VIGILANCE IN COLUMBIAN GROUND SQUIRRELS: THE EFFECTS OF KINSHIP AND MECHANISMS OF THE GROUP-SIZE EFFECT

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VIGILANCE IN COLUMBIAN GROUND SQUIRRELS: THE EFFECTS OF KINSHIP AND MECHANISMS OF THE GROUP-SIZE EFFECT

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THESIS ABSTRACT

VIGILANCE IN COLUMBIAN GROUND SQUIRRELS: THE EFFECTS OF KINSHIP AND MECHANISMS OF THE GROUP-SIZE EFFECT

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Behavioral observations of Columbian ground squirrels (*Spermophilus columbianus*) were made to investigate two factors that can affect vigilance: the group-size effect and the presence of kin. Vigilance was timed in over 700 observations of 230 individuals on 14 meadows in the summers of 2004 and 2005.

One of the goals of this study was distinguish which one of two mechanisms has a greater influence on the group-size effect in Columbian ground squirrels, dilution or detection. To distinguish between the two, equations of the models were fitted to the data and hypotheses were tested by making a number of predictions. If dilution is the main factor in the group-size effect, it was predicted that nearest neighbor distance, and the distance to the edge of the meadow would influence vigilance and that alarm calls and

factors that effect hearing alarm calls (wind speed) would not. The opposite predictions were made for the detection effect. The results of both the model fitting and the hypothesis testing supported detection as the main factor causing the group-size effect in these ground squirrels: nearest neighbor distance and distance to the edge of the meadow had no significant effect on vigilance, whereas alarm calls significantly affected vigilance, and vigilance increased with wind speed. A comparison of our results with those of other studies of dilution and detection suggest that group type as well as means of information transfer about predators may indicate whether dilution or detection is the greater influence producing the group-size effect in a species.

I also examined whether vigilance was affected by the presence of kin in a population. I found that the only group with differing vigilance was females with adult offspring. These females had significantly lower vigilance than other groups (Rank-sum test, 2004 and 2005 pooled: Z=-2.62, P=0.01). Several possible confounding factors, such as group size and current reproduction, were examined and rejected. Mothers' decreased vigilance may be an example of social parasitism, in that mothers may be taking advantage of their adult offspring's vigilance in order to decrease the cost incurred by being vigilant.

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CHAPTER ONE

MECHANISMS OF THE GROUP-SIZE EFFECT ON VIGILANCE IN COLUMBIAN GROUND SQUIRRELS: DILUTION VS. DETECTION

Anti-predator vigilance decreases with group size in many vertebrate prey species. This pattern might be explained by collective detection (increased probability of observing a predator) or risk dilution (decreased likelihood of being captured with larger group size). This is the first study to use both model fitting and hypothesis testing to determine which mechanism had the greater effect. If dilution is the main cause of the group-size effect, nearest-neighbour distances and distance to the edge of the group would affect vigilance, and alarm calling and factors that affect hearing alarm calls would not affect vigilance. The opposite outcomes are expected if detection is the primary influence. We observed vigilance of Columbian ground squirrels (*Spermophilus columbianus*) in 14 populations. Vigilance decreased significantly as group size increased (R^2=0.70, P=0.0002). Model fitting revealed that the detection model fit our data better than the dilution model. We found no significant effect of nearest-neighbour distance on the proportion of time vigilant. Distance of individuals to the edge of the meadow explained a trivial amount of variation in vigilance overall, and was not significant on individual meadows. Alarm calls occurred in 56.1% of observations and had a significant effect on vigilance. Wind speed results for individual meadows were mixed, but overall showed that vigilance increases with wind speed (R^2=0.31, $P < 0.01$). All of these results support the detection hypothesis. Group type and means of information transfer about predators may be indicators of whether detection or dilution has the greater influence on the group-size effect.

INTRODUCTION

Vigilance, scanning the surroundings for predators, is a widespread behaviour of prey species and may be influenced by many factors. One of the most studied factors influencing vigilance is group size, the common finding being a decrease in individual vigilance as group size increases (Lima & Dill, 1990). Two hypotheses most commonly suggested to explain the negative relationship between vigilance and group size are the dilution effect (from Bertram's (1978) "dilution of the predator's effect" and Hamilton's (1971) selfish-herd effect) and increased predator detection (also termed "many eyes," "collective detection," or "detection effect"), advanced by Pulliam (1973). Bertram's (1978) hypothesis suggests that an individual's risk of being captured is decreased with increasing group size because the predator is progressively more likely to capture another individual simply by chance. Hamilton's (1971) selfish-herd effect proposes that having other individuals close-by decreases an individual's risk of capture when the predator chooses the closest prey. Although Hamilton's selfish-herd effect is often equated with Bertram's diluting effect, they are not the same, nor is Bertram's diluting effect a direct result of the selfish-herd effect (Bednekoff & Lima, 1998). However, because both reduce predation risk due to membership in a group, we consider both to be a part of the dilution effect. Alternatively, the detection effect posits that individuals can decrease their vigilance in groups because they can obtain information about approaching predators from group mates (Pulliam, 1973).

Many studies cite dilution and/or detection effects to explain observed group-size effects, with little or no consideration given to which one actually has more effect on the species in question (e.g. Banks, 2001; Cassini, 1991). Several studies suggest models or methods to test between the two possible explanations for the group-size effect, but relatively few studies attempted empirical tests between them (Boland, 2003; Fernandez et al., 2003; Rolando et al., 2001; Childress & Lung, 2003). Three of the four studies concluded that dilution was more important in determining individual vigilance of group members than collective detection, although some conclusions can be questioned on the basis of confounding factors or insufficient methods (Table i, Appendix).

Five additional studies did not specifically test between the two hypotheses, but gave data to suggest one of these effects may be more influential than the other (Blumstein et al., 2001; Smith et al., 2004; Kenward, 1978; Hoogland & Sherman, 1976; Siegfried & Underhill, 1975). In three of the five it can be inferred that detection had a greater influence than dilution (Table ii, Appendix). Most of the species in these nine studies have similar group types and information transfer: ephemeral, travelling, feeding groups that lack a reliable, active, alarm calling system.

Columbian ground squirrels (*Spermophilus columbianus*) provide a very different type of group; a permanent, stationary population with individual territories, and a very high likelihood of transfer of information about approaching predators through active alarm calls (MacWhirter, 1992). The difference in the group type and information transfer as compared to the species in the previous studies may result in differences in the relative influences of dilution and detection. Columbian ground squirrels are appropriate mammals for studying many aspects of vigilance. They live in alpine and sub-alpine meadows where they can be easily observed, and are preyed upon by a variety of predators, both aerial and terrestrial. Adult females establish and defend territories that usually have slight overlap (King, 1989). The animals forage during the day and have an easily observable vigilance behaviour as they forage: they raise their heads, pausing foraging (Arenz and Leger, 2000). Although this vigilance behaviour might also be used for purposes other than anti-predator (e.g. monitoring conspecifics), it probably serves all or many purposes at once, and is likely an accurate measure of anti-predator behaviour.

Before testing between dilution and detection, a group-size effect on vigilance must be shown in Columbian ground squirrels. Because similar sciurids show the effect (Barash, 1973; Carey & Moore, 1986; Hoogland, 1979; Kildaw, 1995), it is likely that Columbian ground squirrels do as well. This study addresses the group-size effect in two ways. I investigated both a population-size effect and a number-active effect. The former may suggest the use of a rule-of-thumb for group size in the squirrels, while the latter implies that the squirrels change vigilance with changes in the number of individuals active on the meadow.

Although dilution and detection are not mutually exclusive, it is likely that one may have a greater influence than the other in a given species or population. We used two methods to determine which of the two effects have the greater influence: model fitting and hypothesis testing. We used models of dilution and detection by Pulliam (1973) and Dehn (1990). We tested between the dilution and detection hypotheses by making several predictions. If dilution is the greater influence on Columbian ground squirrels, then nearest-neighbour distance and distance from the edge of the meadow habitat should influence individual vigilance (Table 3). These factors would be important because they determine an individual's "domain of danger," the area around the individual in which all points are closer to the domain's owner than to any other individual (Hamilton, 1971). An individual with a smaller domain of danger has a smaller chance of being captured by a predator that attacks the nearest prey animal to itself. Roberts (1996) suggested that decreased vigilance with decreased nearest-neighbour distance is also expected for the collective detection effect because information about an approaching predator is easier to obtain from a near individual than a far one. This may be the case in animals without an active alarm calling system, i.e. birds that flush rather than call in the presence of predators. However, in animals such as Columbian ground squirrels, an alarm call can warn all individuals within a rather extensive area. Thus, nearness to other individuals is probably not a predictor for collective detection in ground squirrels. For animals that depend primarily on dilution, alarm calling and response to alarm calls is predicted to be low, and factors that influence hearing alarm calls (e.g. wind) should have little effect on vigilance.

Alternatively, if Columbian ground squirrels are more dependent on collective detection, nearest-neighbour distance and distance to the edge of the meadow should not affect vigilance (Table 3). Alarm calls should coincide with predator sightings and squirrels should respond to alarm calls by increasing vigilance. Additionally, vigilance should increase when the environment limits hearing, such as during high winds (Table iii, Appendix).

METHODS

Observation Methods

Observations were conducted by a single observer (B.F.) on five previously studied populations (hereafter “marked populations”) and nine previously unstudied populations (hereafter “unmarked populations”) in the Sheep River Wildlife Sanctuary in the Kananaskis Country Recreation Area in south-western Alberta, Canada, from 29 May 2004 to 2 July 2004 and 18 May 2005 to 15 July 2005. A foraging squirrel was observed for five to ten minutes and its vigilance timed with a stopwatch; vigilance was defined as lifting the head above the shoulders and pausing all activity except chewing. On the marked populations, observations were taken from raised platforms that have been at each meadow for several years. Squirrels on the marked populations were uniquely marked on the back with black hair dye for individual identification. These populations have been tracked for up to 20 years, so the age/sex for each squirrel was known. These meadows were denoted with flags at 10-m intervals that described Cartesian coordinate systems. Squirrels’ locations were recorded using these reference grids. My access to each marked population depended on the activities of other researchers, so number of observations per meadow varied from 26 to 106 in 2004 and 27 to 106 in 2005. On the unmarked populations, squirrels were monitored from a vantage point that allowed for observations with the least disturbance to the animals. Binoculars and/or a spotting scope were used to make observations. The total area of meadows (in square meters) was estimated from length and width. Nearest-neighbour distances were estimated to the nearest meter after extensive experience in estimation was gained on marked meadows. The unmarked populations were needed to provide a reasonable sample size of populations for testing the population size effect and were also used in tests of nearest-neighbour distance. Due to time limitations and difficult access to the unmarked populations, only 12 observations per unmarked population were made.

