

What is the best way to estimate vigilance? A comparison of two methods for Gunnison's prairie dogs, *Cynomys gunnisoni*



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Vigilance is important for survivorship and reproductive success and is common and conspicuous within hundreds of species across a diverse array of taxa. Vigilance can involve either scanning for predators (antipredator vigilance) or watching conspecifics (social vigilance). From observations of marked Gunnison's prairie dogs, *Cynomys gunnisoni* (Sciuridae), living under natural conditions at Valles Caldera National Preserve, New Mexico, U.S.A., we compared results from the two most common sampling methods used by behavioural ecologists to measure vigilance: focal sampling (i.e. observing an individual for a specific amount of time and recording the amount of time spent vigilant) and scan sampling (i.e. observing all individuals in an area at a single moment and recording whether each individual at that moment is vigilant or nonvigilant). Information from different individuals and from the same individuals over time both revealed that estimates of vigilance from scan sampling were consistently and significantly higher than estimates from focal sampling. These differences probably resulted because non-vigilant behaviours were more difficult to detect in scan samples than in focal samples. Our results have important implications for behavioural ecologists who want to make intraspecific or interspecific comparisons of vigilance.

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Probably because it is so important for survivorship and reproductive success, vigilance is a fundamental behaviour in animals of all kinds, including hundreds of species of insects and other invertebrates (Hamilton & Heithaus, 2001; Wong, Bibeau, Bishop, & Rosenthal, 2005), fishes (Jones & Godin, 2010; Ward, Herbert-Read, Sumpter, & Krause, 2011), amphibians (Martín, Luque-Larena, & Lopez, 2006; Spieler, 2003), reptiles (Ito & Mori, 2010; Robertson et al., 2011), birds (Ge, Beauchamp, & Li, 2011; Xu, Ma, Yang, Blank, Ding, & Zhang, 2013) and mammals (Gaynor & Cords, 2012; Reimers, Lund, & Ergon, 2011; Teichroeb & Sicotte, 2012). Individuals are vigilant for one of two reasons:

to watch for predators (antipredator vigilance), or to watch conspecifics (social vigilance) (Arenz & Leger, 1999; Elgar, 1989; Favreau, Goldizen, & Pays, 2010; Quenette, 1990; Yasukawa, Whittenberger, & Nielsen, 1992). An individual might watch its neighbours to better compete for food (Black, Carbone, Wells, & Owen, 1992; Fernández-Juricic, Beauchamp, & Bastain, 2007; Robinette & Ha, 2001), as part of mate guarding (Hoogland, 1995; Rose & Fedigan, 1995), to watch for trespassers who might be infanticidal (Manno, 2007; Steenbeek, Piek, van Buul, & van Hooff, 1999), or to increase safety by observing a neighbour's reaction to predators (Childress & Lung, 2003; Hare, Campbell, & Senkiw, 2014; Treves, 1999; Ward, 1985). Many studies have focused on the vigilance of nonhunting prey species, but most predators are also vulnerable to capture and show antipredator vigilance (Caro, 1987; Pangle & Holekamp, 2010).

A potential cost of vigilance includes a decrease in time available for other behaviours such as foraging, mating and parental care (Childress & Lung, 2003; Cowlishaw et al., 2004; Fortin, Boyce, Merrill, & Fryxell, 2004; Illius & Fitzgibbon, 1994). The single

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overwhelming benefit of antipredator vigilance is an increased safety that results from the improved ability to detect predators (Hardie & Buchanan-Smith, 1997; Hoogland, 1979; Lazarus, 1979; Lipetz & Bekoff, 1982; Uetz, Boyle, Hieber, & Wilcox, 2002). When animals live in groups, individuals can capitalize on the 'many eyes effect': as the size of a group increases, individuals can decrease their own levels of vigilance because other alert individuals will either intentionally or unintentionally signal a predator's arrival (Carter, Pays, & Goldizen, 2009; Hirsch, 2002; Pulliam, 1973; Roberts, 1996; Sansom, Cresswell, Minderman, & Lind, 2008). Furthermore, individuals in groups can decrease vigilance because of the 'dilution effect': a lower probability of capture when a predator attacks because other individuals are also available for capture (Bertram, 1978; Blumstein & Daniel, 2003; Blumstein, Daniel, & Evans, 2001; Dehn, 1990; Hamilton, 1971).

