

**The Effects of Stranger and Neighbor Presence on the Social Foraging Behavior of
*Peromyscus maniculatus gracilis***

BIOS 35502: Practicum in Environmental Field Biology

Marisa McNally

Advisor: Dr. Michael J. Cramer

2014

Abstract

Animals strive to conserve energy when competing for resources. The dear-enemy effect predicts that animals can do this by forming relationships with familiar, or neighbor, animals which allows them to focus their energy on interactions with unfamiliar, or stranger, animals who pose a greater threat. This study aims to determine the presence of the dear-enemy effect in the foraging behavior of *Peromyscus maniculatus gracilis* at the University of Notre Dame Environmental Research Center in the North Woods of Michigan. This was executed using a three-compartment aquarium where three mice were placed and observed for seed consumption and behavior. The focal mouse was placed in the middle compartment and the neighbor and stranger mice were placed in the two outside compartments. No significant differences were determined in the seed consumption, foraging time, or overall time spent on the neighbor and stranger sides by the focal mouse. However, when the foraging time and overall time spent on the neighbor and stranger sides were compared to the grid location of the sample mice, an interaction occurred between two of the three grids. This interaction revealed that the focal mouse in certain grids did prefer either the stranger or neighbor side to the other. This variation may be due to population density or habitat composition but because the individual grid sample sizes are so small, more research would have to be done to determine actual differences.

Introduction

Territorial animals compete for resources. Animals living in the same habitat frequently interact, thereby establishing relationships which enable them to expend less energy when defending territories from individuals they have already encountered and focus more on strangers who pose a greater threat. Fischer (1954) first noticed this behavior in birds and coined this social phenomenon as the “dear enemy” effect which infers that two familiar animals respond less aggressively toward each other than two unfamiliar animals (Temeles, 1994). This phenomenon has been studied in an array of animals including mammals, fish, amphibians, reptiles, insects, crustaceans, and birds (Temeles, 1994; Briefer *et al.*, 2010; Whiting, 1999; Bee, 2003; Muller *et al.*, 2007; Ochi *et al.*, 2012; Roux *et al.*, 2013; Tierney *et al.*, 2013). Temeles (1994) hypothesized that resident animals weigh the costs of potential predation, energy expenditure, and missed opportunities against the benefits of mating opportunities and territory usage when interacting with each other. The initial encounter between a resident and a stranger

determines the future dominance relationship, which could jeopardize the resident's claim on both territory and mates. When two individuals interact on a neighborly basis, both have already established non-overlapping territories, and the motivation to use resources to establish dominance decreases (Temeles, 1994).

However, not all territorial animals express the dear-enemy effect. Several species including those of mammals, birds, and insects did not react in concurrence with the theory (Temeles, 1994). The variation in animal responses to strangers suggests that territorial behavior does not always result in the dear-enemy effect, and is dependent on the species and the type of area defended. Temeles (1994) specified that the dear enemy effect has not been observed in a feeding habitat while it has been observed in other multi-purpose territories.

Temeles (1994) found that territorial behavior is not a constant in any species but varies depending on the use of territory, breeding or feeding, and the level of familiarity between the individuals. These factors change the level of threat an intruder presents which impacts the resident's response.

This study aims to observe the capacity for the dear enemy effect in the forest deer mouse *Peromyscus maniculatus gracilis*. This species has relatively small home range size between 0.5 -1.5 acres that may divide a much larger population (Whitaker *et al.*, 2009). This divide allows scientists to access many habitats of resident *P. maniculatus* for territorial study. Wolff *et al.* (1983) and Vestal *et al.* (1978) found evidence to support the measurement of this species' relatively small home range. While observing this species under controlled laboratory conditions, they discovered that it was more common for a stronger display of dominance to occur toward the center of the resident's territory as compared to the periphery. The home range of *P.*

maniculatus can therefore be assumed to remain relatively stable due to the species tendency to purposefully interact in a central location as opposed to a peripheral one (Whitaker *et al.*, 1983).