Assumptions

We assumed that vigilance would not be affected by date or time of day. To test these assumptions, we did a Durbin-Watson test on the regressions for nearest-neighbour distance to assess serial correlation. Only one meadow showed a negative serial correlation, which indicates that when one observation has high vigilance the next has low vigilance, and vice versa. Although it did not show a time trend (increase or decrease over the day), the negative serial correlation could indicate non-independence of observations. Therefore an auto-regression was performed for thoroughness to remove the effect of the serial correlation. Durbin-Watson tests were not performed on the regressions other than nearest-neighbour distance because we used average vigilance per x-axis unit (e.g. average vigilance for each wind speed, with a unit size of 0.1m/sec^2). These vigilance averages were taken from observations made throughout the summer, so a serial correlation due to vigilance changes over time was not possible. All datasets used in parametric tests were checked for normality visually using stem-and-leaf plots and normal probability plots, and statistically using the Shapiro-Wilk test (PROC UNIVARIATE).

Group-Size Effect Statistics

To test if global density affects vigilance, we first compared vigilance levels between populations using an ANOVA. Because vigilance levels differed among populations, we did a least-squares linear regression of the average vigilance of each population on population size.

In 2005, we counted the number of squirrels that were active at the time of the each observation to test if individuals change vigilance according to activity level on the meadow. To assess a within-population effect we did three tests: (1) least-squares linear regression of vigilance on number active for each population, (2) an ANCOVA of vigilance with number active as a covariate and population as a class variable (after checking for a covariate by group interaction and finding none), and (3) a regression of "population-free" vigilance residuals on number active to reveal the variation explained by any apparent general pattern. We generated the "population-free" residual data from an ANOVA of vigilance among populations. The first test assess whether different patterns are occurring on different populations. The second test provides a means to combine data from all of the meadows while still looking at a within-population effect, and the third provides an R^2 value for that data. On meadows with observations with over 14 active squirrels, the relationship between vigilance and number active was not linear. A decrease in vigilance followed by an increase is expected if the need to monitor conspecifics becomes necessary at a certain high density. Because this phenomenon seemed to occur at 14 active squirrels, we used observations that had number active below 14.

To assess an among-population effect of number active on vigilance, we averaged number active and vigilance for each viewing station on the marked meadows and regressed average vigilance on average number active for all viewpoints. On some meadows, multiple viewpoints were used. We used each viewpoint for the number-active analysis rather than each meadow because viewpoints differ in the amount of area visible due to topography, distance, and vegetation. Using the average number active for each viewpoint is a more accurate measure of what each squirrel may perceive at that location because many of the squirrels cannot detect all of the meadow. We used only meadows with marked squirrels for this analysis for two reasons: 1.) there was more consistency among viewpoints on marked populations because they were all from raised observation stands, and 2.) the squirrels on marked meadows were habituated to the presence of humans on the stands, whereas the unmarked squirrels vary in their habituation.

Model Testing

Because no pattern between population size and vigilance was apparent, we did not attempt to fit models to this data. Because the number active data showed a group-size effect, we used dilution and detection equations from Pulliam (1973) and Dehn (1990) to discover if one model fit our data better than the other:

DETECTION $$V = \frac{-\ln(1 - P_n)}{Tn}$$

DILUTION $$V = \frac{\ln[n/(n-1)]}{Tn}$$

Where V is vigilance, n is group size, P_n is probability that at least one member of the group detects the predator, T is the time it takes for the predator to make its final uncovered approach.

According to Elgar & Catterall (1981), T is in seconds, and is small for surprise predators such as cats and raptors. P_n will vary with group size and T, but seems to be high for ground squirrels, since at least one squirrel almost always calls before an attack (personal observation). Elgar & Catterall (1981) calculated a P_n values of 0.92 for flock sizes of 8 and T of 2 seconds. We allowed P_n to vary from 0.75 to 0.95, which we felt was a reasonable estimated range for the Columbian ground squirrels. We varied T within a range of 1 to 8 seconds. We used the PROC NLIN procedure in SAS (1999) to find the best fit of each equation to our data, This SAS procedure finds the curve of the model within the given parameter bounds that has the smallest sum of squares. If a model is a good fit to data, the mean of the residuals should be equal to zero ($\mu=0$). We used a t-test to determine if the mean of the residuals was equal to zero (in this case, $\mu=0$ is the null hypothesis, so $P>0.05$ indicates $\mu=0$). If the mean of residuals was equal to zero ($P<0.05$), we considered the model a good fit, if the mean was not zero ($P\leq0$), the model was considered a poor fit.

Hypothesis Testing

To discover if there was an effect of calling on vigilance, we did a t-test on vigilance between observations from 2005 when squirrels in the meadow were and were not calling. Because there was a significant difference, we did the tests twice for nearest-neighbour distance, number active, and population size, first with all observations and then with no-calling observations. The latter tests removed much variation within the data and caused trends to become clearer.

To test for an effect of nearest-neighbour distance, we used least-squares linear regressions on each meadow individually and all meadows combined using vigilance residuals, (see above). We also preformed an ANCOVA with population as a class variable and nearest-neighbour distance as a covariate to test for a relationship between vigilance and nearest-neighbour distance both within and among populations, in the same manner as number active. It is unlikely that a ground squirrel can see another ground squirrel at more than 40 m. At 40 m away, less than 20% of a 70 cm high board was visible to a 26 cm-high observer, which is alert ground squirrel height (MacHutchon & Harestad, 1990). Thus, it is reasonable to assume that a ground squirrel, a less obvious visual target than a 70 cm high board, would be even less visible to ground squirrels than the board. Therefore, nearest neighbours farther than 40 m were removed from these analyses.

We tested the effect of position in group within marked populations (except for the Hay Field population because this area was not mapped) by finding the location of each observed animal and using a map to find the distance to the edge of the meadow. We then regressed vigilance on distance to edge. Additionally, we used an ANCOVA and a regression of vigilance residuals as above.

Finally, we tested for an effect of factors that effect hearing on vigilance by using an EA-2010U La Crosse Technology Hand Held Anemometer (*address*) to measure the average wind speed during each observation on the marked meadows in 2005. These measurements were taken from the observation stands and were used as an index of ambient noise in the environment. We then did the same regression and ANCOVA procedures as above. All analyses were performed using SAS statistical software (1999). Significance determined by $\alpha=0.05$.

RESULTS

Group-Size Effect

Average proportion of vigilance on meadows ranged from 0.22 to 0.70 (Table 2). Although an ANOVA shows that vigilance among populations differed significantly ($F_{17,728}=5.39$, $P<0.01$), population size explained little of the variation (least squares linear regression: $R^2=0.07$, $F_{1,16}=1.25$, $P=0.28$). However, a group-size effect was evident when number of active squirrels during each observation was used rather than population size. We performed a regression of average vigilance on number active (between 1 and 14) for each marked population in 2005, and found a negative relationship within each meadow, although two of the five were not significant (Figure 1; Table v, Appendix).

An ANCOVA with number active as a covariate showed a significant effect of number active on vigilance within the marked meadows ($F_{1,320}=22.95$, $P<0.01$). Residuals of vigilance were obtained to remove the effect of different levels of vigilance among populations. These residuals were averaged for each number active. A regression of these average residuals on number active was performed in order to find the amount of variation in vigilance explained by group size within populations, while using data from all meadows. The regression showed that most of the variation in vigilance within populations was explained by number active ($F_{1,12}$=28.04, P=0.02, R^2=0.70). In a regression of average values among populations, vigilance decreased significantly with average number active ($F_{1,12}$=5.83, P=0.03, R^2=0.33).

Model Fitting

We found the model with the best fit for the data from each meadow. In all but one case, the detection model was a good fit (i.e. $\mu=0$; $0.12 \leq P \leq 0.39$, except Meadow B, where $\mu \neq 0$; P=0.02) and dilution was a poor fit ($P \leq 0.02$; Figure 2). The detection model also had the better fit to the "population-free" residuals of vigilance (detection: t=1.25, P=0.23; dilution: t=4.44, P<0.01; Figure 3) and to the average vigilance versus average number active from each stand (detection: t=0.43, P=0.68; dilution: t=10.56, P<0.01; Figure 4).

Calling

One or more squirrels were calling in 56.1% of my observations in 2005 (calling squirrels are those other than the focal squirrel). The mean proportion of time spent vigilant for observations with no squirrels calling was 0.35±0.01 (X±SE), while the mean vigilance for those observations with calling was 0.40±0.01, a significant difference (t_{456}=-2.62, P=0.01, with and without calling: N=226 and 232 respectively).

Nearest-neighbour Distance

Least-squares linear regressions of proportion of time vigilant on nearest-neighbour distance (excluding ≥40 m) were performed for all 14 meadows (meadows used in both 2004 and 2005 were analyzed separately, e.g. Meadow B 2004 was considered a different meadow than Meadow B 2005; see Table iv in Appendix for average nearest-neighbour distances). No regression was significant, except Meadow B 2005, which was marginally significant, but very little variation was explained by nearest-neighbour distance (F=4.23, 0.04, R^2=0.04). Ethrington showed negative serial correlation (Durbin-Watson: D=3.26, r_1=-0.64). The first-order auto-regression model had a regression R^2 of 0.07, lower than that of the original regression model (F=2.11, P=0.21, R^2=0.30), so the regression shows no effect of nearest-neighbour distance on vigilance before or after correction for serial correlation.

An ANCOVA with nearest-neighbour distance as a covariate showed no significant effect of nearest-neighbour distance ($F_{1,660}$=2.28, P=0.13). When residuals from all populations were regressed on nearest-neighbour distance, the regression was not significant ($F_{1,673}$=2.61, P=0.11, R^2=0.004).

To look for an among-population effect, we regressed average vigilance on average nearest-neighbour distance from each population. The regression was significant ($F_{1,11}$=8.59, p=0.01, R^2=0.44), however all of the significance was due to one outlying data point (outlier removed: $F_{1,10}$=0.77, P=0.4, R^2=0.07). Also, among populations average nearest-neighbour distance and average number active were negatively correlated ($r=-0.72$, $P<0.01$). Nearest-neighbour distance and number active are not correlated within meadows except on meadow C ($0.18 \leq P \leq 0.64$ for all meadow except C. C: $r=-0.33$, $P<0.01$; Table vi, Appendix).

Distance to Edge Effect

We were able to measure the focal animals' distances to the edge of the meadow on three meadows in 2004 and four meadows in 2005. Within-meadow regressions of vigilance on distance to edge showed only one significant result: Meadow B in 2004 ($0.24 \leq P \leq 0.76$ for all meadows except B. B: $F=6.2$, $P=0.02$, $R^2=0.80$; Table vii, Appendix). In 2005, Meadow B did not have a significant relationship between distance to edge and vigilance.

