Functional analysis of concealment: a novel application of prospect and refuge theory.

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

According to prospect-refuge theory, humans prefer to be in spaces that afford protection from threat (refuge), but also provide large fields of view (prospect). These preferences are said to arise from the adaptive advantages of such locations with respect to both avoidance of predation from refuge and survey of opportunities for resource collection by prospect. Prospect-refuge theory in the past has traditionally only been applied to human beings, but many of the same contingencies governing spatial preference ought to also hold true in other animals. If people's spatial preferences are influenced by prospect-refuge considerations, then such preferences ought to be found in other animals that are subject to the same pressures to find safety and resources. The overall objective of this study was to explore spatial preferences of the Mongolian gerbil in situations in which prospect-refuge theory makes specific predictions about which regions of an environment will be preferred. Gerbils were placed in an arena containing three dome shaped refuges that varied in the amount of prospect and refuge. A predator was released during the trial to examine how contextual factors may influence the degree of prospect and refuge preferred. There was a preference for an enclosed refuge at stimulus onset even though this was not reflective of what happened prior to stimulus onset, which suggests there was a shift in preferring refuges with greater concealment upon exposure to a threatening stimulus. These results indicate that shelter preference does in fact depend on contextual factors. An explicit comparison of these preferences in widely divergent species may help to place theories of spatial preference on a firmer biological footing, and may provide a greater understanding of how the principles of spatial cognition might underpin parts of the design process.

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Introduction

Prospect-Refuge Theory:

Aesthetic pleasure from landscapes is derived from the observer experiencing an environment favorable to the satisfaction of their biological needs. Satisfaction experienced from landscapes arises from the perception of landscape features such as colour, shapes, spatial arrangements and other visible attributes that act as stimuli indicative of habitat conditions favorable to survival (Appleton, 1996). In his classic work Appleton (1975), developed a Darwinian theory that explains reactions to landscape paintings using principles of habitat selection and animal behaviour. Appleton's prospect-refuge theory proposed that because the ability to see without being seen allows the satisfaction of many of these biological needs, the ability of an environment to ensure the achievement of this becomes a more direct source of aesthetic satisfaction (Appleton, 1996). According to prospect-refuge theory, human beings prefer to be in spaces that afford protection from threat (refuge), but also provide large fields of view (prospect) (Fischer & Shrout, 2006). A valley seen from a mountain top, or a view from a high-rise balcony are both regarded as views that blend the elements of both prospect and refuge (Hudson, 1993). These preferences arise from the adaptive advantages of such locations with respect to both avoidance of predation, from refuge, and detection of resources, from prospect. Appleton proposes that aesthetic preference does not result exclusively from learning, conditioning, or culture. The aesthetic satisfaction people experience from landscapes is a function of the environment presenting biologically important signs of prospect, an unimpeded opportunity to see, and refuge, an opportunity to hide from hazards (Fischer & Shrout, 2006).

The ability to hide and see are both important for a creature's survival prospects. An environment which provides both a good opportunity to see and hide is more aesthetically satisfying than one which provides neither. Weakness in prospect or refuge may be compensated by strength in the other (Appleton, 1996). Prospect and refuge are not considered a dichotomy or duality and neither are they opposites. Prospect is related to perceiving and receiving information, specifically visual information, and refuge with seeking protection (Ramanujam, 2006).

According to Darwin, natural selection operates on physical and mental abilities. The ability to distinguish, quickly and accurately, environments that are either safe or dangerous is a mental ability with significant evolutionary advantage. According to Darwinian behavioural ecology, fear has definite survival value in wild animals. In nature the most important threat an animal encounters comes from attackers and predators. Consequently, it is essential to maintain constant awareness and have sufficient prospect for areas of an environment from which one can easily move to for safety or places from which an individual can be attacked. Thus, safety and the perception of safety has a strong relationship with range of vision. The chances of survival are enhanced the more an individual can see, in order to detect potential enemies, and the less one can be seen by predators (Ramanujam, 2006).

There is a vast range of literature that seeks to explain landscape preference as a result of human evolutionary history. Current evidence indicates that millions of years of hominid evolution took place in East Africa's savannas. According to Appleton, preference for landscapes may also be due to our biological heritage. It is reasonable to assume that natural selection worked to keep our ancestors in certain environments that

were both high in prospect and refuge such as savannas (Appleton, 1996).

Prospect & Refuge Concepts:

Appleton defines various terms that are commonly used for symbolizing prospect. Direct prospect are views that are observed directly from a point of observation. A restricted view uninterrupted in the immediate foreground is referred to as a closed prospect. Vantage points are structures that provide an observation point from which an extreme field of view can be achieved. Towers, and clearings on forested hills are both examples of vantage points (Appleton, 1996).

The most important basis for differentiating refuges is the kind of hazard they provide protection from. A "hide" is a form of refuge that provides concealment from animate hazards, and a shelter is a type of refuge that provides protection from inanimate hazards. Protection against inanimate hazards such as extreme cold and heat, violent winds, intense solar radiation, rain and snow-storms are vital for human survival even more probably than protection from other humans and animals (Hudson, 1993).

According to Nasar and Fisher (1993) an individual's feelings of safety are not only determined by the extent to which a space provides prospect and refuge, but also to the degree to which a refuge affords the opportunity to escape through an exit (Ramanujam, 2006). If a refuge offers no exit an individual may feel unsafe since they are unable to escape from a potential threat (Nasar & Fisher, 1992). The ease of escape and prospect co-vary since physical boundaries which limit prospect may also reduce the ability to escape (Ramanujam, 2006). Refuges that provide both concealment and prevent entrapment are more likely to be favored and may elicit less fear (Nasar & Jones, 1997).