Few dear-enemy studies have been previously done on this species and there are few studies in general that observe the dear-enemy effect in small mammals. Those that have been performed on *P. maniculatus* and other small animals have been executed using dyadic conditions (Wolff *et al.*, 1983; Rosell, 2008; Vestal *et al.*, 1978). Also, *P. maniculatus* was often accompanied by *Peromyscus leucopus* in trials for interspecific and intraspecific dominance relationships (Vestal *et al.*, 1978; Wolff *et al.*, 1983). Aggressive, investigative, and indifferent behaviors were observed in these trials where physical contact was allowed. Trials were most frequently performed in the natural habitat of the animal as opposed to a laboratory setting. The natural setting was expected to elicit the most authentic response (Wolff *et al.*, 1983). Within the synthetic, neutral, and sometimes circular arenas, two neighbors or strangers of the same sex were observed for their territorial display and site-specific dominance (Vestal *et al.*, 1978; Wolff *et al.*, 1983). The results positively support the existence of the dear enemy effect in *P. maniculatus*.

This study aims to observe the cues generated by resident *P. maniculatus* individuals in a neutral laboratory setting when presented with both a “neighbor” and “stranger” mouse on either side of a three-section aquarium. Replacing the common dyadic enclosure, this partitioned aquarium will allow sight, smell, and sound to transpire through all compartments, but full access to the other mice will not be granted. Rather than direct displays of dominance behavior, the study will observe the feeding behavior of a resident mouse in the presence of two other mice separated by partitions.

This study focuses on the species *P. maniculatus gracilis* that inhabits the northeastern forested regions of North America. The dominating thick canopy of sugar maple (*Acer saccharum*) enables fern growth in the understory, which provides small mammals like *P. maniculatus* protection from aerial predators (Royo and Carson, 2006). The habitat composition of this second-growth forested region, therefore, supports the growth and interaction of these rodent populations. The sugar maple canopy also provides the deer mice with a bountiful supply of seeds, a primary food source in the granivore's diet (Cramer, 2014).

Instead of forcing the animal into an immediate dominance display, the resident mouse will be presented with the decision to feed from the food supply closest to the neighbor mouse or closest to the stranger mouse. Therefore, this study will observe the capacity for stranger and neighbor recognition in the social foraging behavior of *P. maniculatus*. However, it must first be determined whether or not *P. maniculatus* has an interest to forage with others at all. Therefore, this study's null hypothesis states that the presence of other mice will have no effect on the foraging behavior of *P. maniculatus*. If this null hypothesis is rejected, then this study will look at a second null hypothesis that states *P. maniculatus* will have no preference between a familiar and unfamiliar foraging partner.

Materials and Methods

Field

Peromyscus maniculatus gracilis were trapped between July 7th and July 15th of 2014 at the University of Notre Dame Environmental Research Center property in the Upper Peninsula of Michigan's North Woods. Sherman live traps were set at three different plots on the property using sunflowers seeds and oats as bait. These plots were identified as BONO, STRG, and

PCON. Plots on BONO and STRG contained 25 traps set up in a 5 x 5 grid with 15 meters between each trap. The plot on PCON contained 24 traps in a 4 x 6 grid with 15 meters between each trap. The individuals trapped within a plot were assumed to have interacted with each other prior to this experiment. Data recorded at capture for each mouse included species, age class, sex, reproductive condition, weight, body length, and ear length. Each individual was marked with a unique metal ear tag and, if applicable, brought back to the laboratory. Individuals resided in separate holding cages complete with corn bedding, water, shelter and food for a maximum period of 48 hours before released back at the appropriate grid.

Laboratory

Each trial involved three mice and was conducted at night for 30 uninterrupted minutes in a dark room. Prior to testing, the mice were starved 5-6 hours.