ANCOVA results showed distance had a slightly significant effect ($F_{1,571}=4.33$, $P=0.04$; class variable=populations, covariate=distance to edge). There may be a slight negative trend between vigilance and distance to edge, or the significance could be due to the high sample size ($N=579$). Using data from all of the above meadows, a regression of residuals of vigilance (to remove the effect of population differences) on distance to edge showed that distance to edge explained almost none of the variation in vigilance ($F_{1,577}=2.52$, $P=0.11$, $R^2=0.004$; Figure 2).

Wind Speed Effect

The effect of wind speed on vigilance was not the same on all populations (Table 2). Vigilance was averaged at each wind speed (unit=0.1m/s). Although only one of the regressions was significant, the R^2 values of all but one were above 0.18, meaning that a considerable amount of variation in vigilance was explained by wind speed, but the relationship was not the same on all meadows. The insignificance of the regression in some cases may be due to the small sample sizes. When the meadows were pooled and the same regression was done, the regression was significant and positive ($F_{1,19}$=8.34, P=0.01, R^2=0.31). An ANCOVA was not an appropriate test here because the slopes of the regression lines for the various populations were significantly different. A regression of the residuals of vigilance on wind speed approached significance and was positive ($F_{1,19}$=3.84, P=0.07, R^2=0.17). The overall pattern of the effect of wind speed is difficult to ascertain from these results; some of the results show a trend for increased vigilance as wind speed increases, but other result give the opposite pattern. However, we noticed that fewer squirrels ate at high wind speeds, preferring to stand alert or go below ground. Because we used only feeding squirrels as focal animals, this made obtaining data at high wind speeds difficult. Although the statistical results for wind speed are equivocal, the squirrels' unwillingness to eat lends support to the idea that squirrels increase their vigilance at higher wind speeds.

DISCUSSION

Group-Size Effect

Columbian ground squirrels showed the expected group-size effect on vigilance. The results of the regressions of vigilance on population size and number of individuals active suggest that ground squirrels actively changed their vigilance according to the number of squirrels that were active, rather than using a rule-of-thumb based on population size. However, it is possible that there was an effect of population size on individual vigilance that may only be detectable with an extremely large number of meadows or with experimental manipulation.

The trend for increased vigilance at numbers higher than 13 has two possible explanations: 1) at some high group size, individuals must increase vigilance in order to monitor conspecifics or 2) at high group sizes, the likelihood of there being a squirrel calling increases simply because of the number of squirrels, and calling increases vigilance. However the trend was present even when observations taken when squirrels were calling were excluded, so the former explanation is more likely.

Dilution vs. Detection

Our data fit the detection model better than the dilution model. The differences in fits are visually evident on graphs, in addition to the differences in the sum of squares.

The comparison of our results to the predictions of the two proposed mechanisms for the group-size effect lends support to the detection hypothesis. Neither nearest-neighbour distance, nor distance to the edge of the meadow was related to vigilance. Alarm calls did affect vigilance, and although some results are conflicting, wind speed may have also affected vigilance. Our purpose was not to propose that dilution is not in effect at all in the Columbian ground squirrels, only that detection has a greater influence that dilution.

Squirrels were calling in the majority of our observations (56.1%). Calling is clearly an important activity in ground squirrel life. Although it may serve purposes other than anti-predator behaviour (such as territorial defence), calls are almost always given in response to possible predators (MacWhirter, 1992). While the caller's primary purpose may or may not be to warn conspecifics depending on the call, (Sherman, 1977; Sherman, 1985) it would certainly be advantageous for group members to use calls as warnings. Many studies show this to be the case in sciurids (Armitage, 1962; Carey & Moore, 1986; Hanson & Coss, 2001; Hare & Atkins, 2001). My results agree with these previous studies, as seen in the significant difference between vigilance when group mates are and are not calling. This result lends support to the detection hypothesis, as warning from group mates is an essential component of the hypothesis; however this result alone does not preclude the effect of dilution.

Many studies have found an effect of nearest-neighbour distance on vigilance (Olympic marmot: Barash, 1973; Yellow-footed rock wallaby: Blumstein et al., 2001; Red-billed choughs: Rolando et al., 2001; Tamarins: Smith et al., 2004; Teal: Poysa, 1994). However, nearest-neighbour distance does not correlate with vigilance in

Columbian ground squirrels within meadows. The significant regression between average vigilance on average nearest-neighbour distance among meadows disappears when a single outlier was removed. However, the validity of removing of this outlier may be moot, because average nearest-neighbour distance and average number active are correlated among meadows. Considering this correlation and that there is an among-population effect of number active on vigilance, the most plausible explanation of the apparent among-population effect of nearest-neighbour distance is that it is an artefact of its correlation with number active, rather than an actual effect of nearest-neighbour distance.

There are many studies that found a relationship between distance to the edge of the group and vigilance, including in several sciurids (Black-tailed prairie dog: Hoogland, 1979; Yellow-bellied marmots: Armitage, 1962; Black-tailed prairie dog: McDonald, 1998) and non-sciurids (Impalas: Matson et al., 2005; Starling: Jennings & Evans, 1980; Rock dove: Phelan, 1987). Distance to edge may weakly correlate with vigilance in Columbian ground squirrels, but the likelihood of any biological significance is small, as seen in the small R^2 of the regression ($R^2 = 0.004$).

What explains the discrepancy between Columbian ground squirrels and these other species with respect to nearest-neighbour distance and distance to edge? While differences between Columbian ground squirrels and vastly different species such as starlings may be expected, the difference between Columbian ground squirrels and other sciurids is more puzzling. We believe the discrepancy can be explained by the difference between Columbian ground squirrel social groups and those of other species. Columbian ground squirrels are individually territorial, while the above species (both sciurid and non-sciurid) are not, or are only territorial to a limited extent. The sciurids listed above were given high social grades by Michener (1983). These social grades represent social groups consisting of family clusters of one male with many females. Individuals are only territorial toward other families, not individuals within their own family. Compared to these species, Michner assigned Columbian ground squirrels a lower social grade because each squirrel defends a territory. Female kin often have adjacent territories, forming kin groups, but they do not fully share territories (King, 1989b). We found the average nearest-neighbour distance to be 8.8 m, while means given in or estimated from the studies of other species tended to be lower (Olympic marmots: 3.2 m in July, 5 m in August (Barash, 1973), red-billed choughs: estimated 4.9 m (Rolando et al., 2001), saddleback tamarins: estimated between 2-3 m, and moustached tamarins: estimated between 3-5 m (Smith et al., 2004)). Although the previous inter-species comparisons may be questionable due to factors constraining neighbour distances, such as size, the Columbian ground squirrels are smaller than or similar in size to these species. Therefore, one would predict them have comparable or smaller neighbour distances than these species, in contrast to the observed pattern. Thus Columbian ground squirrels are effectively seldom near each other compared to species in which the dilution effect was present, precluding the effective use of the dilution effect through domain-of-danger reduction.

Although the results of the effects of wind speed were mixed, an overall positive relationship between wind speed and vigilance existed. The personal observations that the squirrels stopped feeding at high wind speeds also support the idea that they consider increased wind speed to be a danger. Similarly, McDonald (1998) found that black-tailed prairie dogs increased vigilance and mound use when the prevailing wind was strong and from the centre of the colony, making it difficult for individuals on the edge of the colony (downwind) to be heard by those closer to the centre (upwind). To clarify these effects, an experiment involving introduction of ambient noise would be useful.

In conclusion, in Columbian ground squirrels the group-size effect on vigilance appears to depend more on collective detection than on risk dilution. This conclusion is in contrast to many other studies. We propose that group type and information-transfer type may be important determinants of which mechanism is in effect in any particular species. Groups where individuals are more isolated, due to territoriality or other reasons, and those that have active transfer of predator information are likely to be more reliant on collective detection. Future research should attempt to include a more diverse range of group types and information transfer types when studying the mechanisms of the group-size effect on vigilance.

Table 1. Predictions of the dilution and detection hypotheses

	Dilution predictions	**Detection prediction**
Nearest-neighbour Distance	Vigilance decreases as nearest-neighbour distance increases	Vigilance is unaffected by neighbour distance
Position in group	Vigilance decreases as distance from group edge increases	Vigilance has no relationship to position
Alarm calls	Unimportant/infrequent	Alarm calls accompany predator sightings and vigilance of hearers increases
Response to factors that limit hearing	Little/no response	Increased vigilance

Table 2. Regression results of the wind speed effect

Meadow	**F**	**P**	**R^2**	**Slope**	**N**
B	0.03	0.87	0.00	-0.06	16
C	3.03	0.10	0.18	-0.11	16
D	3.91	0.08	0.30	-0.11	11
Hay Field	2.02	0.19	0.20	0.14	10
4km	6.91	0.02	0.27	0.09	20

Figure 1. Regressions of proportion of time spent vigilant on number active for meadows B, C, D, HF, and 4km for number active below 15. The negative slopes indicate a decrease in vigilance as number active increases.

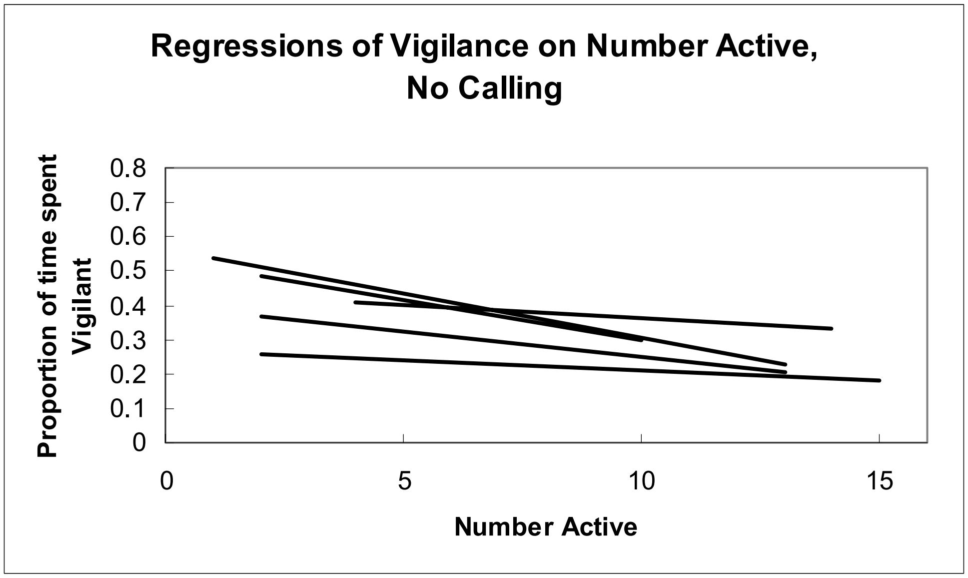


Figure 2. Best fits of the dilution and detection to the observed data on each meadow.

