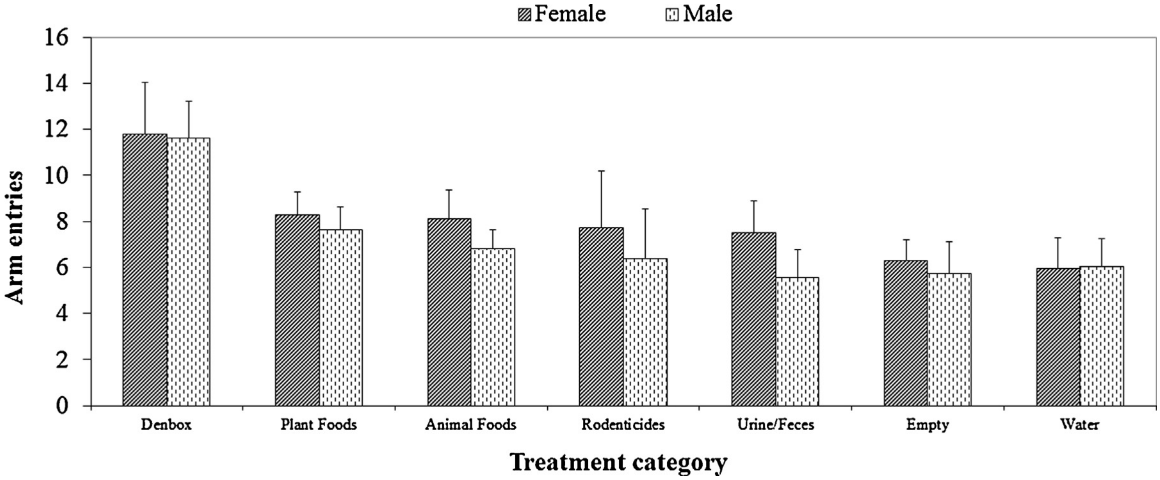

Fig. 1. Mean number of arm entries by treatment category for male and female house mice in a novel environment, radial arm maze. Vertical bars represent the 95% confidence intervals.

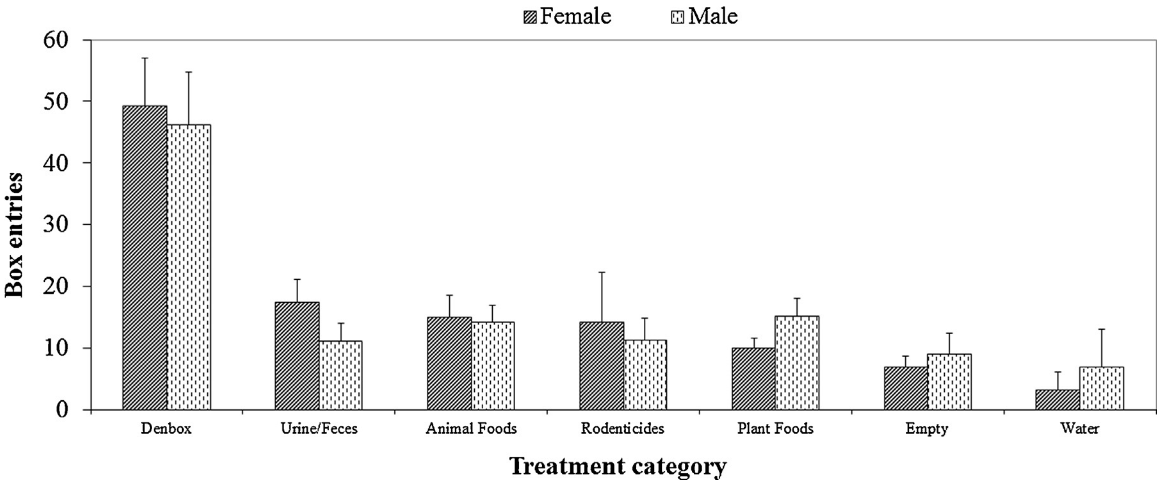

Fig. 2. Mean number of box entries by treatment category for male and female house mice in a novel environment, radial arm maze. Vertical bars represent the 95% confidence intervals.