Each mouse was placed into a compartment of a 1.8 x 0.43 meter aquarium divided into three equal sections 0.6 meters long. These sections were separated by two semi-perforated partitions that allowed sight, smell, and sound to pass through. Two cameras accompanied by two infrared lights were set up to capture the third of each compartment closest to a partition. The middle third of the middle compartment acted as the control and was not recorded. When the focal mouse was not in view of either camera, it was assumed that the mouse was in this middle third and consequently was not showing preference to forage with other mice.

Prior to each trial, the bottom of the aquarium was lined with cellophane and a thick layer of sand. Approximately 10 grams of sunflower seeds were weighed and then sprinkled directly along each side of the two partitions. These seeds were weighed after each trial for differential analysis.

Two neighbor mice captured from the same grid were placed into adjacent compartments of the aquarium. The stranger mouse that had been caught on a different grid from the first two mice was placed into the third outside compartment. The middle “resident” mouse was the focal individual. Between each 30-minute trial, only the focal mouse was removed and only the middle compartment was cleaned and re-assembled. A new focal mouse was used for each trial.

The trial began with a 10 minute acclimation period. This allowed five minutes for the neighbor and stranger mice to acclimate to their compartment before the addition of the focal mouse and another five minutes allowed for all three mice to acclimate together. During the acclimation period, the focal mouse visited both sides of its compartment. Time was recorded using the time count on the two cameras. JWatcher was used to record the amount of time the focal mouse spent on the stranger and neighbor sides and the amount of time spent exhibiting specific behavior. The behaviors recorded were categorized as escape, groom, forage, explore, contact, motion, and motionless.

These behaviors are self-initiated and do not require contact with another mouse. Grooming was noted when the focal mouse licked its paws, fur, or genitalia and when it stroked or scratched itself with its paws or hind foot. Foraging was recorded when the focal mouse handled, consumed, or scavenged for sunflower seeds. The mouse may have picked up the seed and eaten it off camera which was not recorded. Contact occurred when two mice met at the same spot along the partition and appeared to touch noses, as if sniffing each other. Exploratory behavior encompassed all investigative behavior including standing on its hind legs and sniffing the air. Motionless referred to a still mouse that could have fallen asleep. All other non-descript locomotive behavior was categorized as motion. These movements included running, leaping, exhibiting elongated posture, and alertness (Eisenberg, 1962). When accompanied by a stranger

or neighbor mouse, “company” was used to modify the focal mouse’s behavior as a social behavior.

To control for unknown motivations, the neighbor and stranger mice were alternated between the far right and far left compartments in each trial. Due to the limited supply of trapped mice, individuals were reused in several trials in the outside compartments.

Statistical Analysis of Data

Paired t-tests compared the amount of seed consumed, foraging time, and total time spent by the focal mouse on either side of its compartment. Foraging time in the presence of the stranger or neighbor mouse was analyzed using a paired t-test as well. The grid of origin was compared to the time spent on the neighbor and stranger sides with a one-way ANOVA test. All results are reported as means and standard errors.

Results

Twenty-nine mice were trapped and used in 22 trials that measured seed consumption and 18 trials that recorded behavior.

Seed Consumption

The total mass in grams of seeds consumed by the focal mouse on both the stranger (0.509 ± 0.076) and neighbor (0.529 ± 0.116) sides of its compartment at the end of each trial were analyzed with a paired t-test (Fig. 1). There were no significant differences between the amount of seeds consumed near the stranger and neighbor ($t_{17} = 0.872$, $p = 0.395$).

Foraging Time

Proportional foraging time was calculated by JWatcher for the time spent foraging in the presence of a stranger (0.078 ± 0.027) or neighbor (0.097 ± 0.023) mouse. Data were normally distributed (Shapiro-Wilk: $w = 0.938$, $p = 0.272$). After arcsine transformation, the data remained normally distributed. The paired t-test detected no difference between the proportion of foraging time in the presence of another mouse ($t_{17} = 0.549$, $p = 0.590$).