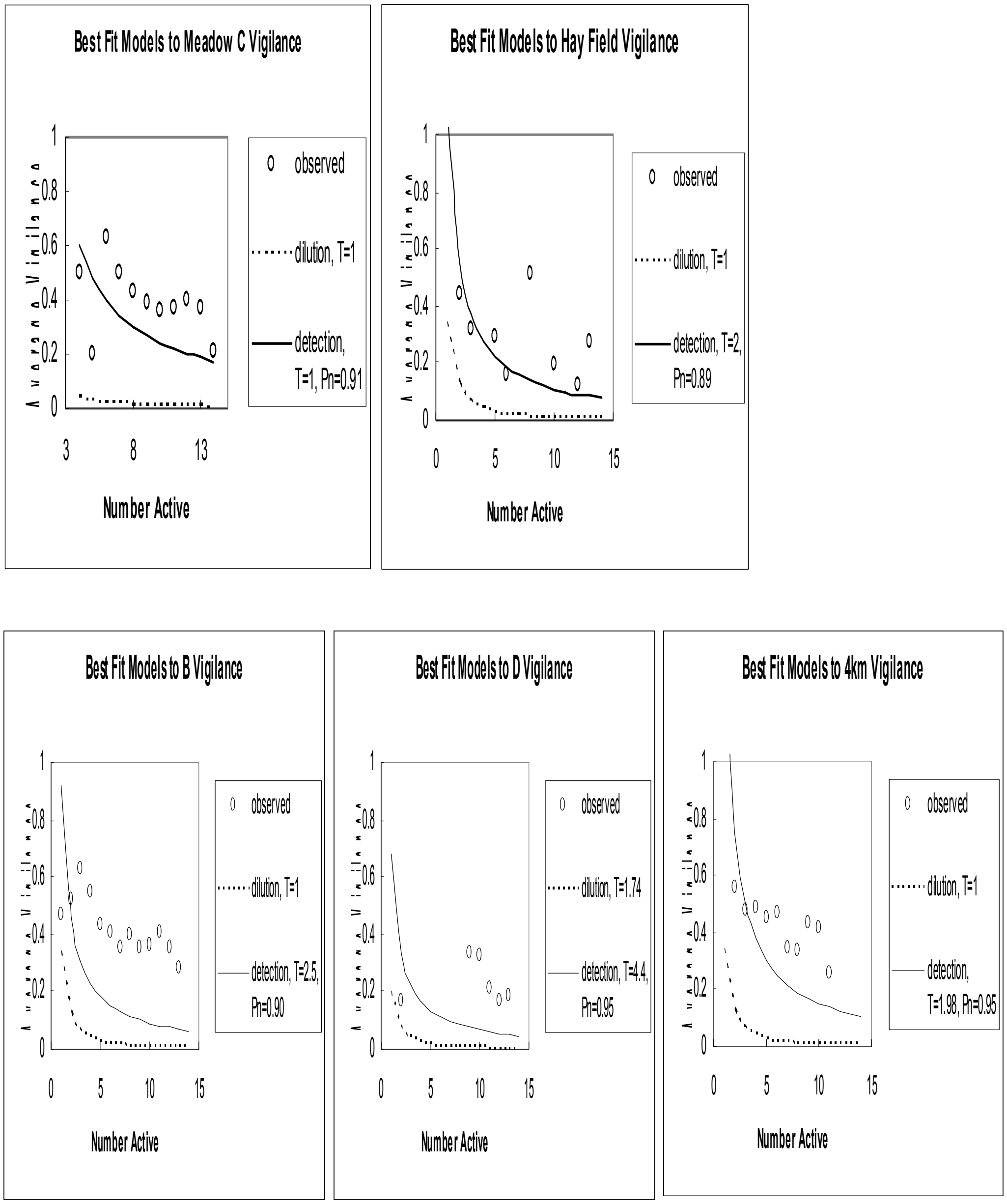


Figure 3. Best fits of the two models to average residuals of regression.

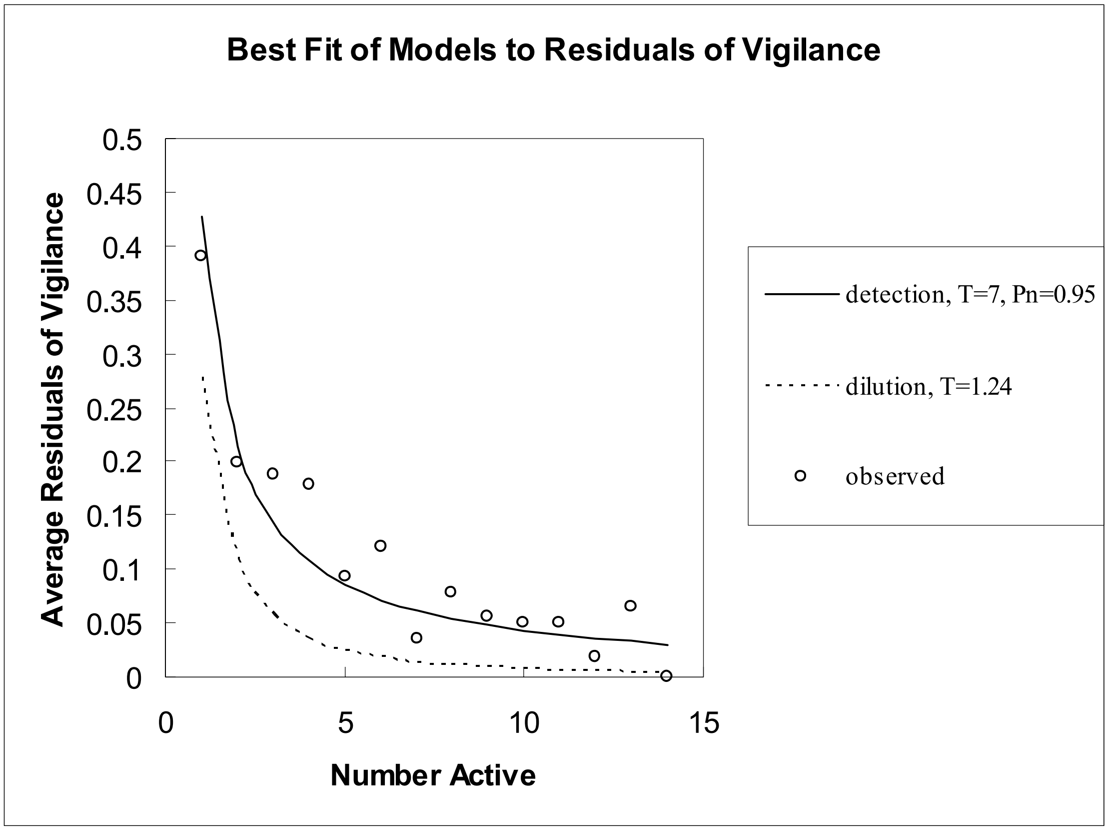


Figure 4. Best fit of the two models to average vigilance from each viewpoint on the five marked populations.

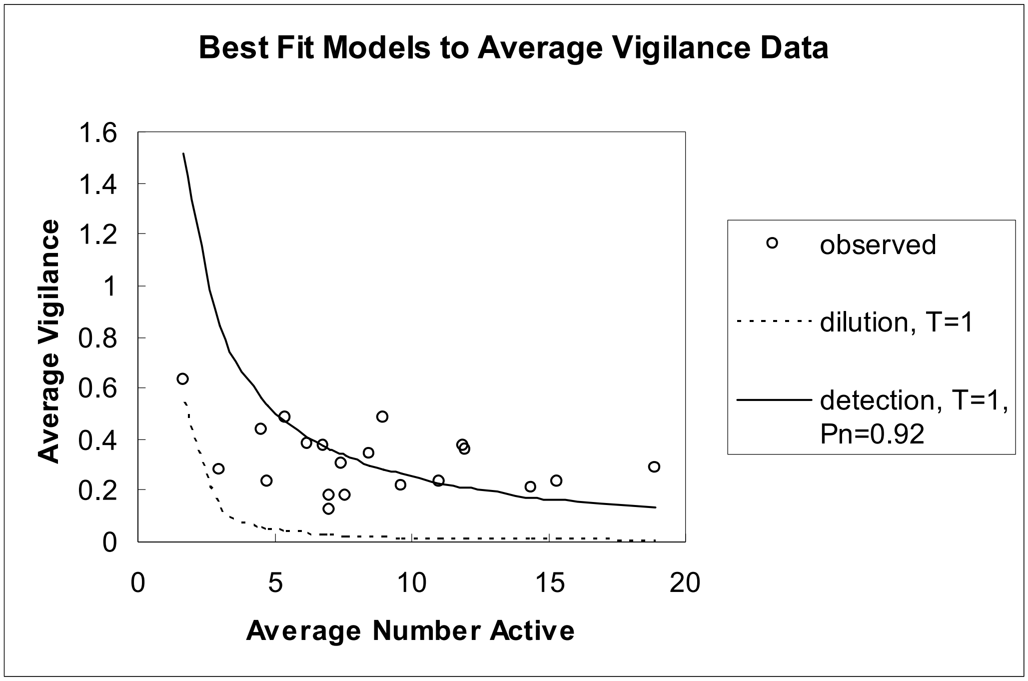
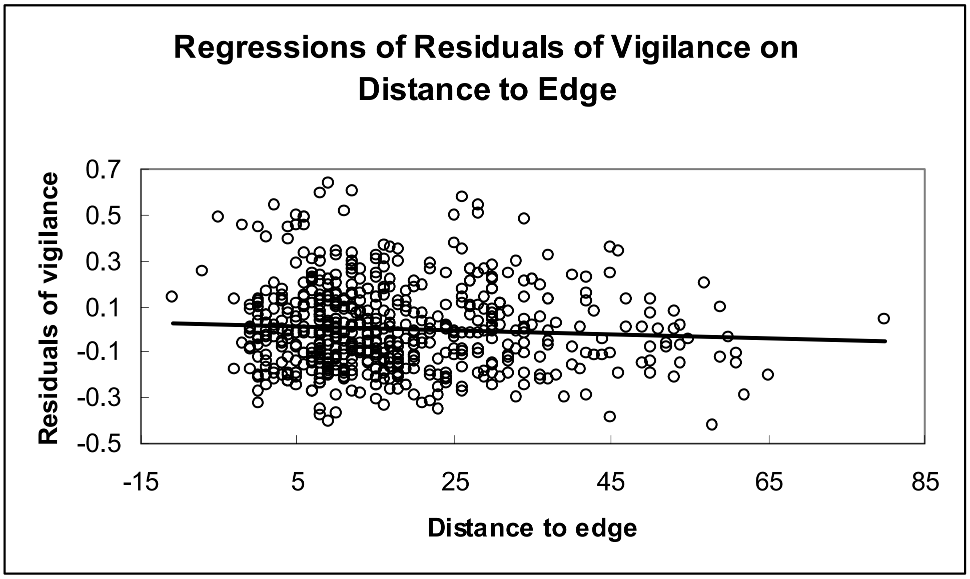


Figure 5. Regression of residuals of vigilance on distance to edge ($F_{1,577}$=2.52, p=0.11, R^2=0.004).