Refuge-seeking is a fairly prevalent phenomenon which involves the animal in a

close relationship with predators and the environment. According to Scott (1958) any animal which can discriminate between various parts of an environment will show some shelter or refuge-seeking behaviour. Refuge-seeking, and exploratory behaviour are also frequently observed in humans as well. Thus, examining animal behaviour provides us with a greater understanding of our evolution (Ramanujam, 2006).

Previous Work:

Previous work has focused on examining prospect and refuge principles in humans rather than in animals. Various measures of fear in relation to environments with extreme prospect, refuge, and entrapment have been examined in several studies. For example, Fisher and Nasar (1992) had 20 participants complete an onsite rating of eight areas using 5-point scales for prospect, refuge, and entrapment. There were significant differences in rating scales among the eight areas. There were higher levels of fear associated with locations that had minimal prospect, or refuge and the ability to escape easily (Nasar & Jones, 1997).

Ironically, previous work has also shown that places that offer prospect and refuge are locations that potential criminals prefer. Potential offenders desire places with concealment and areas high in prospect for detecting victims. Criminals look for site-specific cues in built environments when choosing a burglary target. Studies of interior spaces have shown that robbers select paths and banks that allow them to remain unseen, but at the same time allow them to see as much as possible (Fisher & Nasar, 1992; Tiffany & Ketchel).

Developmental differences for preferences of areas high in prospect and refuge

have also been examined in several studies. Balling and Falk (1982), examined preferences of different aged children for various kinds of environments (Kaplan, 1987). In their widely cited article Balling and Falk (1982) compared children's preferences to visit scenes in photographs of biomes: deciduous forest, coniferous forest, tropical rain forest, desert, and the savanna (Fisher & Shrout, 2006). Savannas are considered environments with both prospect and refuge elements. Given the fact that familiarity and experience have a significant influence on landscape preference, it would be expected that evolutionary influences on biome preference would be the most prominent at a fairly young age since familiarity may not be exerting a very strong influence (Kaplan, 1987). The two youngest age groups, children aged 8 and 10 displayed greater preference for the savanna biome than any of the other biomes. All the other age groups (ninth graders, college students, and older adults) did not display a preference for the savanna and preferred the other biomes instead (Fisher & Shrout, 2006). This study demonstrates how with age, this innate preference for areas high in prospect and refuge, like the savanna, can be modified by experience and familiarity (Kaplan, 1987).

Rationale For The Present Study:

In the past, prospect-refuge theory has only been applied to human beings, but many of the same contingencies governing spatial preference ought to also hold true in other animals. Among vertebrates, habitat selection is a common tendency. In some occasions this even occurs in animals that have been raised in a laboratory and lack any direct exposure with the environment in question (Kaplan, 1987).

The overall objective of this study was to examine how prospect-refuge theory influences environmental preference in Mongolian gerbils. In order to examine their

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spatial preferences, gerbils were placed in an arena containing refuges that varied in the amount of prospect and refuge. The influence of contextual factors such as the presence of a predator was examined to determine if there was a shift towards preferring more prospect or refuge depending upon situational pressures.

In behavioural research, gerbils have gained increasing acceptance as an experimental animal for various practical reasons. Gerbils are curious, lively animals that are fairly good at adapting to laboratory conditions and are well suited for studying active defense strategies (Cheal, 1976; Ellard, 1993). The Mongolian gerbil is preyed on by several aerial and ground predators such as hawks and weasels (Ellard, 1993). Previous work has demonstrated that when gerbils encounter an unexpected overhead stimulus they make evasive movements that are reminiscent of those that are made to aerial predators found in their natural habitat (Ellard, 1996). If a testing field contains a refuge, gerbils usually run towards and enter the refuge, but they also take into consideration the distance between themselves and the refuge. When there is an absence of a refuge in a testing field, gerbils either run away from the predator depending on its trajectory or undercut the stimulus, which suggests that they have developed defense strategies that take into account the biomechanical constraints of predator-prey interactions (Ellard, 1993).

Gerbils live in burrow systems with multiple entrances in their natural habitat (Clark & Bennett, 1979; Ellard, 1993; Agren, et al., 1989). A typical social group of gerbils consists of a collection of 15-20 burrow entrances in which they spend most of their time. When faced by a predator, a gerbil is not only confronted with choices of

entering a refuge or running away, but also has to rapidly decide which of the number of burrows to enter. Similarly, in the present study gerbils were required to choose among three different refuges for shelter. The animal's ability to stand up and look around and orient to distal stimuli allows them to readily explore in tunnels and examine objects in their environment. They also have a well-developed sense of smell and visual system (Cheal, 1976). Their well-developed visual system makes them ideal candidates for this type of study since a good visual system would be essential for detecting predators, and locating areas of space with optimal levels of prospect and refuge. The list of attributes indicate gerbils as an appropriate animal model of behaviour that might be analogous to human behaviours (Cheal, 1976).

In the present study, gerbils were placed in an arena containing dome shaped refuges with varying prospect and refuge levels. Three types of domes were used, an 'enclosed', 'net' and 'open' refuge. The enclosed refuge was sealed from the top and only contained a small opening for animals to enter. The enclosed dome had considerable concealment, but was lacking in prospect. The net refuge contained four openings separated from each other, and had a balance of both prospect and refuge. The open refuge consisted of one large opening at the top, with an area equivalent to the four openings in the net refuge. The large opening allows for considerable prospect, however it does not provide substantial concealment the way the enclosed and net refuges do. A predator was released during the trial to examine how contextual factors may influence the degree of prospect and refuge preferred.