The total foraging time of the focal individual on the neighbor (3.766 ± 0.717) and stranger (2.808 ± 0.523) sides disregarding the presence of the other mouse was recorded through JWatcher as well. Normality was confirmed by the Shapiro-Wilk test ($w = 0.953$, $p = 0.475$). No significant difference was determined between total foraging time and side preference ($t_{17} = 0.872$, $p = 0.395$).

Total Time Spent on Neighbor and Stranger Side

The total time spent by the focal mouse on the neighbor (14.724 ± 1.620) and stranger (13.519 ± 1.604) sides was compared. A Shapiro-Wilk test confirmed the normality of the data ($w = 0.968$, $p = 0.749$). There was no difference between the time spent on the neighbor's side and the stranger's side ($t_{17} = 0.382$, $p = 0.708$).

Grid Effect

Further analysis of the data found a significant interaction between the focal mouse's grid of origin and its overall time spent on the neighbor and stranger sides ($F_{2,29} = 12.640$, $p < 0.001$; Fig. 2). The treatments analyzed were PCON neighbor (19.103 ± 1.985), PCON stranger (9.422 ± 2.985), BONO neighbor (13.538 ± 2.048), BONO stranger (14.778 ± 2.020), STRG neighbor (5.816 ± 0.865), and STRG stranger (21.510 ± 2.715). Independently, the ANOVA determined

no significance between the grid of origin ($F_{2,29} = 0.143$, $p = 0.868$) and the neighbor/ stranger side preference ($F_{1,29} = 0.448$, $p = 0.509$). Individual paired t-tests performed on the three grids (PCON, BONO, and STRG) found differences in the total time spent between stranger and neighbor sides in PCON ($t_7 = 2.472$, $p = 0.043$) and STRG ($t_2 = 4.48$, $p = 0.046$). There was no significant difference observed for mice from BONO ($t_6 = 0.317$, $p = 0.762$).

A significant interaction as also observed in an ANOVA testing the foraging time on the stranger and neighbor sides compared to the focal mouse's grid of origin ($F_{2,29} = 12.891$, $p < 0.001$; Fig. 3). The treatments analyzed were PCON neighbor (6.260 ± 0.978), PCON stranger (1.493 ± 0.314), BONO neighbor (2.299 ± 0.416), BONO stranger (4.216 ± 0.922), STRG neighbor (0.536 ± 0.296), and STRG stranger (3.028 ± 1.607). There was no significant difference between the foraging time ($F_{1,29} = 2.032$, $p = 0.165$) and the grid of origin ($F_{2,29} = 0.708$, $p = 0.501$).

Discussion

Peromyscus maniculatus gracilis appeared to consistently forage throughout this study in the presence of other mice, which supports the idea that forest deer mice can and possibly prefer to forage in the company of other mice. The lack of significance in the seed consumption and behavioral data between stranger and neighbor treatments, however, rejects the idea that forest deer mice overall prefer foraging with one status to the other. Furthermore, my results do not provide sufficient evidence for the presence of the dear-enemy effect in the forest deer mouse.

The total amount of seeds consumed was originally a major determinant to assess the presence of the stranger or neighbor preference on the focal individual's foraging behavior. The lack of significance, however, may be due to other experimental design influences specific to this

study. The 30-minute length of each trial may have masked the mouse's initial decision to forage more on one side than the other. As time continued, the focal mouse became more acclimated and more accustomed to its surroundings causing its reactions to be potentially less specific. Because data was recorded at the end of the trial, more detailed analysis of the time spent in the beginning of the trial would have to be done to determine if this was an influential factor.

Also, the collection process of the seeds after each trial revealed that seeds were being buried and pushed under the barrier. This was not recognized until late in the experiment, so no structural changes were made to the aquarium design to maintain consistency. However, this may have skewed the actual seed data. Given the non-significant p-value this may not be sufficient reasoning for potential significance but the behavior that initiated the seed-pushing could have hidden meaning indicative of preferential behavior. Further studies and analysis would corroborate this observation.

Also, the bounty of seeds provided for the focal mouse, 10 grams on each side, may have been an over-generous amount. With a surplus of seed, the mouse may have not experienced the necessary urgency or motivation to feel the need to choose a side. This would also require a follow up study to assess validity.