CHAPTER TWO

MOM'S NOT LOOKING: FEMALES WITH ADULT OFFSPRING ARE LESS VIGILANT IN COLUMBIAN GROUND SQUIRRELS

Anti-predator vigilance, a vital behaviour in prey species, can be affected by many factors. Few studies have examined the effect of nearby kin on vigilance. In this study, I observed Columbian ground squirrel vigilance for effects of kinship. There are three possible effects of kinship on vigilance: (1) an increase in vigilance, suggesting nepotism in vigilance behaviour, (2) a decrease in vigilance, indicative of either social parasitism or commensalism of kin's vigilance, or (3) no effect on vigilance when kin are present. With one exception, I found that the presence of kin had no effect on vigilance. The exception was that females with adult offspring showed significantly decreased vigilance. Because offspring did not increase vigilance in response to their mother's decreased vigilance, and there were no other obvious costs for the offspring, this seems to be a case of commensalism. It is unexpected that mothers would take advantage of their offspring's vigilance, considering that in other behaviours they act nepotistically. Costliness is suggested as a possible reason for differences in the social exchange (nepotistic versus commensal) of different behaviours.

INTRODUCTION

Vigilance, scanning the surroundings for predators, is a widespread anti-predator behaviour of prey species and can be influenced by many factors (Lima & Dill, 1990). The presence of nearby kin is a rarely studied factor that has been shown to affect vigilance in some species. Siberian jay parents nepotistically increased their vigilance when retained young (mature offspring that remain with the parents to help raise siblings) were present (Griesser, 2003). Similarly, barnacle geese parents increased their vigilance in the winter and autumn if their gosling(s) were with them, however there seemed to be a mutual benefit because parents were also more successful the following year than those without young (Black & Owen, 1989). In Columbian ground squirrels (*Spermophilus columbianus*), MacWhirter (1991) found that lactating females were vigilant for the same amount of time during a foraging bout as nonparous females, but overall spent less time being vigilant when time outside of foraging bouts was included. Gestating and lactating females spent more time foraging than nonparous females. These results are most likely due to the increased need for food of a parous female. However, MacWhirter(1991) did not consider the number of nearby kin of the females, which could be a confounding factor. Another study by MacWhirter (1992) found that parous females were likely to give alarm calls at a stuffed badger. Nonparous females rarely called at the terrestrial predator, regardless of whether their mother and/or sister were nearby. MacWhirter (1992) did not indicate if he classified both littermate and non-littermate sisters as kin, which may be important considering the more recent finding that juvenile Columbian ground squirrels discriminated on the basis of familiarity (shared natal burrow) rather than kinship proper (Hare & Murie, 1996). If familiarity discrimination continues throughout life, differential behaviour toward uterine (mother or littermate) kin would be expected. MacWhirter's (1991; 1992) two studies suggest that increased vigilance is not part of parental care, but risky alarm calling is, and that nepotistic alarm calling is only directed toward offspring. However, because familiarity was not considered in his studies, the possibility of kin-differential vigilance behaviour remains.

Loughry's (1993) study in another sciurid, black-tailed prairie dogs (C*ynomys ludovicianus*), found that parous females were the least vigilant of the reproductive groups (i.e. fathers, non-fathers, and non-parous females), and that they increased vigilance over the course of the season. Loughry suggested that the temporal increase in vigilance may indicate maternal investment in the form of watching for predators that might attack her young, or that it could be a response to decreased energetic demands after weaning of the pups. He speculated the latter because parous females did not increase vigilance above that of other individuals after weaning, but only up to similar levels. MacWhirter's (1991; 1992)and Loughry's (1993) studies suggest that parous females do not nepotistically increase vigilance for young, but rather that the energetic demands of raising young cause parous females to decrease their vigilance.

MacWhirter's and Loughry's studies are the only studies that give insight into kinship effects for vigilance in ground-dwelling sciurids; however, there are studies of nepotistic alarm calling in ground squirrels. Sherman (1977) found that alarm calls given in the presence of terrestrial predators were nepotistic in Belding's ground squirrels even though they are dangerous to give (callers were chased or stalked more often than non-callers). However, in a later study, Sherman (1985) found alarm calls elicited by aerial predators to be self-preservative rather than nepotistic. This unexpected contrast makes the question of the effects of kinship on vigilance all the more intriguing. One would predict a positive relationship between vigilance and number of nearby uterine kin if nepotistic vigilance is occurring in Columbian ground squirrels. Alternatively, there could be social parasitism of nearby kin in vigilance, reaping the benefit of others' vigilance and creating costs for kin. Another possibility is commensalism, which would be indicated if an individual benefited from its kin's vigilance by decreasing its own, but at no cost to the kin. If an individual can depend on her relatives to watch out for her and to warn when danger is present, she may decrease her vigilance in the presence of her kin. Parasitic and/or commensal vigilance may be more common in offspring than in parents or siblings.

I used focal animal sampling to measure vigilance in a population of Columbian ground squirrels with known familial relationships for two summers to determine if nearby kin in the population affected vigilance. Additionally, in the second summer I noted whether or not the focal animals' kin were active (visible above ground) during observations to evaluate whether the activity of kin was important to vigilance.

METHODS

Columbian ground squirrels are appropriate mammals for studying many aspects of vigilance because they live in alpine and sub-alpine meadows where a number of individuals are visible to an observer from a single vantage point. The animals forage during the day and have an easily observable vigilance behaviour: they raise their heads and pause foraging (Arenz & Leger, 2000). Columbian ground squirrels are preyed upon by many carnivores including badgers, goshawks and coyotes. Females often mate with more than one male and multiple paternity within a litter is common (Hare & Murie, 1996). In this study, I used adult and yearling females and yearling males, but excluded adult males because in most cases the identity and number of their offspring was unknown due to their mating system.

I observed a population of Columbian ground squirrels in the Sheep River Wildlife Sanctuary in Kananaskis Country Recreation Area in south-western Alberta, Canada during the summers of 2004 and 2005. This population has been tracked for 20 years, so the age, sex, and kinship for each squirrel are known. Observations were taken from raised platforms that have been on each meadow for several years. I opportunistically observed a foraging squirrel for five to ten minutes and timed its vigilance, defined as lifting the head above the shoulders and pausing all activity except chewing. All squirrels were uniquely marked on the back with hair dye for individual identification. In 2005 I searched for the focal animal's relatives before beginning the observation bout and recorded the number of relatives that were active. Also in 2005, I recorded the number of animals visible during the observation.

I used several statistical tests to evaluate the effects of kin on vigilance. Rank-sum tests were used to test if vigilance was different between animals with and without living relatives in the population for each year separately and both years pooled. I tested whether the activity or inactivity of kin had an effect on vigilance by noting if the focal animal's uterine kin were above ground during each observation. A rank-sum test was performed on those animals with and without active kin in 2005. I used a Kruskal-Wallis test to see if there was a difference in vigilance among animals with different numbers of living relatives. A Kruskal-Wallis test was also used to see if the type of relationship (e.g.

mother, offspring, and sister) affected vigilance. I performed post-hoc tests (Tukey, Bonferroni, and protected LSD) to look for pair-wise differences among groups. Because females that had offspring had consistently different vigilance according to the protected LSD test, I used a rank-sum test to find if females with adult offspring (FWAO) were consistently less vigilant than those with other kin. I then performed a Satterthwaite t-test (due to unequal variances) to look for a difference between number of squirrels visible around FWAO and others to see if the difference in vigilance was due to a group-size effect rather than kinship. A rank-sum test was used to test for differences in vigilance between females with both adult offspring and young-of-the-year compared to females without adult offspring but with young-of-the-year. Finally, to see if age-related differences in vigilance were causing the difference in vigilance between FWAO and others, I performed a Spearman correlation between age and proportion of time spent vigilant on each year and pooled years to see if animals of different ages had different vigilance. I then performed a rank-sum test between ages of FWAO and others for each year and the two years pooled.

Rank-sum tests were used instead of t-tests because of violations to t-tests assumptions of normality. Kruskal-Wallis tests were used instead of ANOVAs because many of the groups had severe outliers and some did not have equal standard deviations. All statistical tests were performed using SAS Statistical Software (SAS, 1999).

RESULTS

No significant difference in vigilance was found between squirrels with and without living relatives in 2004, 2005, or when both years were pooled, (2004: $\square_{\text{with}}=0.40$, $\square_{\text{without}}=0.45$, Z=0.82, P=0.41; 2005: $\square_{\text{with}}=0.41$, $\square_{\text{without}}=0.39$, Z=-0.12, P=0.91; pooled: $\square_{\text{with}}=0.41$, $\square_{\text{without}}=0.42$, Z=0.33, P=0.74). A rank-sum test showed no significant difference in vigilance between squirrels with and without active kin nearby in 2005 ($N_{\text{with}}=34$, $N_{\text{without}}=65$, Z=0.70, P=0.94).

When vigilance and the number of kin were analyzed using Kruskal-Wallis tests, no significant differences in vigilance were found (2004: $\div^2_2=3.43$, P=0.18; 2005: $\div^2_3=1.67$, P=0.18; pooled: $\div^2_3=4.63$; P=0.20). No significant differences in vigilance were found among individuals with different types of active kin (Kruskal-Wallis: $\div^2_5=4.83$, P=0.44). However, there were significant differences in vigilance between types of living kin (2004: $\div^2_4=11.79$, P=0.02; 2005: $\div^2_6=12.72$, P=0.05; pooled: $\div^2_7=16.99$, P=0.02) (Fig 1).