It was hypothesized that the net refuge would be preferred prior to stimulus onset since it provides concealment, but at the same time there is considerable prospect. The enclosed refuge has substantial concealment, however it is lacking in prospect, which is essential for monitoring potential predators. The open refuge is on the other side of the spectrum and has substantial prospect, however does not provide very much concealment compared to the enclosed or net refuge. In summary, it was predicted that the net refuge would be the most favorable since it has a balance of both prospect and refuge.

Another aim of this study was to examine how contextual factors such as the presence of a predator may influence the degree of prospect and refuge preferred. It was expected that once the simulated predator was released, there might be a tendency to prefer the enclosed refuge rather than the net or open refuge since the aerial predator may make concealment a priority over prospect. Being enclosed prevents a gerbil from being seen, and, as a result, may be more adaptive even if prospect is sacrificed in the process. Once a predator is seen prospect may not be as important and concealment may take precedence to prevent detection by a predator. In summary, it was expected that the net refuge would be favored prior to stimuli onset since it has a balance of both prospect and refuge, however once the predator was seen the enclosed refuge may be preferred since being concealed would prevent detection by a predator.

This study addresses whether satisfaction obtained from favorable environments high in prospect and refuge is a basic biological need like eating, sleeping and mating, which we share with animals, or whether it is a particular phenomenon restricted to humans. An explicit comparison of these preferences in widely divergent species may help to place theories of spatial preference on a firmer biological footing.

Method

Subjects

33 male and 27 female Mongolian gerbils were used as subjects. They were approximately 1-3 years of age and were reared in the breeding colony at the University of Waterloo. All animals were housed in plastic cages containing a metal tube, in groups of 2 to 5. Tubes were placed in cages to serve as refuges since such procedures are required to maintain a defensive reactivity to visual stimuli (Ellard, 1993). The room was kept at a constant temperature of 21.1 $^{\circ}$C and testing was conducted during the light phase of a 12-hour light/dark cycle. All animals had free access to food (LabDiet food pellets) and water. The care of the gerbils and their treatment during the experiment was conducted according to the guidelines of the Canadian Council on Animal Care.

Apparatus

All animals were tested in a large open field arena, 2 meters in diameter and 60 cm in height. A mascinite laminate coating was applied to the arena's floor to create traction in order to prevent excessive skidding by the animals. The arena's floor was black and the walls were painted grey to ensure sufficient contrast between the arena's wall and floor. A black polyester curtain surrounded the arena to create uniform lighting and to prevent exposure to visual cues in the room. The curtain was attached to a circular rod mounted to a wooden frame (206 cm x 206 cm x 243 cm) surrounding the arena. A circline fluorescent light attached to the wooden frame illuminated the arena.

The arena contained three dome shaped refuges measuring 22 cm in diameter and 9 cm in height. These domes consisted of soccer balls cut in half that were painted white. Animals could enter all three domes through a hole 8 cm wide and 7 cm high. Three types of domes were used: an enclosed, net and open refuge. The enclosed refuge contained one opening for animals to enter and was completely sealed from above without any other openings. The net refuge contained 4 other openings (5 cm x 5 cm) and there were 5 in total including the entrance. Each of these openings in the net refuge were separated by 2 cm. The open refuge consisted of one large opening at the top, with an area equivalent to the 4 openings in the net refuge. Figure 1 (on the following page), provides an illustration of the refuges.

Refuges:

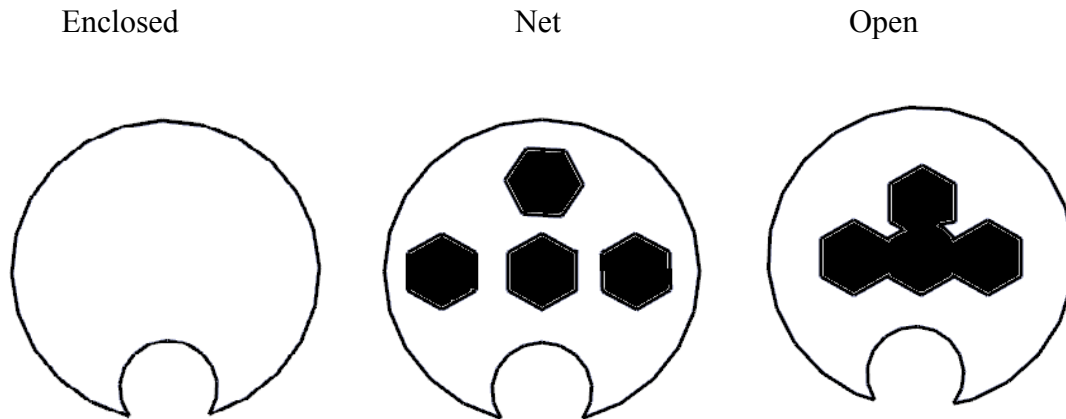Enclosed   Net   Open

Figure 1: Diagram of the enclosed, net and open refuges. The black regions represent

openings and the divots are entrances.

An aerial predator was simulated using a piece of white matte board, 23cm long

and 13 cm wide. The board was attached to 2 parallel nylon wires stretched across the

arena. Each nylon string was stretched across the room at a slope in order for the stimulus

to move along the string by gravity. The stimulus was suspended at the top of the nylon

string and was held in place using an electromagnet. The stimulus was at a height of 243

cm at the top of the release point, and its trajectory was arranged so it passed over the

centre of the arena. An electromagnet was used to trigger the stimulus by turning off the

magnet's current using a power switch. The lack of current to keep the stimulus up

allowed the board to slide across the track with the force of gravity.

Trials were video recorded using a camera attached to the ceiling over the

arena. Video recordings were digitized and analyzed using Ethovision software (Noldus,

Inc).