Other behavioral observations that were not explicitly represented by the statistical analyses included the over abundant occurrence of escape behavior. The expended energy necessary for this activity hinders the mouse's time and ability to forage causing this behavior to occur less frequently than it may in a natural uncontained environment. However, this may be offset if the mice had tried escaping on one side of the aquarium more frequently than on the

other, but this was also not the case as reflected in the non-significant p-value of total overall time spent on both sides.

Vestal *et al.* (1978) found that *P. maniculatus* also did not recognize neighbors or strangers at a significant level even when in direct physical contact with each other. This experiment separated the mice by a barrier, which may have had an even greater impact on their ability to assess and recognize the mouse on the other side. However, there were particular moments where both the focal mouse and the mouse on the other side of the perforated barrier reached their noses up against the barrier as if to touch in several trials. This behavior would appear to refute this idea, however, this occurrence did not happen often enough to be noted as significant.

The tested mice appeared to show no preference, but from observation alone, significant moments of recognition behavior, like that described above, occurred individually. In further analysis, these independent behavioral anomalies were better explained when compared to their grid of origin, BONO, PCON, and STRG. When compared against each other, the mice from both PCON and STRG exhibit a significant difference in their response to the stranger and neighbor treatments. Though the sample sizes for these two grids hold little stock to this statement, the appearance of this pattern requires attention and could be followed up in a future study where more trials are performed with more mice from these grids.

These data suggest that a spatial difference exists within the population of forest deer mice. The mice collected at BONO would, in theory, have a different response as compared to PCON and STRG. BONO's means for total foraging and overall time spent at the stranger and neighbor sites are almost equivalent (Fig. 2 and Fig.3). This could indicate that BONO mice live

in a higher density area and are more accustomed to confronting strangers as much as they are to neighbors. Also, BONO is located roadside which may influence the dispersal of the mice. The BONO mice may be less apt to demonstrate the dear-enemy phenomenon because their individual preferences balance each other out as displayed by the means in both figures. This implies that PCON and STRG mice live in less dense or more diverse areas that allow them to interact with their neighbors without an increased exposure to other mice. This may not as strongly apply to STRG as it does to PCON because STRG mice preferred strangers to neighbors (Fig.2 and Fig. 3).

This difference may also be explained by the variation in habitat composition represented by the three grids. PCON's dominant coniferous canopy may impact the mouse population there differently than BONO's mainly sugar maple canopy. PCON is also a high vole area, which may cause the mice found there to be more discriminatory in who they interact with based upon the highly aggressive tendencies of the vole (Cranford, 1978). PCON mice may prefer neighbors to strangers in order to avoid encountering these aggressive creatures.

On the other hand, the STRG mice favored the stranger treatment, which is coincidentally less vole populated. This may affect the mouse's confidence when interacting with strangers because that increased threat level is decreased. Plus, STRG is unique in that it offers easy access to energy replenishing resources due to the storage shed located within 100 meters of the trapping grid. Although the human-mice interaction rate would increase in this area, the opportunity for shelter and potential food inside and around the shed may override predator risk and could potentially attract mice from greater distances, introducing strangers to the resident STRG population. This would cause a higher interaction rate between this trial's STRG mice with stranger mice. This may contribute to their preference of stranger over neighbor

treatment because the stranger may be an indicator of the storage shed proximity. More trials with mice from these grids are necessary to verify significance.

The grid of origin comparison seems to support the existence of the dear-enemy effect presence in forest deer mice. However, the data from the sample population tested in this experiment are masked by these grid interactions. A possible confounding factor responsible for this masking is the sex of the mice. This variable was not controlled so the sex of the stranger and neighbor mice were random. This could affect the data if one stranger/neighbor was female and the other male. The focal individual may instinctively respond one way toward the female while reacting another toward the male having no regard to the stranger or neighbor treatment. This experiment assumed that the mice would react primarily to the neighbor and stranger treatments over other variables. Further inspection in subsequent trials would be necessary to assess this interaction. Also in future trials, a shorter run time could be implemented to better isolate the behavior performed in direct response to the neighbor and stranger treatments. Overall, the forest deer mouse population at UNDERC shows a varying response to strangers and neighbors in certain locations, but the presence of the dear-enemy effect on property requires further research.