Post-hoc tests that control for experiment-wise Type I error (Tukey and Bonferroni tests) did not show any significant pair-wise differences in means except in 2004 between individuals with both a mother and a sister and those with 2 offspring. However, a protected LSD (which does not control for experiment-wise Type I error) shows several significant differences between groups for 2004, 2005, and both years pooled (Table 1). The groups that are most consistently significantly different from other groups are those that have offspring, i.e. females with adult offspring (FWAO) may be less vigilant than other groups. Using rank-sum tests, I looked for a difference in the vigilance of FWAO compared to the other groups. I found that they were significantly different in 2004 ($\square_{\text{FWAO}}=0.31$, $\square_{\text{others}}=0.44$, $Z=-2.71$, $P=0.01$), and when years were pooled ($\square_{\text{FWAO}}=0.36$, $\square_{\text{others}}=0.44$, $Z=-2.62$, $P=0.01$) (Fig. 2), but not significantly different in 2005 ($\square_{\text{FWAO}}=0.39$, $\square_{\text{others}}=0.42$, $Z=-1.07$, $P=0.28$), although the trend for FWAO to be less vigilant remained. I did not find that offspring with living mothers had different vigilance than others (2004: $\square_{\text{offspring}}=0.46$, $\square_{\text{others}}=0.41$, $Z=1.48$, $P=0.14$; 2005: $\square_{\text{offspring}}=0.43$, $\square_{\text{others}}=0.39$, $Z=1.18$, $P=0.24$; pooled: $\square_{\text{offspring}}=0.44$, $\square_{\text{others}}=0.40$, $Z=1.69$, $P=0.09$).

I searched for several confounding factors. To exclude the possibility that FWAO simply had more squirrels around them, causing a decrease in vigilance due to group size, I performed a t-test between number of squirrels visible in observations of FWAO and number of squirrels visible in observations of others. I found no significant difference ($\square_{\text{FWAO}}=7.14$, $\square_{\text{others}}=7.54$, Satterthwaite $t_{79.8}=-0.783$, $P=0.47$). Additionally, I tested for a difference between FWAO and females without adult offspring due to effects of raising young. Although all of the FWAO were also parous during the observed years, there were many females without adult offspring that were parous (percent of females without adult offspring that were parous: 2004: 81.8%; 2005: 36.4%; pooled: 57.5%). I compared the vigilance level of these two groups and found that FWAO raising young-of-the-year were significantly less vigilant than females with young-of-the-year but no adult offspring (2004: $\square_{\text{parous/FWAO}}=0.31$, $\square_{\text{parous/non-FWAO}}=0.45$, $Z=-2.57$, $P=0.01$; 2005: $\square_{\text{parous/FWAO}}=0.39$, $\square_{\text{parous/non-FWAO}}=0.49$, $Z=2.10$, $P=0.04$; pooled: $\square_{\text{parous/FWAO}}=0.36$,

$\square_{\text{parous/non-FWAO}}=0.46$, Z=-3.04, P=0.002) (Fig. 3). I did not find a pattern of lower vigilance for parous females compared to non-parous females when kinships were disregarded (2004: $\square_{\text{parous}}=0.42$, $\square_{\text{non-parous}}=0.51$, Z=1.56, P=0.12; 2005: $\square_{\text{parous}}=0.43$, $\square_{\text{non-parous}}=0.37$, Z=-1.29, P=0.20; pooled: $\square_{\text{parous}}=0.42$, $\square_{\text{non-parous}}= 0.40$, Z=-0.53, P=0.60). Finally, I found a significant difference in ages between FWAO and others (Rank-sum tests: 2004: $\square_{\text{FWAO}}=6.4$, $\square_{\text{others}}=3.6$, Z=4.71, p<0.0001; 2005: $\square_{\text{FWAO}}=5.6$, $\square_{\text{others}}=2.1$, Z=7.8, p<0.0001; pooled: $\square_{\text{FWAO}}=5.8$, $\square_{\text{others}}=2.8$, Z=7.91, p<0.0001). If squirrels become less vigilant over time, the difference in age between FWAO and others could be causing the observed difference. To test this I found the Spearman correlation coefficient between age and vigilance for each year and pooled years. Only the correlation in 2004 was significant (2004: r=-0.27, P=0.02; 2005: r=-0.08, p=0.45; pooled: r=-0.14, p=0.07), but only marginally significant when the outlying data point of a 10-year-old individual is removed (2004: r=-0.24, p=0.05; pooled: r=-0.09, p=0.24; figure 4).

DISCUSSION

The idea of nepotistic vigilance, especially increased vigilance in mothers for the benefit of offspring, stems from the findings of nepotism in alarm calls. However, nepotism did not occur in the vigilance of Columbian ground squirrels, as seen in the result that individuals with kin (any number or type) did not have significantly higher vigilance than those without kin. In general, parasitism and commensalism does not seem to be occurring either, as seen in the lack of difference in vigilance between animals with different numbers of kin. This implies that the ground squirrels do not depend on kin any more or less for vigilance than they depend on non-relatives.

The single group that may have different vigilance than others is females with adult offspring. Surprisingly, FWAO had lower vigilance than other groups. Although all of the FWAO were parous, there were females without adult offspring that were parous as well, and their vigilance was significantly higher than that of the parous FWAO, discounting young-rearing alone as an effecter of vigilance. MacWhirter's (1991) and Loughry's (1993) studies showed lower overall vigilance in parous females, which would be expected from the increased energetic demands of gestation and/or lactation. MacWhirter (1991) also found no difference in vigilance during feeding bouts between parous and non-parous females. Similarly, I found no difference in vigilance between parous versus non-parous individuals (regardless of kinships) when I measured vigilance during feeding bouts. These patterns suggest that parity had no effect on vigilance during feeding bouts. Therefore, the decreased vigilance of FWAO does not seem to be caused by the demands of raising young. The difference in vigilance of FWAO is not explained by the number of squirrels active either, since the number active is not different for FWAO and others. If squirrels decrease their vigilance as they get older, this may be causing the difference in FWAO vigilance compared to others, because they were significantly older. In 2004, there was a significant correlation between age and vigilance, but it may have been due to an outlying data point. When this outlier is removed, the correlation is marginally significant. Even if the difference in FWAO and others was caused by age differences in 2004, age differences do not explain the difference in 2005 or the general trend from the two years pooled. Hence, I was unable to find any factor that explained the observed patterns better than kinship.

The above patterns indicate that mothers may opportunistically benefit from their adult offspring's vigilance. However, offspring do not respond to their mothers' decreased vigilance; offspring show no difference in vigilance compared to others, lending partial support to the commensal interaction hypothesis. The difference between FWAO and adult offspring vigilance cannot be explained by the fact that FWAO may have many offspring to depend on while offspring can only have one mother. This would suggest that it is simply a numbers game, i.e. number of kin should affect vigilance, but this pattern was not shown. If number of kin was the reason for the reduced vigilance of FWAO, individuals with a mother and two sisters should show similar vigilance to individuals with three offspring, but these two groups are in fact the most different in their vigilance: individuals with a mother and 2 sisters have the highest vigilance, while those with three offspring have the lowest. An experimental study using removal of adult offspring is needed to solidify a causal link between the presence of adult offspring and low vigilance.

Although the offspring do not show a cost in the form of increased vigilance, it is not possible to definitively determine whether the lower vigilance of FWAO is parasitic or commensal in this study, because the offspring may have a cost other than vigilance. The possible parasitism or commensalism by FWAO of their offspring's vigilance is contrasted by their nepotism in risky alarm calls when terrestrial predators are present for young-of-the-year (MacWhirter, 1992). There are no studies of Columbian ground squirrels that show this same nepotism for adult offspring, but Belding's ground squirrels do exhibit nepotism for adult offspring (Sherman, 1977), providing support to the possibility that Columbian ground squirrels may as well. Future studies should investigate vigilance and alarm calling in concert to further elucidate the patterns that are occurring. Although a link between alarm calling and vigilance seems intuitive, if decreased vigilance by FWAO is due to parasitism or commensalism and alarm calling is nepotistic, these two anti-predator behaviours may be quite different in their effectiveness and/or costs. They may therefore be "traded" socially in different ways. For example, alarm calls at terrestrial predators increase the likelihood of capture for callers compared to non-callers, but the increase is from 4% to 8% (Sherman, 1985). Thus, calling is riskier than not calling, but overall the cost may remain minimal in comparison to the benefit, since most callers are not captured and their relatives are likely to escape as well. There are no studies on capture rates of more and less vigilant squirrels, but a known cost of increasing vigilance is decreased time available for other activities such as foraging. The decreased vigilance of parous females suggests that there are situations in which vigilance must be sacrificed in order to meet nutritional requirements. The benefit of increased vigilance is increased predator detection. It is unclear whether this benefit is greater than the cost of decreased time to feed. When living in a social environment, it makes sense that resources that are costly are more likely to be taken from others while those that are inexpensive may be given. Perhaps increased vigilance is more costly than alarm calls, making the former the subject to parasitism or commensalism and the latter appropriate for nepotism.

In conclusion, the presence of kin had little effect on vigilance levels in Columbian ground squirrels. The single exception was a reduction in vigilance by females with adult offspring. This decrease may be a form of social parasitism, where mothers are taking advantage of their adult offspring's vigilance at their offspring's expense, but is more likely commensalism because the offspring do not show a difference in their vigilance level despite their mother's decreased vigilance. An empirical study that removes adult offspring is needed to discover if adult offspring are the cause of mothers' decreased vigilance. Possible costs to the offspring caused by mothers' decreased vigilance should also be sought to determine whether commensalism or parasitism is occurring. Additionally, studies that simultaneously compare the costs of behaviours that are subject to nepotism, commensalism, and parasitism could shed light on why these behaviours have different social exchanges.

Table 1. Pair-wise significant differences shown with protected LSD test.

Year	**Significant pair-wise differences, protected LSD**
2004	Mother/sister-1 offspring Mother/sister-2 offspring Mother-2 offspring None-2 offspring
2005	Mother/2 sisters-mother/sister Mother/2 sisters-3 offspring Mother/sister-mother Mother-3 offspring 1 offspring-3 offspring
pooled	Mother/2 sisters-2 offspring Mother/2 sisters-3 offspring Mother-2 offspring Mother-3 offspring None-2 offspring None-3 offspring

Figure 1. Boxplots of proportion of time spent vigilant versus type of kin living for both years pooled. Whiskers indicate maximum and minimum, filled triangle=median, boxes indicate first and third quartiles.