Testing

On each trial the three spheres were positioned 60 cm from the centre of the arena at a 120° angle from each other. The spheres' positions were rotated to six different sequences to counterbalance the dome's position relative to the arena and each other. Subtle odors or slight differences in light levels in the arena may cause animals to prefer a particular area of the apparatus. In order to take this into account, the spheres were rotated to examine if there was a preference for any of the three refuges regardless of the dome's position relative to the arena. Sixty trials were collected with an equal number of trials with the spheres positioned in each of the six position combinations. After the spheres were placed in a particular position, the animals were brought into the room with a white towel placed over their cage.

Animals were placed on top of a rotating platform positioned in the center of the arena. The platform was rotated approximately three times to ensure that the gerbil was disoriented and could not recall from where they entered the apparatus. The rotating platform was removed from the arena after the gerbil was released.

Each trial was monitored from an adjacent hallway. Animals explored the arena for 7 minutes prior to predator release. The predator was released when the animal was close to the center of the arena (i.e., not standing near the refuge's entrance or inside the refuge) at approximately the 7th minute of a 10 minute trial. The animal's tracks were recorded using Ethovision software. At the end of each trial the apparatus was washed using water and unscented soap to minimize olfactory cues.

Analysis

The arena was divided into 69 different zones (regions) using Ethovision software. 69 regions were selected since zones of this size, covered the area of a single refuge. The duration spent in each zone was recorded to examine if certain regions of the arena were preferred.

Escape responses were classified according to whether the animal ran to the enclosed, net, or open refuge after the predator was released. In addition, the animal's distance to each refuge at stimulus onset was also examined. Entrance into one of the three available refuges within 10 seconds of stimulus onset was considered an escape response. Previous studies have shown that 10 seconds is usually a sufficient amount of time to plan an escape response (Ellard, 1993; Ellard, 2005) All escape responses were further classified according to the refuge visited prior to releasing the predator.

Statistics

Statistical comparisons were made using repeated measures ANOVAs, t-tests, and chi-squared analyses, as appropriate. The accepted value of significance used was $p < 0.05$. Statistical analyses were performed using SPSS Statistical (17.0) software.

Results

Figure 2 (below) provides an illustration of the duration spent in each zone over the entire trial. As demonstrated, there appears to be a preference for the zones containing a refuge rather than the open areas, which is evident by the three peaks. The left peak indicates the duration spent in the enclosed refuge, right peak in the open refuge and the middle peak time spent in the net refuge. Differences were found in the duration spent in the refuges, regardless of the counterbalanced position of the domes (ANOVA: $F(2,179)=3.122$, $p=0.047$). A significantly longer duration was spent in the enclosed refuge compared to the net refuge ($p=0.038$), but the enclosed and open refuges were equally preferred ($p=0.637$). There were also no differences in the duration spent in the open and net refuges ($p=0.264$).
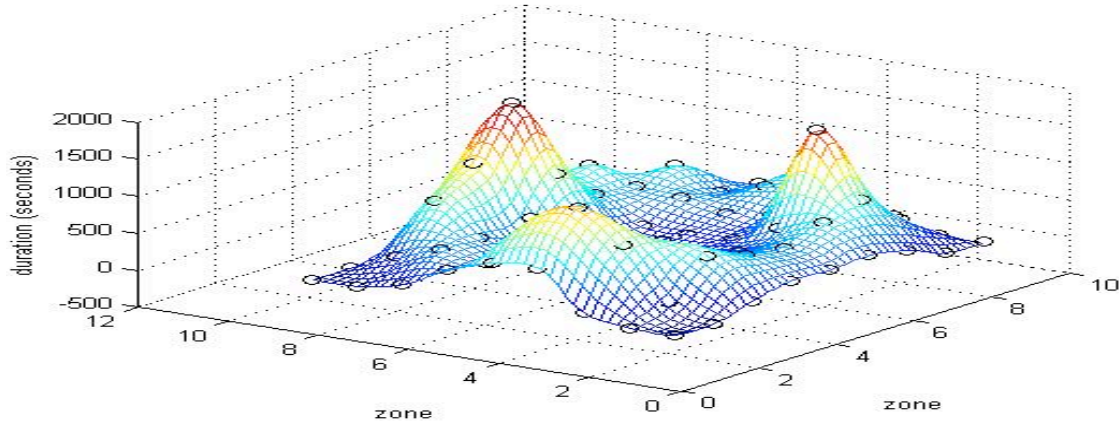

Figure 2: Contour plot of the duration spent in each zone over the entire trial. Each zone represents a square area of the open field. The left peak indicates the duration spent in the enclosed refuge, right peak in the open refuge and the middle peak time spent in the net refuge. The circles represent the corners of a square zone (4 corners indicate the area of one zone).