Acknowledgements

I would first like to thank my advisor, Dr. Michael J. Cramer, for his guidance, support, and positivity throughout this project as well as the extra effort he put forth to help construct my aquarium design. I would also like to thank Kaya Moore and Dana Fineman for their assistance in trapping, housing, and feeding the mice and providing the absolute highest level of teamwork and humor that made this experience unforgettable. I would also like to thank my Saint Mary's

College advisor Dr. Dorris Watt for her patience and collaboration that helped propel this project from the beginning. In addition, I would like to thank the UNDERC class of 2014 for their continual support and excitement that created an unmatchable and extremely enjoyable living and working environment. I would also like to thank Sean Wineland, Kraig Esswein, and Matt Kruchten for helping me with the laboratory set up. Others who deserve my gratitude include the UNDERC director Gary Belovsky and the Bernard J. Hank Family Foundation for providing me with this amazing opportunity and the resources to tackle this project. I am grateful to the teaching assistants Lauren Eckert and Christy Lowney and lab technician Hannah Madson for their unmeasurable enthusiasm and leadership throughout this process. A special thanks to Lauren who worked and communicated with me when Dr. Michael J. Cramer was out of town.

Literature Cited

- Bee, M.A. 2003. A test of the “dear enemy effect” in the strawberry dart-poison frog (*Dendrobates pumilio*). *Behavioral Ecology and Sociobiology* 54: 601-610.
- Cramer, M. 2014. Seeds of doubt: feeding preferences of white-footed deer mice (*Peromyscus leucopus*) and forest deer mice (*Peromyscus maniculatus gracilis*) on maple (*Acer*) seeds. Manuscript submitted for publication.
- Cranford, J. A., Derting, T. L. 1983. Intra and interspecific behavior of *Microtus pennsylvanicus* and *Microtus pinetorum*. *Behavioral Ecology and Sociobiology* 13: 7-11.
- Eisenberg, J.F. 1962. Studies on the behavior of *Peromyscus maniculatus gambelii* and *Peromyscus californicus parasiticus*. *Behaviour* 19: 177-207.
- Fisher, J. 1954. Evolution and bird sociality. In: *Evolution as a Process* (Huxley, J., Hardy, A.C., Ford, E.B., eds). Allen & Unwin, London.
- Jaeger, R.G. 1981. Dear enemy recognition and the costs of aggression between salamanders. *The American Naturalist* 117: 962-974.
- Kurta, A. 1995. Deer mouse. In: *Mammals of the Great Lakes Region* (Douglas, M.M., ed). The University of Michigan Press, Ann Arbor, MI, pp. 153-156.
- Muller, C.A. Manser, B.M. 2007. ‘Nasty neighbours’ rather than ‘dear enemies’ in a social carnivore. *Proceedings of the Royal Society of Biological Sciences* 274: 959-965.

Ochi, H., Awata, S., Kohda, M. 2012. Differential attack by a cichlid fish on resident and non-resident fish of another cichlid species. *Behaviour* 149: 99-109.

Rosell, F., Gunderson, G., le Galliard, J.-F. 2008. Territory ownership and familiarity status affect how much male root voles (*Microtus oeconomus*) invest in territory defense. *Behavioral Ecology and Sociobiology* 62: 1559-1568.

Roux, O., Rossi, V., Cereghino, R., Compin, A., Martin, J.-M., Dejean, A. 2013. How to coexist with fire ants: the roles of behavior and cuticular compounds. *Behavioural Processes* 98: 51-57

Royo, A. A., Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36: 1345-1362.