Many factors affect vigilance, including sex, age, dominance, site-specific vulnerability to predation and availability of resources (Favreau et al., 2015; Hirsch, 2002; Lehtonen & Jaatinen, 2016; Xu, Ma, & Wu, 2010). Probably for this reason, levels of vigilance can vary tremendously among individuals within and across species (Beauchamp, 2010; Hoogland, Hale, Kirk, & Sui, 2013; McDonough & Loughry, 1995; Roche & Brown, 2013).

Behavioural ecologists frequently use two different sampling methods for estimating vigilance for animals living under natural conditions: 'focal sampling' and 'scan sampling'. A focal sample involves observing an individual for a specific amount of time and recording the amount of time spent vigilant (Alberts, 1994; Altmann, 1974; Robinette & Ha, 2001; Rose & Fedigan, 1995; Stojan-Dolar & Heymann, 2010). A scan sample, also called an instantaneous sample (Altmann, 1974), involves observing all individuals in a population at a single moment and recording whether each individual at that moment is either vigilant or non-vigilant (Hoogland et al., 2013; Paolosso & Hames, 2010). Behavioural ecologists are more likely to use focal sampling for solitary individuals, or for colonial individuals that are easily identifiable by either natural or applied marks (Altmann, 1974; Mann, 1999). Scan sampling is more suitable for highly colonial species for which identification of individuals is difficult (Fragaszy, Boinski, & Whipple, 1992; Gilby, Pokempner, & Wrangham, 2010; Mann, 1999).

In theory, focal sampling and scan sampling should yield identical results. Several studies have shown how focal sampling and scan sampling can lead to different conclusions for a variety of behaviours, including vigilance (Choi, Nam, & Lee, 2007; Fragaszy et al., 1992; Gilby et al., 2010; Mitlöhner, Marrow-Tesch, Wilson, Dailey, & McGlone, 2001). To our knowledge, no previous study has specifically focused on whether estimates of vigilance from focal samples and scan samples from the same marked individuals yield equivalent results, and why differences between the two methods, if they exist, might occur. To address this shortcoming, we compared focal sampling versus scan sampling for estimating vigilance of marked Gunnison's prairie dogs, *Cynomys gunnisoni* (hereafter simply 'prairie dogs'), living under natural conditions at Valles Caldera National Preserve (VCNP) in New Mexico, U.S.A.

METHODS

Study Animals

We studied a portion (the 'study area', approximately 5 ha) of a large colony (>30 ha) of prairie dogs in the Redondo Meadow (35°51'37.29"N, 106°36'09.47"W; elevation ca. 2500 m) of VCNP, Sandoval County, New Mexico, U.S.A., from March through early July 2014. Anschuetz and Merlin (2007) and Coop and Givnish (2007) described the flora, fauna and topography of VCNP.

Prairie dogs are medium-sized (300–900 g for adults), diurnal, colonial ground-dwelling rodents of the squirrel family (Sciuridae) (Fitzgerald & Lechleitner, 1974; Hoogland, 1999; Rayor, 1988). Adults (≥ 9 months old) typically first appear aboveground from their burrows at dawn and remain aboveground until dusk. At the entrance to each burrow is a large mound of soil, and the prairie dogs frequently use these mounds as highpoints to scan for predators. Colonies are divided into family groups called clans, which typically contain one breeding male, three to four breeding females, one to two nonbreeding yearling males, and (in late spring) 5–10 juveniles (≤ 2 months after weaning) (Hoogland, 1999). Our study area contained 34 clans in 2014. Terrestrial predators on prairie dogs at VCNP include American badgers, *Taxidea taxus*, coyotes, *Canis latrans*, and bobcats, *Lynx rufus*. Avian predators include golden eagles, *Aquila chrysaetos*, red-tailed hawks, *Buteo jamaicensis*, and prairie falcons, *Falco mexicanus*.