Figure 3 illustrates frequencies of the refuge visited at stimulus onset. Only visits within 10 seconds of stimulus onset were included. As illustrated, a large proportion of animals did not visit any refuge when the predator was released. Most gerbils that did respond to the stimulus, ran to the enclosed refuge (N=17; X^2=9.5046, df=2, p<0.01) rather than to the net (N=6) or the open refuge (N=5).
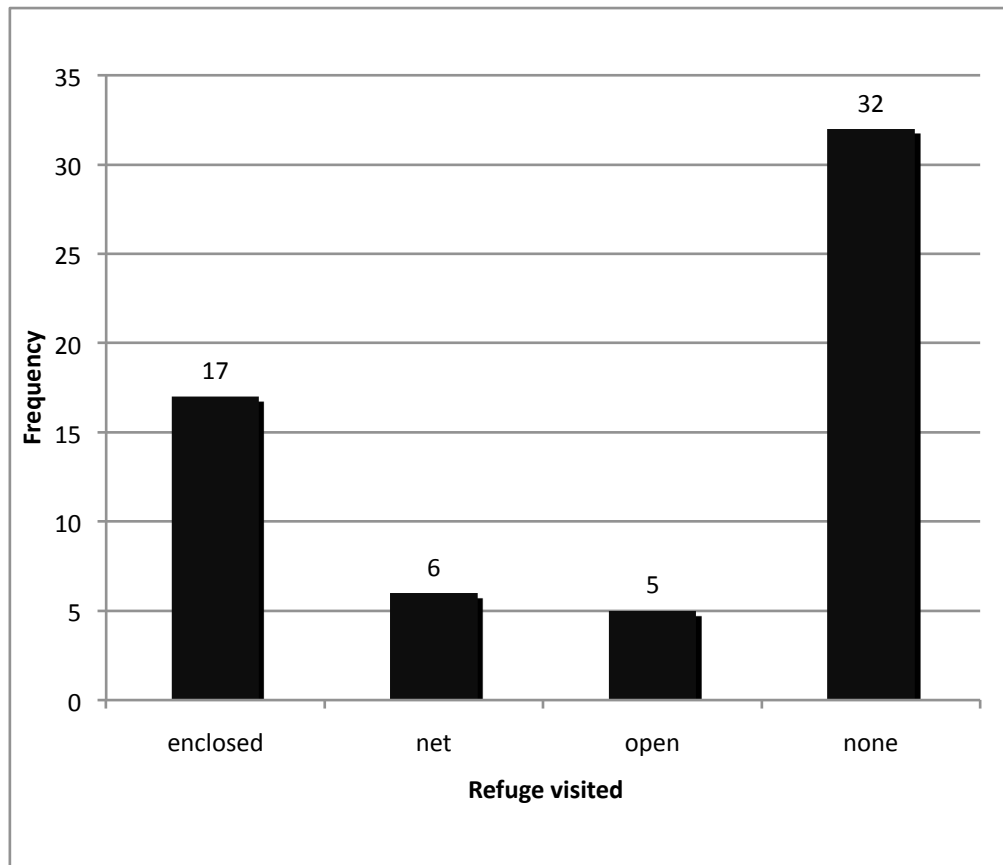

Figure 3: Refuge visited at stimulus onset. Only visits within 10 seconds of stimulus onset were included.

In order to examine if there was a lingering preference for an enclosure in the animals that responded to the predator, the duration spent in each refuge 3 minutes prior to stimulus onset was compared to the time spent 3 minutes immediately after the predator was released (Figure 4). The duration spent in the enclosed refuge prior to and after stimulus onset did not differ (enclosed: $t(27)=0.630$, $p=0.534$). Differences were also not found in the duration spent in the net and open refuges before and after release of the predator (net: $t(27)=-1.592$, $p=0.123$; open: $t(27)=-1.022$, $p=0.316$). The total duration spent in all three refuges combined, before, and after stimulus onset was also compared, however a significant difference was not found ($p=0.198$).
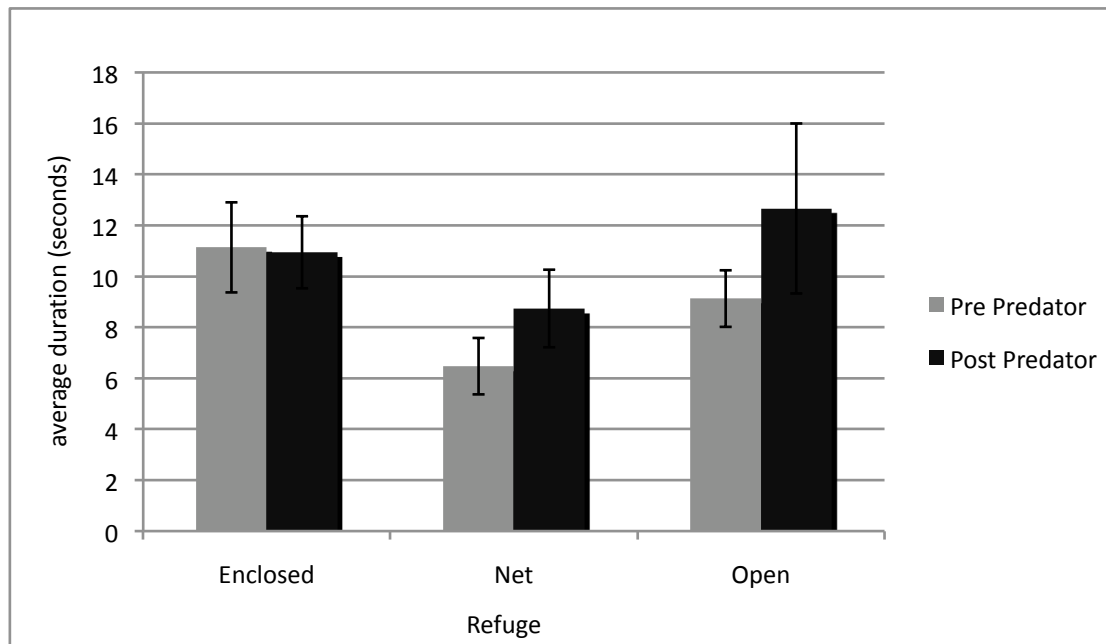
Figure 4: The duration spent in each refuge 3 minutes prior to stimulus onset was compared to the time spent 3 minutes immediately after the predator was released.

