

## Variation in Vigilance in White-tailed Deer (*Odocoileus virginianus*) in Northeastern Kansas

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ABSTRACT.—This study was designed to test hypotheses regarding vigilance (a state of alertness that allows an animal to detect the presence of predators or other threats) in white-tailed deer (*Odocoileus virginianus*). Based on findings on other species, we predicted that: (1) increasing group size would result in decreased individual vigilance; (2) juveniles would be less vigilant than adults; and (3) males would be less vigilant than females. Deer were observed from a tower in northeastern Kansas from May through Jul. 2001 at dawn and dusk. In accordance with other species, individual vigilance was negatively correlated with group size and juveniles spent less time vigilant than adults. However, there was no apparent difference in vigilance levels between the sexes in adults. We conclude that deer exploit loose aggregations to maximize foraging time by decreasing individual vigilance (without increasing risk) and that the trade off between vigilance and foraging intensity changes with maturation.

### INTRODUCTION

Time allocation by animals is of interest because many activities have corresponding costs. For example, foraging may increase exposure to predation in desert rodents (Kotler *et al.*, 1991). Because of this, an animal must be alert for predators while feeding. The costs of this alertness are obvious: while scanning the environment for a potential threat, the animal loses valuable foraging time (Lima and Dill, 1990; Lima, 1995a; Roberts, 1996; Treves, 2000). Thus, a decrease in vigilance, defined by Arenz and Leger (1999a:97) as “visual scanning that varies with predation risk,” allows more time for other activities, especially feeding (Roberts, 1996). One hypothetical advantage of aggregation in many animals, such as fish, mammals and birds (Lima and Bednekoff, 1999), is that vigilance is shared among group members, allowing each individual proportionately more time for foraging. Thus, aggregation is considered an adaptive behavior, because it benefits the individual (Hamilton, 1971; McNamara and Houston, 1992; Bednekoff and Lima, 1998a).

Proposed benefits of group living are numerous, but perhaps one of the major benefits of being associated with a group is that of collective detection (Lima, 1995a), or the “many eyes” hypothesis (Pulliam, 1973). Each individual need not be as vigilant as it would if solitary because the probability of predator detection is presumed to increase with group size (Hamilton, 1971; McNamara and Houston, 1992; Lima, 1995b; Bednekoff and Lima, 1998b; Hilton *et al.*, 1999; Lima *et al.*, 1999). Pulliam (1973) assumed that every member of the group is alerted to danger the instant a predator is detected by just one individual; collective detection, however, is imperfect, and group members that detect a threat possess an advantage over non-detecting members because detectors may react faster (McNamara and Houston, 1992; Lima, 1994, 1995a, 1995b; Bednekoff and Lima, 1998a, 1998b; Hilton *et al.*, 1999). Thus, all individuals retain vigilant behavior, though at a reduced level, even in a very large group. In fact, the behavior may persist even after many generations in the

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absence of predators (Blumstein *et al.*, 2001) suggesting that there is a strong innate component (Treves, 2000). Furthermore, group predator detection can be so effective that some animals will form mixed-species flocks to increase group size (Metcalf, 1984b; Bshary and Noe, 1997).

In addition to factors that influence general levels of vigilance, individuals vary in degree of vigilance. Subordinate animals are often more vigilant than are dominant individuals (Valone and Wheelbarger, 1998; Domenech and Senar, 1999). In addition to watching for predators, subordinates, which may be females or young males, must also be alert to the presence of dominant individuals to avoid confrontation and guard against kleptoparasitism (Metcalf, 1984b). Thus, vigilance may increase from threats other than predation (Arenz and Leger, 1997, 1999b; Bednekoff and Lima, 1998a; Valone and Wheelbarger, 1998; Treves, 2000). It also has been suggested that, in mammals, females with young may be more vigilant than males or barren females (Burger and Gochfeld, 1994; Swaisgood *et al.*, 1999; Toigo, 1999; Childress and Lung, 2003; Wolff and Van Horn, 2003). Juveniles may be less vigilant than adults because nutritional demands of juveniles for growth and development dictate more time foraging, perhaps contributing to higher mortality in young (Arenz and Leger, 1997, 2000).