We live-trapped, eartagged and marked all 109 prairie dogs in our study area with Nyanzol black fur dye for behavioural observations from a distance of ≤ 150 m (as described in Hoogland, 1995). Eight of these 109 (7%) individuals were difficult to observe either because of tall vegetation or because they were too far from the nearest observation tower, so we did not attempt to estimate their vigilance; therefore, we estimated vigilance for 101 prairie dogs. The combination of eartags and Nyanzol enabled us to identify with absolute certainty the same prairie dogs within and across years. Five observers used both scan sampling and focal sampling to estimate vigilance. Because categorizing an individual as either vigilant or nonvigilant was so straightforward, interobserver variability probably was minimal, but we did not rigorously investigate the possibility of interobserver differences in our estimates of vigilance. The same observer was responsible for all scan samples and all focal samples from the same marked prairie dogs ($N \sim 20$; see immediately below) near his or her observation tower over the 3 months of our research.

Scan Samples

From five 2 m observation towers, we recorded scan samples from 15 March 2014 through 1 June 2014. Each observer had approximately 20 marked prairie dogs available for watching in a roughly circular area with a diameter of about 100 m surrounding his or her tower. We usually used binoculars to identify vigilance, but sometimes marked prairie dogs were close enough to observe with the naked eye. Once per hour, an observer recorded an individual as either alert (i.e. vigilant) or nonalert at the first moment it was seen. Locating and scoring the 20 prairie dogs around each tower for scan samples usually took 2–3 min. An individual was scored as nonalert if its head was down, if it was on all four feet feeding, or if it was interacting with another prairie dog (e.g. fight, chase or territorial dispute; see Hoogland et al., 2013). An individual was scored as alert if it was standing on its two hind feet scanning its surroundings, or if it was either standing or on all four feet on a burrow-mound with its head raised (Hoogland et al., 2013).

For scan sampling, we used only one (the first) score of vigilance or nonvigilance per hour per individual, and we had data from 101 marked prairie dogs. During periods when the frequency of behavioural interactions was low (e.g. when females were lactating), we recorded scan samples once every 60 min. When the frequency of behavioural interactions was higher (e.g. when copulations were occurring and we wanted to know the exact location of every prairie dog as often as possible while still allowing time to record behavioural interactions), we recorded scan samples once every 20 min. Shorter intervals (i.e. < 20 min) between scan samples might have made it difficult to distinguish between scan samples and focal samples (Altmann, 1974). Furthermore, even

though scan samples were important, the primary focus of our research was to document as many behavioural interactions as we could (Hoogland, 1995, 1999); higher frequencies of scan samples would have interfered with that primary focus. For consistency across the entire field season, we used only one scan sample (the first) per hour for each marked prairie dog for our statistical analyses.

The mean \pm SD number of days for each prairie dog for which we recorded scan samples was 60.5 ± 11.8 (range 27–78) days. If we did not see an individual at any point within an hour, we did not score it. We calculated the percentage of time each prairie dog spent alert during each day by dividing the number of observations of alertness by the total number of observations taken throughout the day. We only calculated a daily mean for a given prairie dog if we had at least three records of vigilance or nonvigilance for it on a given day. For 101 prairie dogs, we calculated a total of 6151 daily mean estimates of vigilance from scan samples. From these daily means of scan samples, we calculated the overall mean \pm SD time spent alert during the entire season for each prairie dog; for this calculation, we only used prairie dogs for which we recorded scan samples for ≥ 27 days.

Focal Samples

From our towers we recorded focal samples from 18 March 2014 through 1 June 2014. Focal sampling involved observing a marked prairie dog for 15 min using a timer and a stopwatch. The observer started the timer when a prairie dog was foraging, and started the stopwatch every time the individual was alert; the observer stopped the stopwatch when the individual ceased being alert. We used the same alert/nonalert criteria for focal samples as for scan samples (see above). A focal sample was only started when an individual was feeding and showed no signs of vigilance.

Occasionally during a focal sample, an animal would leave an observer's field of view by moving outside the study area, by going behind tall vegetation, or by submerging into a burrow. When a focal prairie dog disappeared for one of these reasons, the observer stopped the timer. If the individual became visible again, the observer restarted the timer when the individual was foraging in order to get a full 15 min of data. Some prairie dogs were easier to focal-sample than others, but we never recorded more than one focal sample per prairie dog per day. For each focal sample, we recorded the date, the individual, the start time, the cumulative time spent watching and the total time the individual spent alert. The time devoted to alertness was then divided by the cumulative time spent watching to yield a percentage of time spent vigilant. From these daily focal samples, we calculated an overall mean \pm SD alertness for each prairie dog over the 3 months of our research. We only used data from prairie dogs for which we obtained ≥ 10 focal samples for our statistical analyses, and we only used a focal sample if we were able to observe the prairie dog for ≥ 10 min. For 60 prairie dogs, we calculated a total of 1058 daily mean estimates from focal sampling.