The duration spent in the minute prior to stimulus onset was also compared to the minute immediately after the predator was released (Figure 5). The release of the predator did not seem to have an influence on the amount of time spent in any of the three refuges (Enclosed: t(59)=1.522, p=0.133; Net: t(59)=0.680, p=0.499, Open: t(59)=176, p=0.861)
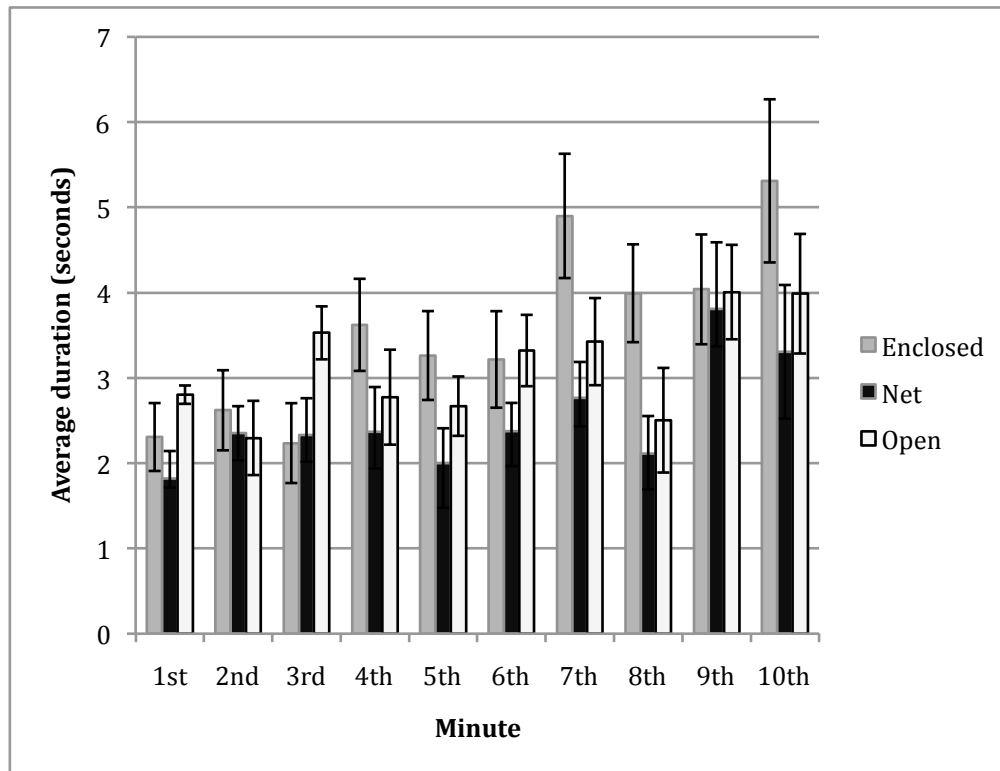
Figure 5: Average duration spent in the enclosed, open and net refuge during each minute over the entire 10 minute trial.

The large proportion of animals that ran to the enclosed refuge probably did not prefer the enclosure because they were in that sphere prior to stimulus onset. As illustrated in table 1, prior to stimulus onset, the refuges were equally visited (X^2=1.6, df=2, p>0.50; Enclosed: N= 20, Net: N=24, Open: N =16), however once the predator was released most ran to the enclosed refuge (Table 1: N=17; X^2=9.5046, df=2, p<0.01).

Table 1: Frequencies of the last refuge visited *prior* to predator release compared to the the refuge visited *after* predator release.

		Refuge visited at stimulus onset			
		Enclosed	Net	Open	Total
Last refuge visited prior to predator release	Enclosed	5	1	2	8
	Net	8	2	3	**13**
	Open	4	3	0	7
	Total	**17**	6	5	

The animals also probably did not run to the enclosure simply because they were closer to that refuge at stimulus onset. As illustrated in table 2, of the animals that ran to the enclosed refuge (row 1), they were at an approximately equal distance to the other refuges yet they still preferred the enclosure. The animals were equally likely to run to the closest refuge or to the ones further away ($X^2=0.2056$, df=1, p>0.90).

Table 2: Distance to each refuge for those that ran to the 1) Enclosed 2) Net and 3) Open refuge at stimulus onset.

		Average distance to each refuge at stimulus onset			
		Enclosed	Net	Open	Average
Refuge visited at stimulus onset	1) Enclosed	98.01 cm	82.83 cm	82.54 cm	87.79 cm
	2) Net	69.98 cm	98.32 cm	88.59 cm	85.63 cm
	3) Open	66.33 cm	76.33 cm	98.99 cm	80.55 cm
	Average	78.10 cm	85.83 cm	90.04 cm	

It is also unlikely that the animals ran to the enclosed refuge due to a home base in that region. A home base is a location where animals frequently return after they explore their territory, and is often chosen based on subtle differences in illumination or odors. In order to determine if this preference for the enclosure was due to a home base in that region, the home base for each animal was determined (table 3) and was correlated with the refuge fled to after predator release. An animal's home base was determined according to the longest duration spent in a refuge. Most animals did not run to the enclosed refuge due to a home base in that area since there does not appear to be a significant correlation between an animal's home base and the refuge visited at stimulus onset (r=0.29539; t_{crit}=1.578, df=26, p>0.05).

Table 3: Comparison of an animal's home base to the refuge visited at stimulus onset.