Location of foraging may also influence vigilance. Animals may forage longer or more often in areas of lower predation risk. For some animals, especially birds, this may include areas with nearby cover where the prey can flee to avoid a predator (Metcalf, 1984a; Pöysä, 1994; Slotow and Coumi, 2000). Metcalf (1984a) has also shown that birds increase vigilance as habitat becomes increasingly complex with more visual obstructions that may conceal encroaching predators and block an individual's view of conspecifics. Thus, reduced visibility increases vigilance, perhaps in response to a heightened sense of vulnerability (Metcalf, 1984a; Arenz and Leger, 1997, 1999a; Harkin *et al.*, 2000). For animals that depend on speed and maneuverability to avoid predators, open areas where vision is least obscured, may allow most rapid response to presence of a predator (Stankowich and Blumstein, 2005). However, if the quality of food in a "risky" site is high enough, animals might hazard feeding there; in such cases, they should adjust their vigilance levels accordingly (Bednekoff & Lima, 1998a; Brown, 1999; White *et al.*, 2001). Mule deer (*Odocoileus hemionus*) are known to vary both their vigilance and foraging intensity with habitat (Altendorf *et al.*, 2001). However, white-tailed deer (*O. virginianus*) differ from mule deer in both their habitat preferences and response to coyotes (Lingle and Wilson, 2001).

The central hypotheses of this study were that vigilance was influenced by group size, age and sex in the white-tailed deer. Based on work in other species (reviewed in Stankowich and Blumstein, 2005), we predicted that: (1) as group size increases, vigilance levels of individuals within the group should decrease; (2) juveniles would be less vigilant than adults; and (3) females, especially those with young, should be more vigilant than males. To the best of our knowledge, there are no previous studies of these questions in the large body of literature on white-tailed deer.

#### METHODS

We conducted our study approximately 12 km (7.5 mi) northeast of the University of Kansas (Lawrence, KS, U.S.A.) at the Nelson Environmental Study Area (NESA) in Jefferson County. Deer were observed from a 10-m tower on the fragmentation study site at NESA, described briefly by Robinson *et al.* (1992). Vegetation on the site was a mosaic of grasses with imbedded successional woodland plots that consisted of various trees (*e.g.*, eastern red

cedar, *Juniperus virginiana*; slippery elm, *Ulmus rubra*; and rough-leaved dogwood, *Cornus drummondii*) and bushes (including blackberries, *Rubus* spp.) that attracted foraging deer. The fragmented site encompassed 6.9 ha, and was surrounded on three sides by woodlands. The tower acted as a blind and offered a vantage point from which to see most of the area despite trees that would obscure the view at ground level.

Deer were observed from 24 May to 9 Jul. 2001 for a total of approximately 50 h. Observations were conducted at dawn (~0500–0700 h) and dusk (~1930–2100 h), when deer were most likely to be foraging and visible. Data were recorded either by direct observation (for animals near the tower), or, for animals farther away, with the assistance of 10 × 50 binoculars. After a deer or group of deer was sighted, a focal individual was arbitrarily chosen, and the amount of time it was vigilant (head raised above parallel to the ground, scanning its environment) was measured using a stopwatch. Ideally, the animals were observed for five min (300 s). However, the focal animal often wandered out of sight behind a shrub or tree. When this happened, vigilance was simply recorded for the time the animal was visible. The proportion of time spent vigilant then could be calculated by dividing the number of seconds the animal spent with its head raised by the length of the observation period. This was done for each member of the group and care was taken not to record data on the same individual more than once per day. When each individual had been sampled, attention was then focused on a different group. Generally ≤3 members in a single group were sampled. Groups >5 often dispersed or moved out of sight or daylight waned before all individuals could be observed.

We noted age (juvenile or adult) and sex of the focal animal, the number of individuals in its group, and the group constitution (number of males, females and juveniles). Juveniles were distinguished from adults primarily by size (somewhat smaller than adults) and were primarily yearlings; only two fawns were seen during the study, presumably because they hid in the nearby woods or tall grass while their mothers foraged. As the study progressed and the yearlings grew, it became increasingly difficult to distinguish them from adult females. Age was more reliably estimated among males—*i.e.*, it was assumed that a male with antler buds or spikes was younger than one with more than two points. The number of antler points was recorded for males beginning 13 Jun. (for a total of 29 observations). This information was then used to further examine the relationship between vigilance and age. The presence or absence of antlers determined sex (in adults), but sex of juveniles was impossible to determine from the tower. Ninety-seven animals (32 solitary individuals and 65 in groups ranging from two to nine) were successfully timed. No animal was timed twice in one day, but because animals were not individually marked, it is possible that individuals were sampled on several different days. The deer population on the Fitch Natural History Reservation that bordered our study area is large (>100), but probably only a few dozen deer frequented the 6+ ha visible from the permanent tower. We treated observations on different days and observations of several animals in the same group as independent in our statistical analyses.