We took both scan samples and focal samples throughout the day from shortly after dawn until shortly before sunset, but we did not investigate whether vigilance was consistently higher at certain times of the day. For all analyses, we used two-tailed nonparametric statistical tests.

Ethical Note

Research with prairie dogs at VCNP complied with current laws of the United States, and our proposal for handling and studying prairie dogs (SUB 15A13, Hoogland) was approved by the Institutional Animal Care and Use Committee (IACUC) of the University of

Maryland Center for Environmental Science. Our approved protocol includes many procedures to minimize adverse impacts on the welfare of the prairie dogs that we studied.

RESULTS

We recorded scan samples from 15 March 2014 through 1 June 2014 for 101 marked prairie dogs, and we recorded focal samples from 18 March 2014 through 1 June 2014 for 60 marked prairie dogs. For 60 individuals, we were able to obtain both focal and scan samples on the same day. The mean \pm SD number of daily estimates of vigilance per prairie dog from scan samples was 60.5 ± 11.8 (range 27–78). The mean \pm SD number of estimates of vigilance per prairie dog from focal samples (1 per day) was 17.6 ± 5.4 (range 10–32).

Figure 1 shows the distribution of the overall mean vigilance from scan samples from 101 prairie dogs and the distribution of the overall mean vigilance from focal samples from 60 prairie dogs. None of the estimates of overall mean vigilance from scan samples were $\leq 10\%$, but 21.7% of the estimates of overall mean vigilance from focal samples were $\leq 10\%$. On the other hand, none of the estimates of overall mean vigilance from focal samples were $> 50\%$, but 9.9% of the estimates of overall mean vigilance from scan samples were $> 50\%$.

The mean overall vigilance estimated from scan samples was $31.3 \pm 11.7\%$ ($N = 101$), and the mean overall vigilance estimated from focal samples was $18.6 \pm 10\%$ ($N = 60$). These differences were significant (Mann–Whitney U test: $U = 2469$, $P < 0.001$).

We also compared the overall estimates for the prairie dogs for which we had both scan and focal samples ($N = 60$). For 53 of the 60 prairie dogs (88%), the mean overall vigilance estimated from scan samples was higher than the mean overall vigilance estimated from focal samples, and these differences were significant (Wilcoxon matched-pairs signed-ranks test: T critical = 648.26, $P < 0.001$).

Because we had both scan samples and focal samples from 60 individuals, we compared vigilance estimates from both methods when we had data from the same individual on the same day. We only made these comparisons when we had at least 10 days of data from both methods on the same day. For 27 of the 60 prairie dogs (45%), the differences in vigilance between the two methods for paired data from the same days were significant (**Table 1**). For 26 of these 27 prairie dogs (96%), scan sampling yielded higher overall estimates of vigilance than focal sampling (Wilcoxon matched-pairs signed-ranks test: T critical = 106.92, $P < 0.001$).

DISCUSSION

Watching for predators and monitoring the activities of nearby conspecifics are often important for survivorship and reproductive success (Arenz & Leger, 1999; Elgar, 1989; Favreau et al., 2010; Quenette, 1990; Yasukawa et al., 1992). Vigilance is therefore common and conspicuous for animals ranging from insects and other arthropods to primates (Gaynor & Cords, 2012; Ge et al., 2011; Hamilton & Heithaus, 2001; Ito & Mori, 2010; Jones & Godin, 2010; Spieler, 2003), and behavioural ecologists have been studying vigilance among hundreds of invertebrate and vertebrate species for more than 140 years (Caine & Marra, 1988; Cowlishaw, 1998; Di Blanco & Hirsch, 2006; Galton, 1871; Hall, 1960; Pulliam, 1973). In this study, we compared the two most common sampling methods for estimating vigilance, namely focal sampling and scan sampling. A major advantage of our study was the ability to observe marked individuals ($N = 101$), which allowed us to compare focal sampling versus scan sampling for the same individuals ($N = 60$) over time.