		Refuge visited at stimulus onset (frequency)			
		Enclosed	Net	Open	Total
Home base	Enclosed	4	0	5	9
	Net	3	5	0	8
	Open	10	1	0	11
	Total	17	6	5	

Discussion

Initially, it was hypothesized that the net refuge would be preferred the most prior to stimulus onset since it has a balance of both prospect and refuge. Contrary to what was predicted, the net refuge was in fact preferred the least and instead a higher duration was spent in the enclosed and open refuges. A substantial amount of time was spent exploring the arena rather than remaining in a refuge. On average, the gerbils spent 80 seconds in all three refuges and the remaining time of a 10 minute trial was spent exploring the rest of the arena outside the enclosures. Given that a substantial amount of time was spent outside the refuges, the animals had considerable prospect of the arena for a large proportion of the trial. The substantial amount of time spent outside the refuge may have allowed them to fully explore their environment for potential predators and resources. A longer duration may have been spent in the enclosed refuge even prior to stimulus onset rather than the net and open refuge which have more prospect, since they may have already explored their environment and further prospect is unlikely to provide any further environmental information.

This preference for exploring environments may be due to an innate hunger for information. This craving begins with a simple preference for certain stimuli and then leads to more sophisticated levels of cognition and perception that draw on associations the brain makes with prior experiences. When this hunger for information becomes even the slightest bit starved boredom occurs, such as when starring at a blank wall. This craving for information only occurs when other motives are not engaged. When animals are trying to satisfy other needs such as for food, avoidance from harm or are engaged in some goal-oriented behaviour, then the desire for information takes a less active role. The

infovre (information) system is designed to maximize the rate at which information is acquired under conditions in which there may not be an immediate need for the information. The knowledge gained may have some practical value in the future and even if there is no direct use of the new information, there can still be an adaptive value to acquiring it.The infovre system is so valuable that the brain has molecular and cellular mechanisms that facilitate the acquisition of information. A system has been identified that is associated with a reward network, which relies on opioids in the brain (Biederman & Vessel, 2006; Yue et al., 2006).

Furthermore, the net refuge was also preferred less than the open refuge. According to Nasar and Fisher (1993) an individual's feelings of safety are not only determined by the extent to which a space provides prospect and refuge, but also to the degree to which a refuge affords the opportunity to escape through an exit (Ramanujam, 2006). The open refuge provides the same ground level concealment as the net refuge, however the open refuge offers rapid escape because the gerbil can exit out of the large top opening, whereas the animals is unable to escape easily from the net refuge. Consequently, there may have been a slight preference for the open refuge compared to the net refuge due the large opening which allows animals to escape easily.

The results of this study also suggest that the degree of prospect and refuge preferred can in fact change depending on contextual factors. The animals showed a preference for the enclosed refuge at stimulus onset, but this is not reflective of what happened prior to stimulus onset. Gerbils preferred running to enclosure after the predator was released, but it was not the most frequently visited refuge immediately prior to stimulus onset. The fact that most gerbils ran to the enclosed refuge after the predator

was released even though immediately prior to stimulus onset the refuges were equally visited suggests that there may have been a shift in preference for concealment rather than prospect due to the environmental circumstance (Table 1). This makes intuitive sense since seeking concealment from a refuge is more adaptive in the presence of a predator, rather than having substantial prospect for potential resources. Given the fact that the predator is already detected, further prospect would probably play a minimal role in their survival, and consequently most may have run to the enclosed refuge rather than to the net and open refuges even though they have greater prospect.

Previous work has shown that gerbils have a tendency to prefer locations that they have visited prior to presentation of a threatening stimuli (Ellard, 1993). As illustrated in table 1, it is unlikely that there was a tendency to seek refuge in the enclosed refuge simply because they had visited that refuge prior to stimulus onset since even the group of gerbils that visited the net or open refuge also had a tendency to run to the enclosed refuge. Prior to stimulus onset, the refuges were equally visited, however once the predator was released most animals still ran to the enclosed refuge.

Preference for the enclosure does not appear to be related to the gerbil's distance to the enclosed refuge prior to stimulus onset. It is unlikely that the animals ran to the enclosure simply because they were closer to that refuge when the predator was released. As illustrated in table 2, the animals that ran to the enclosed refuge were at an equal distance to the other refuges, yet they still preferred the enclosed shelter. The findings suggests that prospect and refuge considerations may have influenced the refuge chosen rather than proximity to the various shelters.

It is also unlikely that the animals ran to the enclosed refuge due to a home base in that region. It has been shown that mammals have a home base to which they frequently return after they explore their territory or home range. The location of a home base may influence an animal's choice of refuge. A home base is often a place where an animal spends the longest cumulative duration, and it has a pervasive influence on the way an animal progresses throughout an environment. The most reliable feature of a home base's location appears to be the time spent there and the large number of visits (Eilam & Golani, 1989). A home base's location is not completely arbitrary, and is often determined by subtle differences in sound qualities, odors, or illumination, for instance, that could have existed in the testing arena used in the present study (Ellard, 1993). Differences in illumination due to shadows from refuges may have influenced the location of the home bases. Most animals probably did not run to the enclosed refuge due to a home base in that region since there does not appear to be a strong correlation between an animal's home base and the refuge visited at stimulus onset. As illustrated, these results suggest that the choice of refuge was not simply based on the location of a home base, but perhaps rather due to differences in prospect and refuge levels among the shelters.

Even though several animals ran to the enclosed refuge after the predator was released, a large proportion did not flee to any refuge. The lack of response in so many animals suggests that prospect and refuge levels cannot always conclusively predict an animal's spatial preference, however it still may be one of several important factors. The absence of a fleeing response by several animals is probably not because they did not perceive the threat as an actual predator. Responses to this overhead predator have been

examined in previous studies and their responses are similar to those that gerbils make to actual aerial predators, such as falcons and other predators found in natural habitats (Ellard, 1996; Agren, et al., 1989). In the past, gerbils have responded to this simulated aerial predator by making maneuvers that take into account the trajectory of the stimulus and the locations of refuges (Ellard, 1996). Gerbils will run from almost anything regardless of its size, shape, trajectory or speed when it is in the upper field (Ellard, 1996; Ellard & Chapman, 1991; Ellard & Goodale, 1988). Animals can have a fear response to a stimulus because of its physical characteristics, such as its intensity, movement, duration proximity or suddenness. These stimuli are not species specific and are associated with the context of predation. For example, a flying hawk is more likely to elicit a fear response than the same predator that is perched and does not move. It is also not very likely that the animals could not see the predator since Ingle and Shock (1985) have demonstrated that gerbils are sensitive to visual properties that are substantially more subtle than used with this aerial predator (Ellard, 1996; Emerson & Baker, 1983).

