The effect of familiarity on vigilance behaviour in grey squirrels

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ABSTRACT

Introduction: Vigilance enables an animal to obtain information about the environment but often at a cost of reduced foraging rate. Some environmental information may not change rapidly, so vigilance might be safely reduced with familiarity with an area. Studies have noted this decline in vigilance with familiarity, but the reason for this decline has not been tested. **Methods**: I proposed and tested two hypotheses to explain this decline in vigilance. The Safe Experience hypothesis suggests the probability of a predator being nearby but undetected decreases with time spent in an area, enabling an animal to decrease its vigilance due to the reduced risk. The Visual Experience hypothesis suggests that as time progresses vigilant animals acquire more information from their surroundings (e.g. refuge locations) allowing for a decrease in vigilance because an animal would not need to detect a predator as early if reaching a refuge required less time. Grey squirrels (*Sciurus carolinensis*) were used to test these hypotheses by feeding them peanut butter in an apparatus that limited their access to visual information by varying degrees. **Results**: An effect of familiarity was evident by a sharp decline in vigilance rates within trials. Squirrels adjusted vigilance postures to the different treatments, but the rate of decline in vigilance was unaffected by treatment. **Discussion**: While vigilance is related to visual information, the decline in vigilance with familiarity is not related to the amount of visual information obtained from the environment, giving provisional support to the Safe Experience hypothesis.

KEYWORDS

Vigilance, foraging, familiarity

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INTRODUCTION

The act of vigilance enables an animal to obtain information on its surroundings *(1)*, such as information on nearby refuges, escape routes, predator approaches, and conspecifics *(2)*. Unfamiliar environments have been found to elicit higher vigilance *(3, 4)*, likely because potential sources and locations of danger, as well as locations of refuge, are not known. Familiarity with an area is important for survival because an animal can benefit from knowing the types and locations of food *(5)* and refuge *(6)* available. Animals in unfamiliar locations take longer to find refuge *(7-9)*, and consequently are at higher risk of predation *(6, 7, 10, 11)*.

Previous studies have found that vigilance decreases with increased familiarity with the surroundings: in Holstein dairy cows *(4)*, eastern chipmunks, *Tamias striatus (3)*, grey squirrels, *Sciu-*

rus carolinensis (12) and barbary doves, *Streptopelia risoria (13)*. However, there has been little consideration of why this decrease in vigilance occurs, and consequently no studies have attempted to predict what affects the relationship between vigilance and familiarity. The decrease in vigilance could be related to the increase in knowledge of the surroundings (such as refuge locations) with time, or the decrease in vigilance could be related to predation risk as the probability that a predator is present but undetected decreases with time spent in an area *(3)*.

In this study, I proposed and tested two hypotheses to explain this decrease in vigilance. The Safe Experience hypothesis suggests that since the probability of a predator being nearby but undetected decreases with time spent in an area, an animal can decrease its time spent being vigilant, because of the lower risk of no predators in the vicinity, and the arrival of a predator would involve movement that would be more easily detected *(11, 14)*. The Visual Experience hypothesis suggests that the more time an animal spends being vigilant, the more information is obtained from the surroundings (e.g. location of refuges and escape routes). This leads to a decrease in vigilance, as the knowledge of possible refuges allows for a slightly later detection of a predator. The Visual Experience hypothesis predicts that vigilance will decrease as the amount of visual information obtained from the surroundings increases, whereas the Safe Experience hypothesis predicts a decrease in vigilance regardless of the amount of visual information obtained.

To distinguish between these hypotheses, I studied the effect of familiarity on vigilance in grey squirrels (*Sciurus carolinensis*) during visits to a food patch, using a feeding apparatus with walls of varying heights (treatments). The apparatus added two elements of unfamiliarity to the environment: it was a novel object and a novel food patch for the squirrels. The different treatments made it possible to vary the amount of visual information that could be obtained by being vigilant. The Visual Experience hypothesis predicts differences between treatments on the rate of decline in vigilance, because if familiarization is affected by visual information then more rapid familiarization would be expected when the amount of visual information obtained is greater. Conversely, the Safe Experience hypothesis predicts no difference between treatments on the rate of decline of vigilance since the rate is independent of the amount of visual information obtained from the surroundings.