Temeles, E.J. 1994. The role of neighbours in territorial systems: when are they ‘dear enemies’? *Animal Behaviour* 47: 339-350.

Tierney, A.J., Andrews, K., Happer, K.R., White, M.K.M. 2013. Dear enemies and nasty neighbors in crayfish: effects of social status and sex on responses to familiar and unfamiliar conspecifics. *Behavioural Processes* 99: 47-51.

Vestal, B.M., Hellack, J.J. 1978. Comparison of neighbor recognition in two species of deer mice (*Peromyscus*). *Journal of Mammalogy* 59: 339-346.

Whitaker, J.O., Mumford, R.E. 2009. Prairie deer mouse. In: *Mammals of Indiana*. Indiana University Press, IN, pp. 418-437.

Wolff, J.O., Freeberg, M.H., Dueser, R.D. 1983. Interspecific territoriality in two sympatric species of *Peromyscus* (Rodentia: Cricetidae). *Behavioral Ecology and Sociobiology* 12: 237-242.

Figures

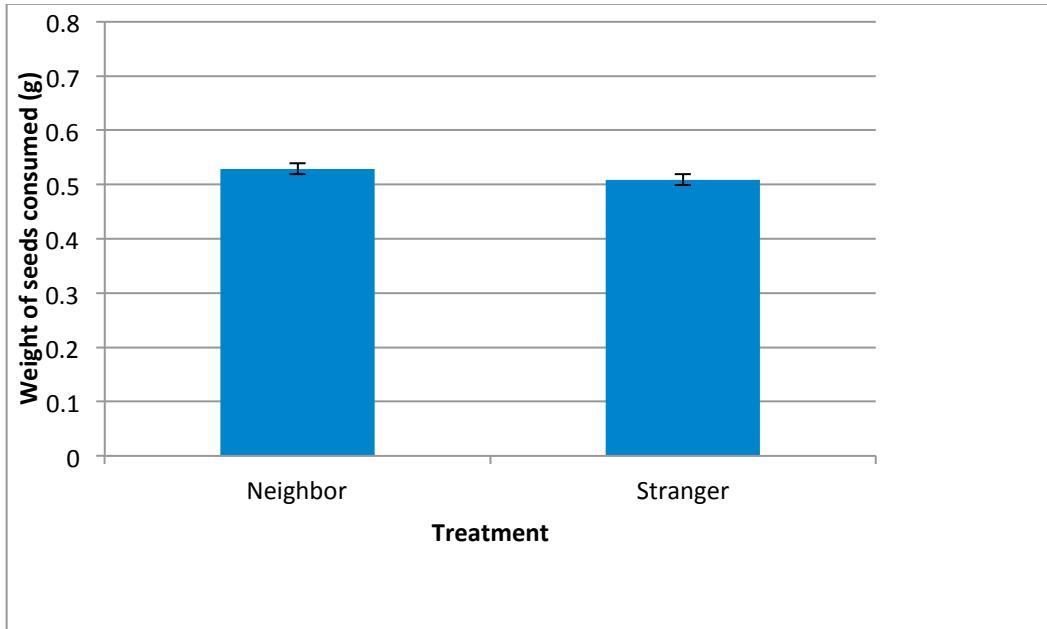


Figure 1. The mean seeds consumed in grams by the focal mouse in 22 trials on the neighbor and stranger sides.