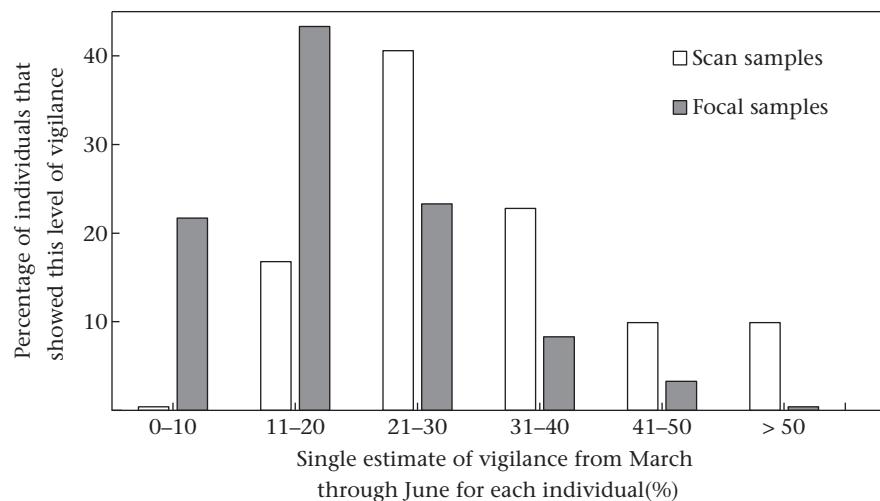


Figure 1. Percentages of different overall levels of vigilance from scan samples ($N = 101$ individuals) versus focal samples ($N = 60$ individuals) in 2014 for Gunnison's prairie dogs at Valles Caldera National Preserve, New Mexico, U.S.A. The differences shown here were significant ($P < 0.001$; see text for details).

Table 1

Gunnison's prairie dogs at the Valles Caldera National Preserve, U.S.A., for which estimates of vigilance using scan samples differed significantly from estimates using focal samples collected on the same day (Wilcoxon matched-pairs signed-ranks test: $N = 27$, $P < 0.001$)

Prairie dog	Sex	Number of days for which both scan and focal samples were available	Overall mean percentage \pm SD		<i>P</i>
			Scan samples	Focal samples	
03	Male	31	25 \pm 21	8 \pm 11	<0.001
05	Male	17	23 \pm 17	11 \pm 10	0.048
17	Male	23	58 \pm 17	27 \pm 21	<0.001
32	Male	32	36 \pm 30	12 \pm 12	<0.001
47	Male	21	28 \pm 15	17 \pm 17	0.005
104	Male	24	23 \pm 17	16 \pm 16	0.015
R12	Male	14	41 \pm 22	22 \pm 14	0.030
R14	Male	21	18 \pm 15	11 \pm 13	0.044
R16	Male	16	48 \pm 23	33 \pm 23	0.049
R33	Male	24	22 \pm 13	10 \pm 9	<0.001
R37	Male	13	33 \pm 18	15 \pm 17	0.016
BB0	Female	19	31 \pm 17	9 \pm 7	<0.001
BB5	Female	12	37 \pm 17	18 \pm 12	0.004
BS4	Female	23	29 \pm 20	7 \pm 7	<0.001
C2	Female	16	27 \pm 15	12 \pm 8	0.005
FR	Female	29	27 \pm 14	8 \pm 10	<0.001
HWA	Female	16	35 \pm 18	15 \pm 13	0.002
H6	Female	20	33 \pm 19	20 \pm 22	0.003
RB3	Female	12	34 \pm 22	16 \pm 10	0.023
RSBB	Female	29	25 \pm 22	13 \pm 17	0.006
RSBS	Female	12	15 \pm 14	6 \pm 4	0.034
RSRAB	Female	10	36 \pm 18	13 \pm 14	0.017
RR2	Female	21	29 \pm 15	19 \pm 18	0.013
RR5	Female	14	14 \pm 14	30 \pm 21	0.036
RR8	Female	21	18 \pm 15	9 \pm 16	0.025
5SBS	Female	16	32 \pm 20	13 \pm 10	0.008
6STR	Female	18	25 \pm 19	9 \pm 7	0.008

For each day of data, we used one focal sample and the single mean of all the scan samples for each prairie dog. For 33 other prairie dogs for which we had information from both scan samples and focal samples on the same day, the differences were not significant.