All observations were made in open habitat or at the edge of wooded habitat fragments so we had no opportunity to observe the influence of habitat type on vigilance, but we did estimate distance from wooded cover to focal individuals. We fit general linear models with proportion vigilance as the dependent variable and group size, sex, age and distance to wooded cover as predictor variables.

To determine relationships between percent vigilance and group size, we first calculated percent vigilance for all observations, categorized into one to ≥7 individuals (there was one observation from a group of eight and two for individuals in a group of nine, so the ≥7

TABLE 1.—Median percent vigilance ( $\pm$ SD) in white-tailed deer for group sizes 1 to  $\geq 7$ 

Group Size	Number of groups	Number of individual observations	Median % vigilance
1	32	32	9.83 ( $\pm 7.97$ )
2	15	21	7.00 ( $\pm 8.63$ )
3	6	9	7.00 ( $\pm 6.44$ )
4	7	13	4.17 ( $\pm 3.18$ )
5	3	5	1.33 ( $\pm 1.91$ )
6	3	9	2.67 ( $\pm 4.01$ )
$\geq 7$	6	8	5.17 ( $\pm 6.00$ )
Total	72	97	

group was created to eliminate the confounding effects of small sample sizes). All data were analyzed via SPSS for Windows, version 10.1. Because data deviated from assumptions of normality, and because they could not be normalized by various transformations, all statistical analyses were non-parametric and we report median percent vigilance. In tests involving more than one factor, we used ranked percent vigilance, rather than raw data.

#### RESULTS

We were unable to include age and sex in the same statistical model because we could not determine sex for young animals. Our preliminary general linear model on rank percent vigilance versus group-size, distance-to-cover and sex indicated that neither of the latter two terms had a significant influence on vigilance ( $P = 0.245$  and  $0.915$ , respectively) as a main effect or in any interaction terms. A second linear model indicated that both age and group-size effects were significant ( $P \leq 0.01$ ). Deer decreased individual vigilance when associated with increasingly larger groups. There was a significant inverse relationship between median percent vigilance and group size (Spearman's coefficient,  $r_s = -0.75$ , one-tailed  $P = 0.026$ , Table 1). Solitary individuals were especially vigilant.

Small deer, which we classified as young, were less vigilant than adults. The median percent vigilance for young ( $M \pm SD = 1.83 \pm 2.86\%$ ;  $n = 12$ ) was significantly less than for adults ( $5.83 \pm 7.57\%$ ;  $n = 85$ ;  $P = 0.004$ , one-tailed Mann-Whitney U). It was possible that, because young deer were more likely to be members of groups (11 of 12 observations of young versus 54 of 85 observations of adults), age differences might be due to a group size effect, but the partial effect (age adjusted for group size) was significant in the linear model. Males with antler buds or spikes also were less vigilant than males with 2 or more antler points ( $n = 29$ ,  $P = 0.037$ ; one-tailed Mann-Whitney U). We also found a significant positive association between mean percent vigilance and number of antler points (ranging from 1 to 5 on a single antler;  $r_s = 0.458$ ,  $P = 0.006$ ). Thus, even though antler size may not be a strong correlate of age, all statistical analyses indicated that younger deer were less vigilant than older deer.

Finally, we compared vigilance levels between adult males and adult females in additional analyses. The median percent vigilance for males ( $7.00 \pm 7.59\%$ ;  $n = 48$ ) did not differ significantly from that of females ( $5.33 \pm 7.57\%$ ;  $n = 37$ ;  $P = 0.777$ ; one-tailed Mann-Whitney U). Using a matched pairs comparison of males and females in the same groups, we again found no significant differences between sexes ( $P = 0.917$ ,  $n = 6$  matched pairs; two-tailed Wilcoxon signed ranks test). Thus, we found no significant differences in vigilance between adult male and female deer.