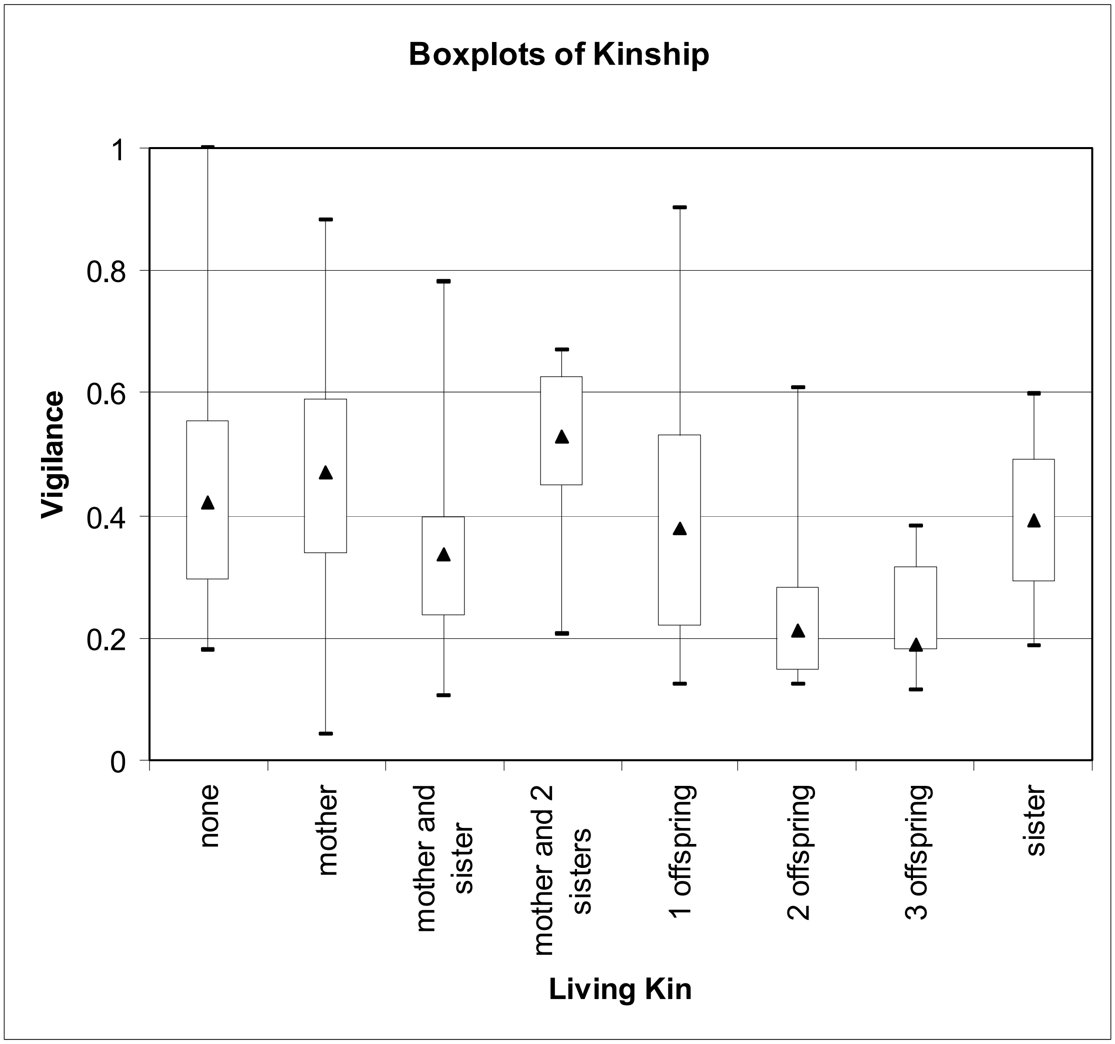


Figure 2. Differences in vigilance levels of females with adult offspring and others for pooled years.

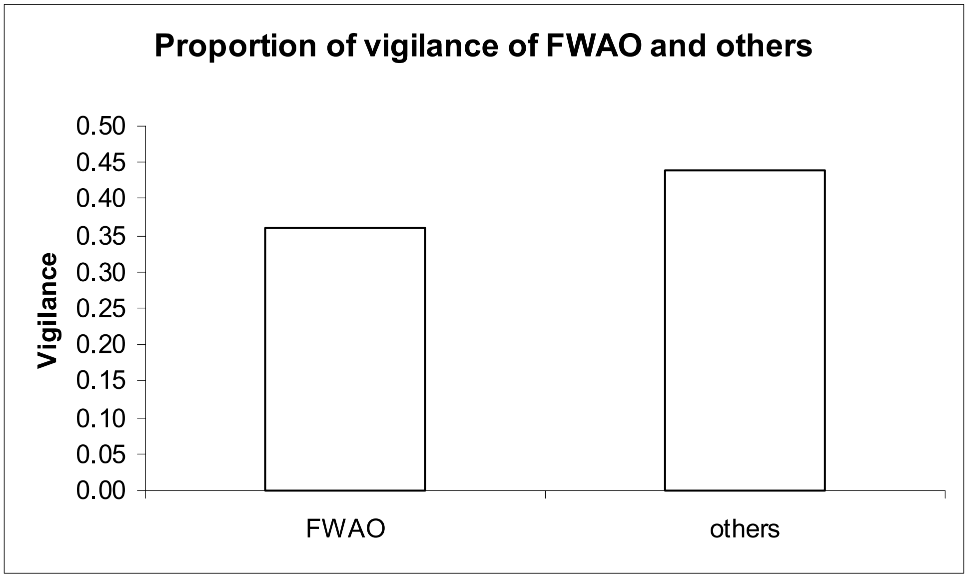


Figure 3. Difference in vigilance levels between females with young-of-the-year and adult offspring and females with young-of-the-year but no adult offspring for pooled years.

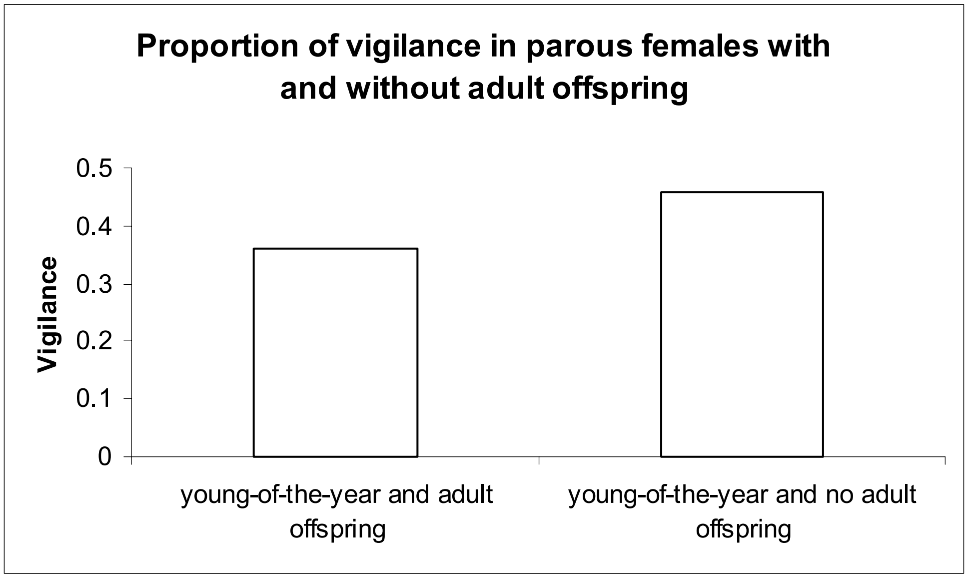
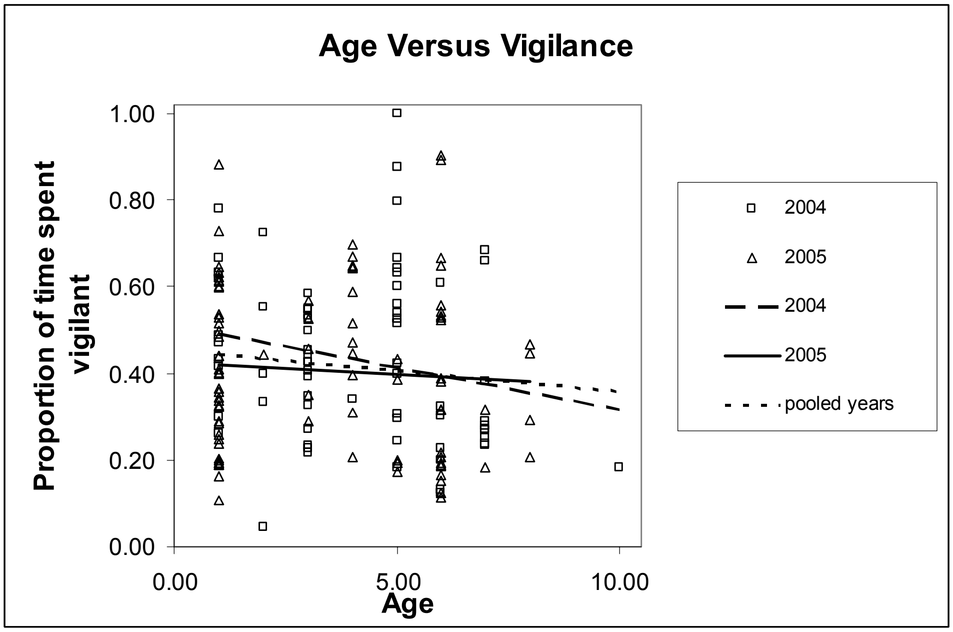
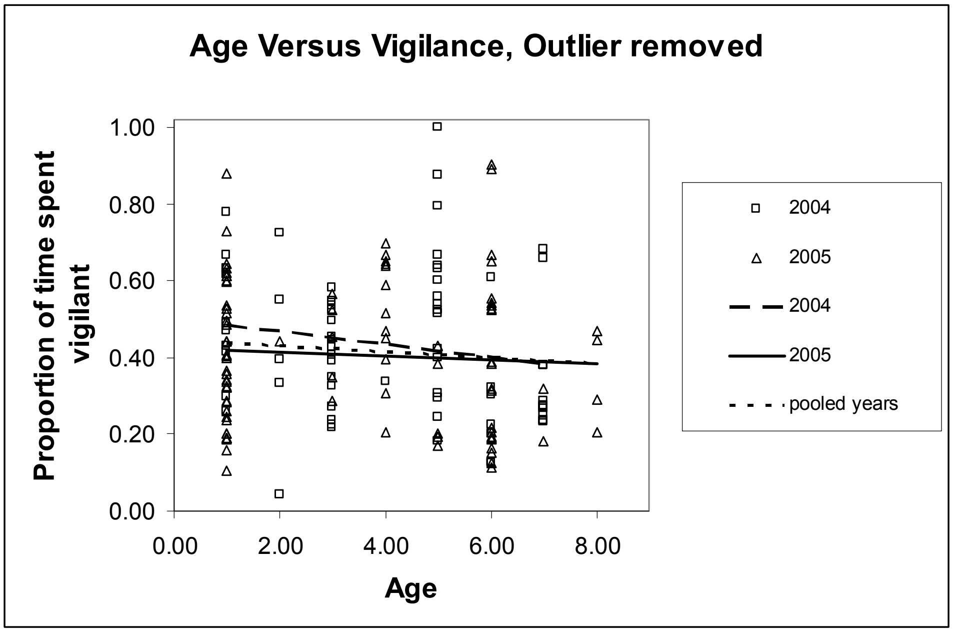


Figure 4. Graphs of age versus vigilance, with trendlines for each year and years pooled. The single data point of a 10-year-old individual in 2004 has a strong influence on the trendlines for 2004 and the pooled years.