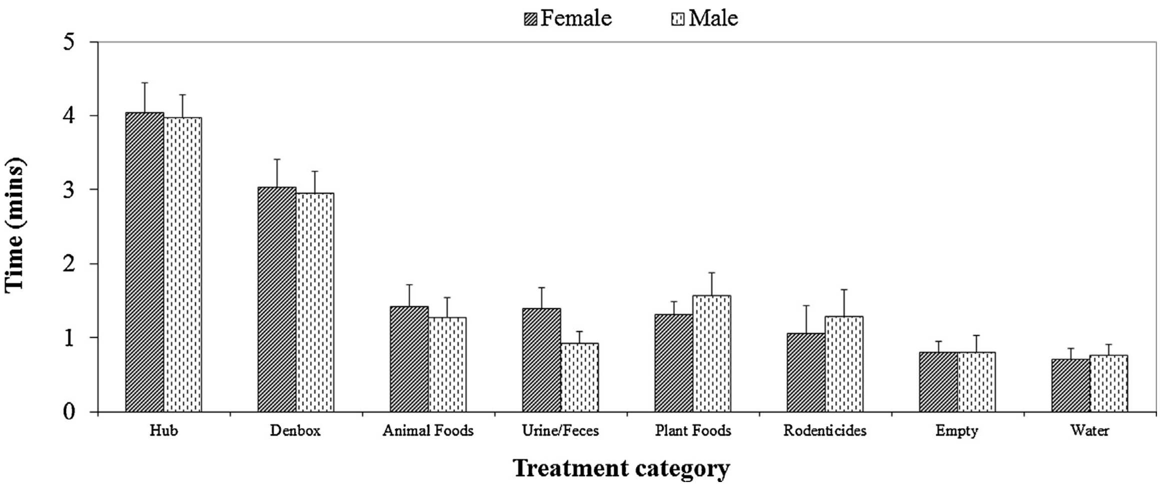

Fig. 3. Mean time (in min) partitioned by location for male and female house mice in a novel environment, radial arm maze. Vertical bars represent the 95% confidence intervals.

extract, and peanut butter (Table 2). The least visited treatments were the empty (control) and water treatments. Sex of the mice and the interaction of treatment × sex did not influence the number of arm entries, box entries, and amount of time spent in each treatment arm (all $P \geq 0.071$; Table 3). However, we noted that females visited male feces and urine odors ($\mu = 17$ visits) more than males visited female feces and urine odors ($\mu = 11$ visits).

4. Discussion

This study differs from many other rodent behavior studies, in part, because we used wild-caught house mice rather than laboratory strains of rodents. There are marked differences in behaviors and activities of laboratory versus wild rodents (Barnett, 1988; Berdoy and Macdonald, 1991; Boice, 1971; Mitchell, 1976; Shepherd and Inglis, 1987). Therefore, our study can easily relate to wild populations of house mice, especially those that might find themselves in a new environment.

We found that, in a novel environment, house mice initially focused most on a den box compared to all other treatment categories. These results were similar to three species of wild rats (*Rattus* spp.), which all utilized the den box more often than other treatment types in radial arm maze trials (Witmer, 2009). A den box likely provided cover and a more secure environment (Witmer, 2009). Although this has not been shown before with house mice, these results would seem to be consistent with the findings of Russell (2007), whose radio-collared Norway rats (*Rattus norvegicus*) stayed under cover and moved very little for the first several days after being placed on a novel island. Because the house mice primarily focused on the den box, we suggest that locating a safe covered area might be a primary need for house mice when moving into a new environment (e.g., invading an island).

The house mice also spent a considerable amount of time in the central hub. Witmer (2009) also found this was the case with three species of wild rats in a similar study. Based on that finding, we surmised that invading house mice will likely spend some time assessing a new environment before deciding on a course of action. The central hub was the only location in the radial arm maze where the mice had to choose between multiple attractants. The mice may have spent considerable time in the hub investigating the various treatment types (mainly odors), and deciding on a direction to explore. Also, the central hub is where each mouse spent the 1 min acclimation period; therefore, it may represent the most familiar environment for the mice. Other researchers have reported that wild mice of both sexes had lower activity levels and higher avoidance of open areas than laboratory strains of mice (Augustsson and Meyerson, 2004; Augustsson et al., 2005). They also mentioned that once the mice had assessed the various areas as non-risky, they explored all zones. Additionally, Wolfe (1969) noted that house mice are more exploratory than some other rodents and exhibit a less strong and prolonged period of neophobia.