## DISCUSSION

In many animal aggregations, individual vigilance levels decrease with increasing group size (Hamilton, 1971; McNamara and Houston, 1992; Lima, 1995b; Bednekoff and Lima, 1998b; Lima *et al.*, 1999; Hilton *et al.*, 1999). We found deer observed in this study to be no exception. The proportion of time spent vigilant by individual white-tailed deer was negatively correlated with the number of animals in a group. Shared vigilance might be particularly beneficial in white-tailed deer because of communal signaling of the presence of intruders via foot-stamping, snorting, or tail-flagging (but as a secondary function of the latter; Bildstein, 1983; Caro *et al.*, 1995).

Juvenile thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) spend proportionately more time foraging, thus less time vigilant, than do adults. Young ground squirrels have high nutritional demands because they must deposit enough fat during the spring, summer, and autumn to survive hibernation (Arenz and Leger, 2000). Similarly, young deer also may spend more time foraging due to heightened nutritional demands of growth, development and winter stress as in other ungulates (White *et al.*, 2001).

Contrary to our initial prediction, we found no significant differences in relative frequency of vigilance between males and females. Vigilance should be related to potential threats, and while deer were protected from hunting on our area, they were susceptible to seasonal hunting in surrounding areas. In addition they could be harassed by dogs (*Canis familiaris*), coyotes (*Canis latrans*) and bobcats (*Lynx rufus*), all of which were numerous locally. Cougars (*Puma concolor*) also have been reported, but not confirmed in the area. Perhaps female deer with independent young did not perceive a threat of predation from any of these sources and so did not increase vigilance. Female blacktailed deer (*Odocoileus hemionus*) with fawns may actually reduce their response to intruders (Stankowich and Coss, 2007). White-tailed deer do not appear to exhibit male dominance as seen in some other mammals, thus females need not increase vigilance to avoid conflict with males in summer (see Valone and Wheelbarger, 1998; Domenech and Senar, 1999). Another, admittedly speculative, possibility is that antlers increase prominence, requiring increased male vigilance to a level comparable with that of females, which presumably have young nearby during the spring and summer months. This idea is consistent with the positive association we found between percent vigilance and antler size, as is the proposition that males might be more exposed to hunting. Stankowich and Coss (2006) attributed heightened response of male blacktailed deer to approaching humans to male deer being exposed to heavier hunting pressure than were females. Both sexes were hunted in our region, including a special antlerless-only season in recent years, so it would be interesting to repeat our observations following the regular and again after the supplemental hunting seasons. In our study, vigilance was not directed toward a specific stimulus (*e.g.*, human or animal model), so perhaps it was not surprising to find no sexual difference. There might be compensating differences between the sexes in response to a variety of intruders.

Single deer were most commonly observed (32 of 72 observed groups) and the relative frequency of groups generally decreased as group size increased. However, 154 of 186 deer were seen at least in pairs, and more individual deer (45) were seen in groups  $\geq 7$  than groups of any other size. This suggests that white-tailed deer commonly forage in groups, at least in the summer. It might be worthwhile to determine if there is an optimal group size above which additional group members have no effect on individual vigilance, or are even detrimental to the group (*e.g.*, making the group more visible to predators). Such a relationship might make vigilance an asymptotic or parabolic function of group size, consistent with our observation that median percent vigilance for groups  $\geq 7$  animals was

greater than for groups of size 3 to 6. However, a lack-of-fit test on the raw data indicated that a more complex mathematical function was not statistically better than a straight line relating group size to vigilance.

Distance to cover can affect levels of vigilance (White *et al.*, 2001; Blumstein *et al.*, 2003), however in this study, deer did not vary significantly in vigilance levels in response to distance from cover after accounting for the influence of group size. This may be due to the open nature of our study area, and the fact that white-tailed deer can escape by running from any common predator (*e.g.*, dogs or coyotes) in the area.

It must be noted that the animals we observed were not individually marked, so we have no solution to potential statistical problems introduced by resampling individuals. We took care to observe individuals only once per day and to sample multiple groups per day, but the same animals might have been sampled on different days. Both size and spatial location of groups varied among days, suggesting that individuals that may have been resampled were observed in different spatial and social contexts. Coss *et al.* (2005) used Monte Carlo simulations to demonstrate that resampling actually reduced the power of their statistical analyses, so the true influence of resampling is difficult to estimate. Despite this caveat, our findings support many of the existing hypotheses on antipredator vigilance in gregarious animals and imply that white-tailed deer benefit from foraging in groups. They also illustrate that there may be other factors in addition to group size that influence individual vigilance.

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