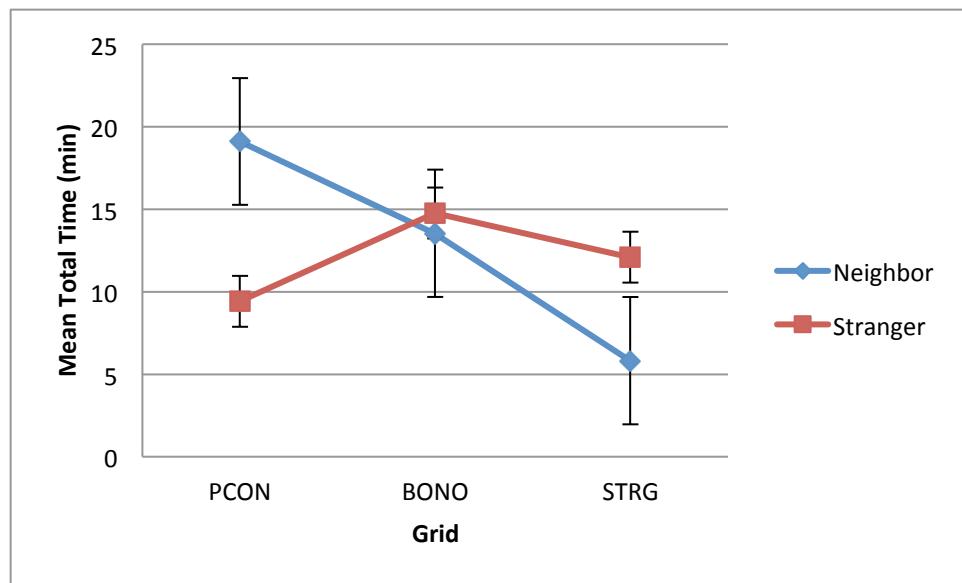


Figure 2. The effect of grid on the total overall time spent by the focal mouse on the neighbor and stranger side. The time was recorded in milliseconds and converted into minutes. There is significant interaction between the PCON mice and the STORAGE mice ($F_{2, 29} = 12.64, p < 0.001$).

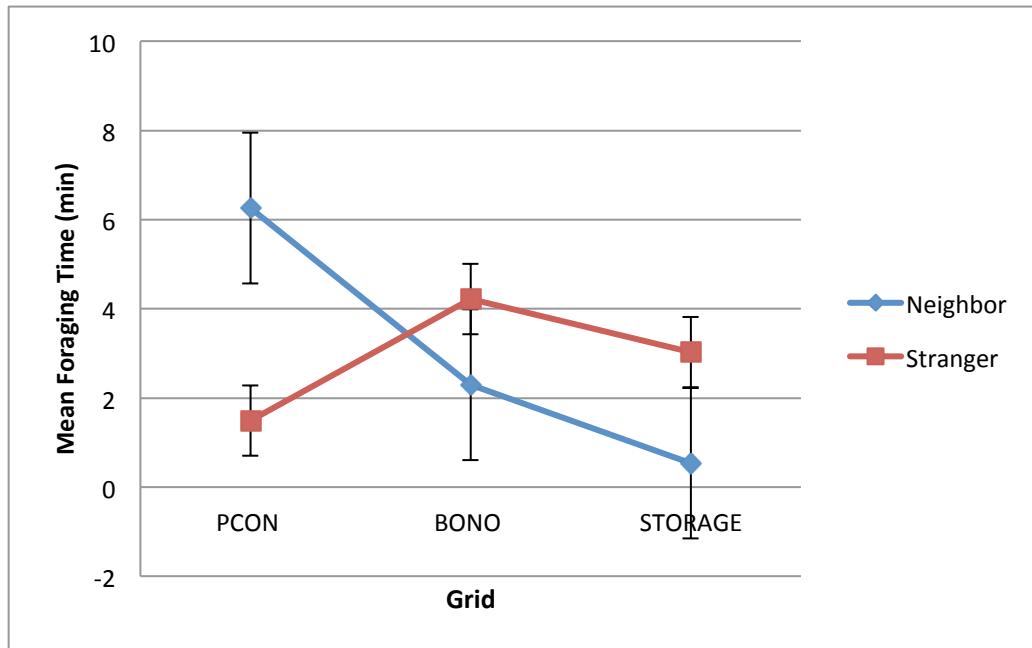


Figure 3. The effect of grid on total foraging time spent on the neighbor and stranger sides. The time was measured in milliseconds and converted into minutes. There is significant interaction between the PCON mice and the STORAGE mice ($F_{2,29} = 12.8914, p < 0.001$).