There are various plausible explanations that may account for the lack of response in several animals. There is an implicit assumption that animals flee as soon as they see a predator and that detection is equivalent to response (Ydenberg & Dill, 1986). This is a false premise since fleeing has costs in time and energy taken from other activities and as a result animals may not necessarily flee as soon as a predator is detected (Kramer & Bonefant, 1996). The large proportion of animals that did not respond may have rather spent their time and energy grooming or exploring their environment for more threatening predators instead.

Several animals may have also not run to a refuge after the predator was released because under natural conditions, the cessation of locomotor activity or freezing is fairly common when a predator is initially detected. Freezing serves several different functions and can often be adaptive. If a predator is seen before the prey has been detected, freezing can help to reduce detection. Various predators rely almost exclusively on moving visual cues to identify and capture a prey. Freezing can facilitate in concealing an animal due to the lack of motion. Furthermore, prey movement may cause the predator to expect even further movement. If a prey animal freezes, the predator may shift its attention for a short period of time and this may prevent further pursuit (Suarez & Gallup, 1981). Even in laboratory conditions, freezing has been demonstrated to be a prepotent response and appears to be a species-specific defense reaction (Suarez & Gallup, 1981; Bolles, 1970). A large proportion of animals, specifically older gerbils that cannot run as fast, may have chosen to freeze rather than flee since it may have been more adaptive. Previous studies have shown that gerbils are usually fairly responsive to this aerial predator, for instance in a study by Ellard (2005) 82% responded and in another study (Ellard, 1993), 73% responded. Since these animals are now 1-2 years older than those in these previous studies, freezing or minimizing movement may have been a more adaptive alternative to prevent detection rather than fleeing to a refuge.

As illustrated, there are a wide range of factors that may have contributed to a lack of refuge-seeking behaviour in so many animals. Even though several gerbils did not flee to a refuge due to the reasons discussed, the animals that choose to flee seem to have taken prospect and refuge features into consideration when choosing the most optimal refuge. Of the 28 gerbils that did have a fleeing response, most ran to the

enclosed refuge rather than to the net or open refuge. The results indicate that this shift in preference for concealment was not very long lasting, which is suggested by the lack of increase in duration spent in the enclosure even 3 minutes after exposure to the predator. The preference may not have been very long lasting since the absence of a predator may not have provided a motive to remain in the enclosure. Despite the fact that the duration spent in the enclosure did not increase after stimulus onset, there was still a tendency to run to the enclosed refuge immediately after the predator was released. As illustrated, this tendency to run to the enclosure at stimulus onset provides evidence that predation may in fact play some role in the degree of prospect and refuge preferred.

This preference for the enclosure at stimulus onset also indicates that gerbils may have formed a vector representation of the refuges locations and that they are able to distinguish between them. Animals navigate through environments using an internal representation of the spatial arrangement among objects in their environment (Singer et al., 2006). If the animals had not formed a vector representation of the refuge locations, they may not have been able to locate the enclosed refuge (Archer, 1990). An animal's location in an environment is encoded by the firing of hippocampal place cells. An animal's location relative to a landmark determines which specific place cells will fire (Collett & Graham, 2004).

Latent learning models have allowed the direct assessment of exploratory behaviour using representations of space upon later learning performance (Archer, 1990). Latent learning occurs when learning is not immediately expressed and manifests itself later when an appropriate motivation or circumstance arises. It appears that animals are capable of building a vector representation of an object's location that they are able to use

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later when motivated (Tolman, 1948). Similarity, in the present study the gerbils may have "learned" the refuge's locations even prior to stimulus onset, however this vector representation may not have manifested itself until the animals were required to locate and choose the most optimal refuge upon exposure to the predator.

In conclusion, the present study suggests that the amount of visible space and its arrangement does appear to influence refuge preference. The results indicate that upon exposure to a threatening stimulus there is a shift towards preferring refuges with greater concealment rather than prospect. Animals displayed a strong preference for the enclosed refuge at stimulus onset, but this is not reflective of what happened prior to stimulus onset. These results suggest that the degree of prospect and refuge preferred is in fact influenced by contextual factors, such as predation. The findings also indicate that this preference for the enclosure is probably due to its optimal level of prospect and refuge rather than due to various other factors such as the animal's distance to the enclosed refuge, the last refuge visited or due to a home base close to the enclosure. This preference for the enclosure also suggests that the gerbils may have developed a vector representation of the refuge's locations and that they were able to distinguish between them, since otherwise they would not be able to locate the enclosed refuge.

Satisfaction obtained from favorable environments with prospect and refuge appears to be one of those basic biological needs that we share with animals. Appleton's (1975), theory uses a strategic approach in explaining perceptions of safety and danger. A greater understanding of the similarities between animal and human spatial preference provides further justification in taking animal behaviour models into account when designing urban spaces. An explicit comparison of these preferences in widely divergent

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species has helped place theories of spatial preference on a firmer biological footing, and

provides a greater understanding of how the principles of spatial cognition might

underpin parts of the design process.

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