Previous investigators have assumed that estimates of vigilance from focal samples and scan samples are equal (Hill & Cowlishaw, 2002; Smith, Kelez, & Buchanan-Smith, 2004), and several studies have used both sampling methods to quantify vigilance (Blumstein, 1996; Kutsukake, 2006; Marino & Baldi, 2008; McDonough & Loughry, 1995). However, rigorous research to

investigate the equivalence of estimates of vigilance from focal samples versus scan samples is scarce. Here we show that estimates of the percentage of time spent vigilant from scan sampling were consistently higher than estimates from focal sampling.

Prairie dogs usually stand when they are looking for predators or conspecifics and are therefore easy for behavioural ecologists to see during a scan sample (Hoogland et al., 2013; see also Martin, Bateson, & Bateson, 1993). However, nonalert foraging individuals are difficult to see during a scan sample. By contrast, both alertness and nonalertness are easy to quantify during a focal sample that involves careful observation of a single marked prairie dog. Furthermore, we only began a focal sample when a prairie dog was feeding (and therefore not vigilant; see also Frid, 1997). Detecting nonvigilance is therefore more likely in focal samples than in scan samples for these two reasons, and these reasons are probably primarily responsible for our finding that scan samples consistently yielded higher estimates of vigilance than focal samples for our prairie dogs living under natural conditions. Note, for example, that none of our single overall estimates of vigilance from scan samples were $\leq 10\%$, but 21.7% of our single overall estimates of vigilance from focal samples were $\leq 10\%$. Contrarily, none of the estimates of overall mean vigilance from focal samples were $> 50\%$, but 9.9% of the estimates of overall mean vigilance from scan samples were $> 50\%$.

When studying vigilance, distinguishing between vigilance for predators and vigilance for conspecifics can be difficult (Edwards, Best, Blomberg, & Goldizen, 2013; Favreau et al., 2010; Hoogland et al., 2013; Klose, Welbergen, Goldizen, & Kalko, 2009; Treves, 2000). Because of the position of the eyes on a prairie dog's head, we could not determine the direction of an individual's gaze to determine whether it was looking for, or at, a predator or a conspecific. We therefore did not attempt to distinguish between antipredator vigilance versus social vigilance (see also Hoogland et al., 2013). Instead, we focused on the percentage of time individuals devoted to vigilance for either predators or conspecifics.

The lower antipredator vigilance of individuals expected in large groups might result either from an increase in probability of detecting a predator ('many eyes effect': Carter et al., 2009; Lima & Dill, 1990; Pulliam, 1973; Sansom et al., 2008) or from an individual's lower probability of getting captured ('dilution effect': Bertram, 1978; Hamilton, 1971). Several studies have indicated that the many eyes effect is probably more important than the dilution

effect for the reduced vigilance of individuals of larger groups (Boland, 2003; Fairbanks & Dobson, 2007), but other studies have indicated the opposite trend (Childress & Lung, 2003; Fernandez, Capurro, & Reboreda, 2003; Rolando, Caldroni, Sanctis, & Laiolo, 2001; Thomas & Towell, 1982). Discriminating between lower vigilance from the many eyes effect and the dilution effect is difficult for animals in general (Fairbanks & Dobson, 2007; Krause & Ruxton, 2002) and for prairie dogs in particular. We made no attempt to make this discrimination in our research, but emphasize that such an attempt probably will involve either focal sampling or scan sampling.

We present perhaps the best documentation to date that the two most common sampling methods for estimating vigilance for animals under natural conditions do not yield an equivalent result. Our results should be important to other behavioural ecologists who want to make intraspecific or interspecific comparisons of vigilance. Estimates of vigilance from scan samples were higher than estimates from focal samples from the same marked prairie dogs in 88% of our comparisons. We have not demonstrated that one method is necessarily more accurate or better than the other, however; only that these methods yield different results. Indeed, this difference is the most important conclusion of our research. The species under investigation should play a major role in the decision of which sampling method to use. Additional studies that compare the two methods for estimating vigilance for other animals will be valuable, and we predict that these studies also will show that estimates of vigilance from focal sampling versus scan sampling are not equivalent.

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