Our findings also suggested that the house mice were interested in the animal foods, plant foods, and rodenticide baits. Because the mice were fasted for 12 h before trial, we surmise that they sought the most attractive food options, given a choice of various foods. Similarly, Wallace (2003) reported that when Norway rats were food deprived, they tended to find a food source and then feed, followed by extended bouts of food retrieval (e.g., caching and hoarding). Contrarily to that study, however, we suspect that the food odors we presented to the mice were novel odors. Some researchers have noted the novel odors often invoke risk assessment behaviors and avoidance by house mice, sometimes apparently suppressing their appetites (Garbe et al., 1993). Regardless of the novelty, based on our findings, we expect some food items that we tested could be useful for attracting wild house mice into a trap or a detection device. This would perhaps be more effective if the invading mice were more food-deprived than our lightly fasted mice. The time and amount of visits to the various food odors were all comparable among attractants types; however, the highest amounts of visits were to cheese, bacon grease, almond extract and peanut butter. Interestingly, we noticed that the rodenticide baits were not the most visited food odors, suggesting that perhaps there is room for improvement regarding the attractiveness of those baits. Acceptance of rodenticides baits by wild house mice has been found to be, in general, lower than acceptance by wild rats (Fisher, 2005; Witmer, 2007).

The urine and feces odors and the food odors were visited a similar number of times. Scent marking is known to be a very important feature of rodent behavior, and is often done for communication (Roberts, 2007). Additionally, the complex nature of conspecific odors (e.g., urine) on the social dynamics and reproduction behaviors of house mice and rats has been well documented (Drickhamer, 1997; Drickhamer et al., 1992; Meehan, 1984). This has also been shown for other rodents, such as voles (*Microtus* spp.; Ferkin, 1999; Solomon and Rumbaugh, 1997; Solomon et al., 1999). Some researchers have even noted that live traps which had previously held a rodent were more likely to capture another rodent (e.g., Temme, 1980). Based on those findings and our results from the maze, we surmise that house mice will spend a considerable amount of time seeking a conspecific when introduced to a novel environment. We found that female mice focused somewhat more on the urine and feces from male mice than vice versa. Witmer (2009) noticed the opposite effects with Norway rats and black rats (*Rattus rattus*), where the males tended to visit the urine and feces of females far more than females visited the urine and feces of males. Those conflicting results are likely beyond what we can discern with this study. Dominance ranking in males and estrus cycles in females are important components in the variation in attractiveness, but we did not monitor those parameters.

We found that house mice showed relatively little interest in the empty box or in the water bottle. This result was not unexpected because those boxes did not emit odors. Additionally, house mice do not require free water, therefore may not readily seek it, because they can meet their need for water from metabolizing foods (Witmer and Jojola, 2006). We surmise that the low amount of interest shown by house mice in those two arms provides some

assurance that the attractants we tested were indeed effective at discerning some of the immediate focuses of house mice in a novel environment.

5. Conclusions

We identified some immediate needs of house mice in a novel environment, thereby providing new information for developing detection and removal devices for invading house mice. It appears that a den box, which provides a secure place for house mice to acclimate to a novel setting, would be sought by newly-arrived house mice. A den box could also "hold" the mice at that location for a period before they disperse or explore the new setting, therefore giving an opportunity to expose them to a well-placed toxicant, trap or detection device. Additionally, food items like bacon grease, peanut butter, and cheese located in or near a den box might further maintain the mice in a limited area. These materials could be utilized for early detection and response to newly-invading house mice, similar to what been proposed for invading Gambian giant pouched rats (*Cricetomys gambianus*; Witmer et al., 2010).

Conflict of interest

The authors declare that there are no conflict of interest.

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All methods used in this study, QA-1628, were approved under the National Wildlife Research Center's Institutional Animal Care and Use Committee. Reference to trade names does not imply U.S. government endorsement of commercial products or exclusion of similar products with equal or better effectiveness.

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