

Functional analysis of concealment: A novel application of prospect and refuge theory

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ABSTRACT

According to prospect–refuge theory, humans prefer environments that afford protection from threat (refuge), but also provide large fields of view (prospect). Prospect–refuge theory in the past has traditionally only been applied to humans, but many of the same contingencies governing spatial preference ought to also hold true in animals. The focus of this study was to examine if this phenomena also occurs in animals. Gerbils were placed in an arena containing three dome shaped refuges that varied in prospect–refuge levels. A simulated predator was released during the trial to examine how contextual factors may influence the degree of prospect and refuge preferred. The results indicate a preference for the enclosed refuge at stimulus onset even though this was not reflective of what happened prior to predator release. The results suggest spatial preferences in animals are influenced by prospect–refuge considerations in certain contexts.

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1. Introduction

According to habitat theory, esthetic pleasure in 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 color, shapes, spatial arrangements and other visible attributes that act as stimuli indicative of habitat conditions favorable to survival (Appleton, 1975). Habitat theory is one of the first theories that connects human behavior and the environment. According to ‘Habitat theory’ humans interact with the environment, the same way animals do with their habitat. 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. In nature the most important threat an animal encounters come from attackers and predators. Consequently, chances of survival are greatly enhanced the more an individual can see in order to detect potential enemies and the less one can be seen from predators (Appleton, 1975; Ramanujam, 2006).

In his classic work Appleton (1975) developed a Darwinian theory that explains reactions to landscape paintings using principles of habitat selection and animal behavior. Appleton’s prospect–refuge theory proposes 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 esthetic satisfaction (Appleton, 1975). According to Appleton’s prospect–refuge theory, humans prefer to be in environments that not only afford protection from threat (refuge), but also provide large fields of view (prospect) (Appleton, 1975; Fisher and Shrout, 2006). Prospect refers to having an overview of an environment and refuge involves having a safe place to hide (Appleton, 1975; Kaplan, 1987). Appleton proposes that we prefer environments that offer both prospect and refuge because such places aid survival by making it possible to anticipate threats and opportunities, as well as by providing protective space to keep oneself from being harmed (Appleton, 1975; Fisher and Nasar, 1992). A valley seen from a hilltop, an open landscape viewed from a cave mouth, or savannah environments that consist of widely scattered trees, all contain elements of both prospect and refuge (Appleton, 1975; Hudson, 1993).

According to Konrad Lorenz, animals appear to take prospect–refuge features into consideration as well. When animals approach open areas with prospect from an enclosure animals stop at the edge of the forest and survey open fields before crossing into areas with prospect. Lorenz’ phrase “to see without being seen” effectively describes Appleton’s prospect–refuge concept. It is advantageous for a predator to see its prey, however without being seen to prevent a fleeing response from its victim. Prey have a somewhat different objective and are concerned with seeking refuge to prevent being seen, however need to be able to see an environment to remain vigilant of a possible attack (Lorenz, 1954; Appleton, 1975).

The overall objective of this study was to explore spatial preferences of the Mongolian gerbil in situations in which

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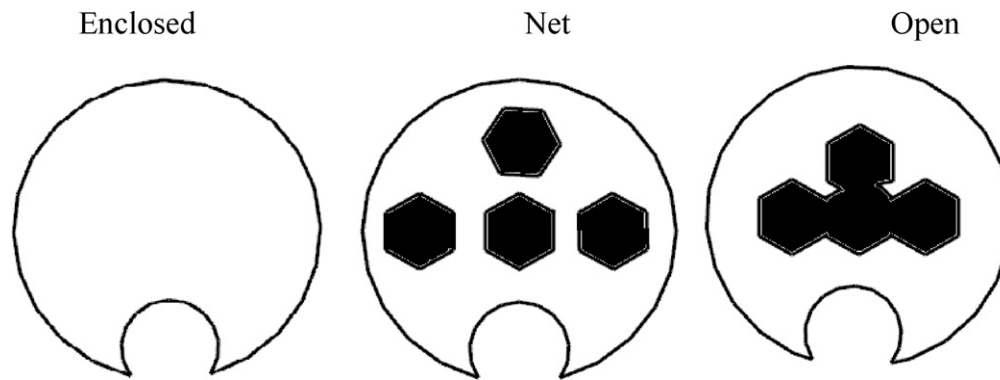


Fig. 1. Diagram of the enclosed, net and open refuges. The black regions represent openings.

prospect–refuge theory makes specific predictions about environmental regions preferred. Lorenz's work suggests that animals take prospect–refuge features into consideration, however little is known about the impact of contextual factors on these preferences. Environments with certain levels of prospect and refuge may be preferred in certain contexts, but not in others. An explicit comparison of these preferences in widely divergent species may help to place theories of spatial preference on a firmer biological footing (Lorenz, 1954).

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. Three types of domes were used, an 'enclosed', 'net' and 'open' refuge, as illustrated in Fig. 1. 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 and provided prospect, but minimal refuge. It was hypothesized that the net refuge would be preferred prior to stimulus onset since it provides concealment and considerable prospect.

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 predator was released, there might be a tendency to prefer the enclosed refuge rather than the net or open refuge since concealment may take 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. In summary, it was expected that the net refuge would be favored prior to stimuli onset since it had a balance of both prospect and refuge, however once the predator is seen the enclosed refuge may be preferred since being concealed would be of greater importance than having prospect.

In behavioral 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). Gerbils live in burrow systems with multiple entrances in their natural habitat (Clark and Bennett, 1979; Ellard, 1993; Agren et al., 1989). When faced by a predator, a gerbil is not only confronted with the choice 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 various different refuges for shelter the way they would in their natural habitat. 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 (Cheal, 1976).

2. Materials and methods

2.1. Subjects and housing

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. The room was kept at a constant temperature of 21.1 °C and testing was conducted during the light phase of a 12-h light/dark cycle. All animals had free access to food (LabDiet food pellets) and water. Treatment of animals during the experiment was conducted according to the guidelines of the Canadian Council on Animal Care.

2.2. Procedure

On each trial three domes were positioned 60 cm from the center of an arena (2 m in diameter, with a perimeter wall 60 cm high) at a 120° angle from each other. The arena contained three dome shaped refuges measuring 22 cm in diameter and 9 cm in height. The domes' positions were rotated to six different sequences to counterbalance their position relative to the arena and each other. Sixty trials were collected with an equal number of trials with the spheres positioned in each of the six position combinations. Each animal was tested only once to minimize the effects of habituation. After the spheres were placed in a particular position, the animals were brought into the room in a cloth-covered cage. Animals were placed in an arena containing a rotating platform positioned in the center.

The platform was rotated approximately three times to ensure that the gerbil was disoriented and could not recall where they entered the apparatus. The rotating platform was removed from the arena after the gerbil was released. Each trial was 10 min in duration. The predator was released when the animal was close to the center of the arena (i.e., not standing near the refuges' entrance or inside the refuge) at approximately the 7th minute of a 10 min trial. An aerial predator was simulated using a piece of rectangular (23 cm × 13 cm) white matte board 2 mm thick, that was attached to 2 parallel nylon wires. 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 center 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.

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