I also looked at whether the type of vigilance posture was affected by access to visual information. Squirrels exhibit several different vigilance postures of varying heights (in a range from quadrupedal to bipedal postures *(15)*, that allow them to get a better view of their surroundings by increasing their viewing range *(16)*. I expected squirrels to adjust their vigilance postures to the different wall heights of the different treatments, based on the assumption that access to visual information influences vigilance posture.

METHODS

EXPERIMENTAL APPARATUS

The experimental apparatus consisted of three walls positioned around a food source (Fig. 1), a glass plate with 30ml of evenly spread smooth peanut butter. As grey squirrels have been shown to be vigilant while handling food items in a bipedal position *(12)*, the peanut butter setup forced squirrels to eat with their

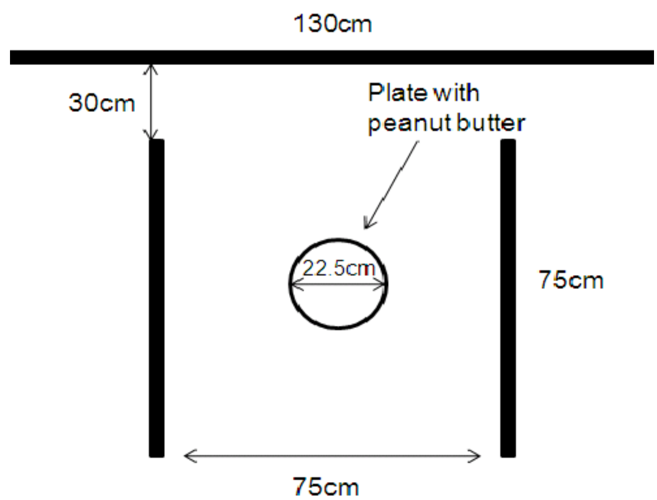

Fig 1. The design and spatial layout of the experimental apparatus (seen from above) used to test the effect of familiarity on vigilance. The height of the walls surrounding the food source varied with the different treatments: 6cm for the low walls treatment, 15cm for the medium walls treatment, and 40cm for the high walls treatment.

Posture	Type	Description
Low head raise	Quadrupedal	Head raised with eyes below the highest part of the squirrel's back
High head raise	Quadrupedal	Head raised with eyes above the highest part of the squirrel's back
Semi-upright	BIPEDAL	Sitting on back feet with back noticeably arched
Upright	Bipedal	Sitting on back feet with back straight, more fully upright than the semi-upright posture

Table 1. Descriptions of the different vigilance postures exhibited by grey squirrels.

heads down. Each wall of the apparatus consisted of two wooden poles pounded into the ground, with black gardening fabric stretched between them. Once the squirrel entered the apparatus, the walls blocked the squirrel's view in three directions. The open end of the apparatus provided a clear view to videotape the vigilance behaviour of the squirrel. The apparatus did not have a roof because previous studies using overhead blocks found they have no effect on vigilance *(12, 17, 18)*.

Four different treatments were used with varying wall heights: low walls were 6cm in height, medium walls were 15cm in height, and the high walls were 40cm in height. The fourth treatment consisted of only the plate with peanut butter (referred to as the 'no walls' treatment). The design of the low and medium walls treatment was such that squirrels could still obtain information from their surroundings if they adjusted their vigilance posture to the wall height. Based on a few pilot trials, I determined that squirrels were able to see over the low walls using a quadrupedal vigilance posture, and squirrels were able to see over the medium walls using a bipedal vigilance posture. The high walls treatment blocked the squirrel's view even in bipedal vigilance postures.

FIELD TRIALS

Study sites were located in several Montreal parks, with 3 trials in the area surrounding Lac aux Castors on Mont Royal, 14 trials in Angrignon Park, and 19 trials in Maisonneuve Park. Trials were conducted in open grassy areas where trees were spaced more than 3m apart. I conducted a total of 36 trials were conducted between 10:00 and 16:00 h from October 21 to December 2, 2006, on days without rain.