CONCLUSIONS

Two aspects of Columbian ground squirrel vigilance were investigated: 1) the mechanisms of the group-size effect on vigilance and 2) the effects of the presence of kin on vigilance. The ease of observation that the ground squirrels provided, and the extensive previous knowledge of many of the populations made them an appropriate subject for adding to general scientific knowledge of factors affecting vigilance behavior.

The study of the mechanisms of the group-size effect on vigilance sought to discover which factor influenced Columbian ground squirrel vigilance more, dilution or detection. The dilution effect involves a decrease in an individual's predation risk as the number of individuals increase. Vigilance is decreased because the chances of being preyed upon decrease. The detection effect is a decrease in vigilance due to an increased likelihood of detecting a predator before it attacks through the vigilance of others in the group. The detection effect depends on information about a predator being passed between group members. The information transfer may be inadvertent, in that escape behavior or increased vigilance in an individual may be a signal to others that a predator is present, or it may be actively communicated in alarm calls or other communication modes. In species with active communication of predators' presence, the detection effect may be expected to have a greater influence on the group-size effect. Dilution and detection are not necessarily mutually exclusive, and they may both occur simultaneously in a species, however it is likely that one will have a greater influence than another. I predicted that if the dilution effect was the greater influence on the group-size effect in the ground squirrels that vigilance would have a positive relationship with nearest neighbor distance and a negative relationship with the distance to the edge of the meadow habitat. Additionally alarm calls would have little effect, as would factors that affect hearing alarm calls, such as wind speed. I predicted that if the detection effect had a greater influence on the group-size effect that vigilance would not be related to nearest neighbor distance or distance to the edge of the habitat, and that alarm calls and factors that affect hearing alarm calls would increase vigilance.

The ground squirrels exhibited a group-size effect on vigilance that is common among social prey species; they decreased their vigilance as the number of individuals increased. Nearest neighbor distance and the distance to the edge of the meadow did not influence vigilance, while alarm calls were associated with increased vigilance. The results for the relationship between wind speed and vigilance were difficult to interpret because the pattern was not the same on all of the meadows. However, an overall pattern of increased vigilance with increased wind speed was present, and I observed a tendency for the squirrels to stop foraging at high wind speeds. These results indicate that detection has a greater influence than dilution in the group-size effect in Columbian ground squirrels. This result contrasts with three out of four studies that tested between dilution and detection in other species (Boland, 2003; Fernandez et al., 2003; Rolando et al., 2001; Childress & Lung, 2003), as well as three of five conclusions about dilution and detection that I inferred from other studies(Blumstein et al., 2001; Smith et al., 2004; Kenward, 1978; Hoogland & Sherman, 1976; Siegfried & Underhill, 1975). The reason for the differences in dilution and detection between these different species may be indicated by the group type and information transfer of the species. Ground squirrels have individual territories and are relatively more spread out when compared to many of the species that show greater dependence on dilution. Additionally, ground squirrels have an active alarm calling system, whereas many of the species that indicate greater dependence on dilution do not have active communication about predators. Therefore, I propose that group type and information transfer be considered as an indicator of the mechanism of greater influence in the group-size effect. Tests of this hypothesis should be studied by using prey species with a variety of group types and information transfer when searching for the mechanisms of the group-size effect.

The effects of kinship on vigilance are not well studied, but some research has shown that the presence of kin can affect vigilance levels. Two studies found that parents increase their vigilance when offspring remain with them after the offspring were physically capable of being on their own (Black & Owen, 1989; Griesser, 2003). In one instance, this was considered nepotistic vigilance, because the parents did not obviously benefit from the increased vigilance, however in the other study, the parents that retained young were more successful in the following year, thus the increase in vigilance was mutualistic.

Columbian ground squirrels females are philopatric with respect to their territories and can temporally co-occur with kin (King, 1989), and may therefore adjust vigilance according to the presence of kin. The change in vigilance may be described as any one of several types of interactions, depending on the direction of the change and the cost and/or benefits to the individuals involved. Nepotistic vigilance occurs if individuals increase their vigilance in the presence of kin. Individuals can be socially parasitic in regard to vigilance if one individual benefits by decreasing vigilance and another individual pays a cost, such as increased vigilance. Alternatively, the interaction could be commensal if one individual reduces its vigilance and the other individual is unaffected. My results showed that in general, the ground squirrels did not change their vigilance in the presence of kin. There was one exception: females with adult offspring had lower vigilance than any other group. Because the adult offspring showed no change in vigilance, the interaction appears to be commensal. This is an unexpected result considering that other species showed a nepotistic or mutualistic increase in vigilance when adult offspring were present and that ground squirrels have been shown to give nepotistic alarm calls when adult offspring were present (Sherman, 1977).

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APPENDIX

Table i. Summary of studies that test between dilution and detection hypotheses

Species	**Conclusion (dilution/detection/both)**	**Group type/ information transfer**	**Source**
Emu	Both	Ephemeral, travelling/passive*	(Boland, 2003)
Greater Rhea	Dilution	Ephemeral, travelling/?	(Fernandez et al., 2003)
Red-billed Chough	Dilution	Ephemeral, travelling/?	(Rolando et al., 2001)
Rocky mountai elk	Dilution	Ephemeral, travelling/Active**	(Childress & Lung, 2003) Info. transfer: (Thomas et al., 1982)

*Passive information transfer: Departure/intense vigilance of one individual can signal danger to others, but information is not actively ("purposefully") passed between individuals.

**Active information transfer: Presence or suspected presence of danger is actively communicated to other group members via auditory or visual communication.

Table ii. Summary of studies that give data suggestive of one hypothesis or the other

Species	**Inferred conclusion (dilution/detection/both)**	**Group type/ information transfer**	**Source**
Yellow-footed rock wallabies	Dilution	Ephemeral, travelling/Active	(Blumstein et al., 2001) Info transfer: (Griffin & Evans, 2003)
Saddleback / moustached tamarins	Dilution	Ephemeral, travelling/Active	(Smith et al., 2004) Info. transfer: (Hardie & Buchanan-Smith, 1997)
Woodpigeons	Detection	Ephemeral, travelling/?	(Kenward, 1978)
Bank swallows	Detection	(semi)permanent, stationary/Active	(Hoogland & Sherman, 1976)
Laughing doves	Detection	Ephemeral, travelling/?	(Siegfried & Underhill, 1975)

Table iii. Predictions of the dilution and detection hypotheses

	Dilution predictions	**Detection prediction**
Nearest-neighbour Distance	Vigilance decreases as nearest-neighbour distance increases	Vigilance is unaffected by neighbour distance
Position in group	Vigilance decreases as distance from group edge increases	Vigilance has no relationship to position
Alarm calls	Unimportant/infrequent	Alarm calls accompany predator sightings and vigilance of hearers increases
Response to factors that limit hearing	Little/no response	Increased vigilance

Table iv. Summary of data averages and standard deviations for each meadow (X±SD)

Meadow* and Year	Meadow area	Population size**	Average proportion of time spent vigilant	Average proportion of time spent vigilant, no calling	Average nearest-neighbour distance**	Average number active
B 2004	28900	30	0.43±0.19		18.8±13.8	
D 2004	11700	102	0.42±0.19		11.1±9.6	
Hay Field 2004	252000	400-600	0.26±0.18		17.9±12.0	
4 km 2004	2400	40	0.37±0.17		13.1±12.5	
B 2005	28900	37	0.40±0.19	0.35±0.16	19.1±16.7	9.9±2.5
C 2005	4900	48	0.40±0.21	0.38±0.19	10.8±7.8	10.4±5.0
D 2005	11700	79	0.32±0.19	0.24±0.14	7.3±4.7	10.6±5.6
Hay Field 2005	252000	300-500	0.32±0.17	0.31±0.15	19.9±37.7	7.6±3.2
4 km 2005	2400	38	0.43±0.19	0.38±0.13	13.1±9.5	7.8±2.1
U1 2005	20000	28	0.38±0.16	0.29±0.20	4.2±5.3	20.5±2.8
U2 2005	15000	11	0.70±0.22	0.58±0.22	29.5±22.8	3 (est)
U3 2005	10000	15	0.30±0.15	0.24±0.04	14.3±11.4	4.8±2.6
U4 2005	14000	7	0.44±0.17	0.52±0.19	17.8±15.2	3.1±2.0
U5 2005	9000	35	0.22±0.06	0.22±0.07	10.2±5.6	11.5±2.8
U6 2005	10000	22	0.53±0.19	0.44±0.11	13.5±12.7	10.4±2.6
U7 2005	2700	10	0.23±0.13	0.13±0.03	10.2±1.7	7±1.7
U8 2005	45000	13	0.27±0.16	0.18±0.11		7.6±3.3
U9 2005	14400	28	0.28±0.15	0.25±0.15	11.3±12.8	

* Named meadows indicate marked populations, U# indicates unmarked population.

**Estimated on unmarked populations.

Table v. Results of least-squares linear regression of average vigilance on number active for each meadow (number active under 14)

Meadow		**F**	**p**	**R^2**	**Direction of relationship**
B	no calling	17.94	0.0014	0.62	-
	all	20.16	0.0009	0.65	-
C	no calling	0.23	0.64	0.02	-
	all	8.76	0.01	0.47	-
D	all	2.86	0.12	0.22	-
HF	no calling	1.53	0.26	0.20	-
	all	1.17	0.31	0.10	-
4km	no calling	6.25	0.04	0.47	-
	all	15.33	0.004	0.66	-

“No calling” indicates that only observations with no squirrels calling were used in the analysis. “All” indicates that all observations were used, both those with squirrels calling and those without. Sample size for no calling on Meadow D was too small to regress.

Table vi. Spearman correlations between number active and nearest-neighbour distance on meadows where both variables were recorded

Meadow	**r**	**p**
Meadow B 2005	-0.05	0.64
Meadow C 2005	-0.33	0.002
Death Valley 2005	0.33	0.28
Meadow D 2005	-0.06	0.59
Hay Field 2005	-0.19	0.33
Highwood Pass 2005	0.29	0.42
3 hills	-0.16	0.59
4km 2005	-0.09	0.40
Windy Point Base	0.71	0.18

Table vii. Results of regressions of vigilance on distance to edge for each meadow

Meadow	**F**	**p**	**R^2**	**Direction of relationship**
B 2004	6.2	0.02	0.8	-
B 2005	0.85	0.36	0.008	-
C 2005	0.77	0.38	0.009	+
D 2004	1.46	0.24	0.04	+
D 2005	1.3	0.26	0.02	-
4km 2004	0.27	0.6	0.003	-
4km 2005	0.09	0.76	0.001	-