I conducted trials in sets of the four treatments to keep samples sizes consistent across treatments (9 trials in each treatment), with the order of the treatments and the orientation of the open end of the apparatus (north, east, south or west) randomized in each set. I attracted a squirrel to the apparatus by throwing a couple nuts (either peanuts or sunflower seeds) towards the apparatus. For each trial I set up the apparatus 2-5m from a large tree (> 20cm in diameter), and filmed the behaviour of the squirrel with a video camera (Panasonic Digital Palmcorder, PV-DV400-K) on a tripod positioned 10m from the open end of the apparatus. Trials were spaced at least 100m apart to minimize the likelihood of retesting the same individual. The trial began when the squirrel first entered the apparatus (no prior familiarization), and ended when the squirrel exited the apparatus of its own accord to forage or in some cases was chased out of the apparatus by a conspecific or domestic dog (*Canis familiaris*). I minimized interruptions of trials by conspecifics by distracting other squirrels in the vicinity with nuts (peanuts, sunflower seeds, and hazelnuts).

DATA EXTRACTION AND ANALYSIS

From each videotaped trial, I counted the number of vigilance bouts in each minute to get a rate of vigilance per minute, which was used as the response variable in subsequent analyses. Only the first three minutes were analyzed because of small sample sizes after three minutes (i.e. most squirrels exited the apparatus after three minutes). Each vigilance bout was classified into one of several different posture types (Table 1), as previously described in other studies on vigilance behaviour in squirrels *(15, 19)*. Nonparametric tests were used because the data were not normally distributed (Shapiro-Wilk normality test, $p<0.001$). Statistical analyses were done using SYSTAT® Version 12, with an alpha significance level of 0.05.

RESULTS

THE EFFECT OF TIME AND TREATMENT

Vigilance rates were similar between treatments, with all four treatments showing a sharp decline in vigilance rate from the first to the second minute, and remaining relatively constant from the second to the third minute (Fig. 2). There were no significant differences in vigilance rates in the first three minutes of trials between different treatments. (Kruskal-Wallis test: 1st minute interval H_3=3.239, p=0.356; 2nd minute interval H_3=1.933, p=0.586; 3rd minute interval H_3=4.942, p=0.176). Since treatment had no effect on vigilance, all treatments were combined to test for the effect of time. Time had a strong effect on vigilance rate (Friedman test: Q=17.721, $p<$ 0.001), and vigilance rate sharply declined by 62% from the first to the second minute (Wilcoxon signed ranks test: $p<0.001$). The rate of vigilance remained relatively constant after the first minute and there was no significant difference in vigilance rate during the second and third minute (Wilcoxon signed ranks test: p=0.5).

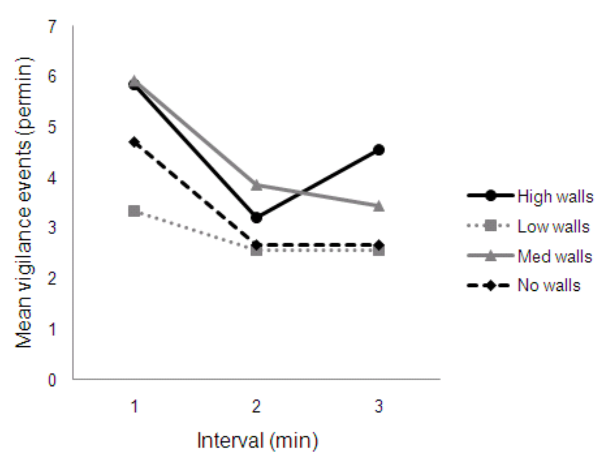

Fig 2. Mean number of vigilance events per minute for each of the four treatments for the first three minutes of each trial.

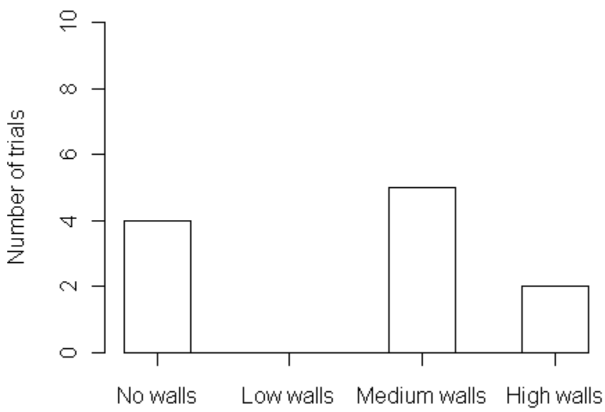

Fig 3. Number of trials with the occurrence of either of the two bipedal vigilance postures (semi-upright and upright).

VIGILANCE POSTURES

The quadrupedal vigilance postures, the low and high head raises (Table 1), were the most common types of vigilance postures. The different treatments ranged from a mean of 90%-100% quadrupedal postures out of the total number of vigilance postures that occurred in the first three minutes of each trial. Bipedal vigilance postures, semi-upright and upright, were used less often and accounted for a mean of 0-10% bipedal postures out of the total vigilance postures that occurred in the first three minutes of each trial. The number of trials where the squirrel used bipedal vigilance postures differed between the treatments (G test of independence: G=10.051, p=0.018; Fig. 3).

DISCUSSION

Squirrels responded to the various treatments by modifying their vigilance postures to the different wall heights. The occurrence of bipedal vigilance postures (semi-upright and upright) differed between treatments, with bipedal postures occurring more frequently in trials with the medium walls treatment and less frequently in the low walls and high walls treatment. This was expected because the medium walls treatment was the only treatment that allowed better access to visual information with the use of bipedal vigilance postures. Quadrupedal vigilance postures were sufficient to see over the walls in the low wall height treatment, and in the high walls treatment neither vigilance posture was effective in accessing visual information. The no walls treatment also had a high occurrence of bipedal postures, and although it is not clear why this was the case, it might have been due to uncontrolled environmental factors such as grass height, or other vegetation that might have affected access to visual information in these trials. My results support previous evidence that vigilance postures are related to the gain of visual information. They are consistent with other studies that found bipedal postures were used more often in habitats where better views of the surroundings could be gained by their use of bipedal postures.

Vigilance rates declined sharply (62%) with increased time feeding in the apparatus, primarily between the first and second minute of the trials. This suggests that familiarization in grey squirrels in an urban setting occurs mainly in the first minute of exposure to a novel situation. Other studies have found an effect of familiarity between repeated visits to a novel location where food was provided. For example, a study on dairy cows found a 41% decrease in the time spent vigilant over 11 trials *(4)*, and a study on barbary doves found an 80% decrease in time spent vigilant over 7 trials *(13)*. A study on eastern chipmunks also found a significant decline in vigilance among successive trips to a food patch *(3)*. There is almost no previous evidence, however, for familiarity affecting vigilance over the course of a single visit to a food patch (which has been demonstrated in this study). In a study on eastern chipmunks, a non-significant decline in vigilance rate within a single visit to the food patch was documented; however, the chipmunks made three familiarization trips to the food patch prior to data collection *(3)*.

CONCLUSION

I found that varying access to visual information had no effect on vigilance rates of grey squirrels over the first three minutes of the trials, giving provisional support to the Safe Experience hypothesis. This suggests that the decline in vigilance in grey squirrels due to familiarity is not a result of increased information about the surroundings, but is instead due to a presumed decrease in predation risk as an animal forages without any sign of a predator in the vicinity. Although more work in this area is necessary to conclude with certainty which hypothesis best explains the decline in vigilance with familiarity, this study provides the first step in establishing how familiarity affects vigilance by proposing and testing hypotheses to explain the observed decrease in vigilance rate. The approach used in this study of varying the amount of visual information and the design of the apparatus provides a useful way of testing for effects of familiarity and could be important for later studies addressing similar questions.

This study was done on grey squirrels in an urban setting, and the results on the effects of familiarity raise an interesting question as to whether there are differences between grey squirrels in urban and natural areas in regards to the time it takes to become familiar with their surroundings. It is possible that the effect of familiarization on vigilance behaviour would differ between squirrels in urban areas and squirrels living in natural areas because of different stimuli from their environments and differences in predatory risk *(21)*. Familiarization might play an important role for animals adapting to urban environments, since novel situations may occur more often and animals that familiarize more quickly could benefit by decreasing their foraging costs.

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