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What have we been looking at? A call for consistency in studies of primate vigilance

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Abstract:

Vigilance functions to detect threats. In primates, these threats emerge from both predators and conspecifics, but a host of other social, demographic and ecological factors have been shown to influence primate vigilance patterns. The primate vigilance literature is thus characterized by considerable variation in findings, with inconsistent or contradictory results reported not only across different species but also within species and populations across studies. Some of this variation could emerge from fundamental differences in the methods employed, making comparisons across species and groups challenging. Furthermore, identifying consistent behavioral markers for the state of vigilance appears to have proved challenging in primates, leading to a range of definitions being developed. Deviation at this level leads directly into concomitant variation at the level of sampling methodologies. As a result, the primate vigilance literature currently presents a diverse series of approaches to exploring subtly different behaviors and phenomena. This review calls for a greater consistency in studying vigilance, with the aim of encouraging future research to follow similar principles leading to more comparable results. Identifying whether an animal is in a vigilant state is challenging for most field researchers; identifying and recording a more general behavior of 'looking' should though be more achievable. Experimental approaches could then be employed to understand the compatibility 'looking' has with predator detection (and other threats) in individual study systems. The outcome of this approach will allow researchers to understand the key determinants of looking in their study groups and explore threat detection probabilities given an individual or group's relative level of looking.

1 | INTRODUCTION

Group-living is widespread throughout the animal kingdom, with most adaptive explanations centering on its antipredator benefits. Early explanations for grouping suggested that that animals benefited from forming aggregations as it decreased individual risk of predation (Bates, 1863; Belt, 1874). Despite there being clear evidence that group-living or aggregation formation can aid in predation avoidance, research has struggled to identify the precise mechanisms governing its evolutionary selection (Beauchamp, 2015). Typically, research interested in these mechanisms has explored two principle pathways, namely risk-dilution (Hamilton, 1971; Vine, 1971) and the group-vigilance hypotheses (Pulliam, 1973).

The group-vigilance hypothesis, otherwise known as the ‘many-eyes effect’ (Powell, 1974) or ‘collective detection’ (Lima, 1995), suggests that gregariousness carries the advantage of cumulative senses, increasing the likelihood of early detection of predators (Miller, 1922). As group size increases, therefore, the level of vigilance performed by individual group members should decrease. Reduction in individual vigilance allows animals to take advantage of the relative safety of groups by devoting more time to other fitness enhancing tasks such as foraging (Bednekoff & Lima, 1998; Dehm, 1990; McNamara & Houston, 1992; Pulliam, 1973; Roberts, 1996). The prediction of an inverse relationship between group size and vigilance was initially well supported, and became known as the ‘group-size effect on vigilance’ (Elgar, 1989; Lima, 1995). Interestingly, however, an increasing number of studies, particularly on primates, do not report a group-size effect on vigilance (Treves, 2000).

Treves (2000) explored possible explanations for this lack of consistent support for the group-size effect in primates, focusing on several assumptions consistently made about predator and prey species. For example, one specific assumption was the idea of a trade-off between vigilance and feeding, or put another way, the assumption that vigilance and feeding were incompatible. Primates can feed upright or use their hands to harvest and manipulate food, potentially allowing them to handle food and scan concurrently (Cowlishaw et al., 2004). However, Treves (2000) found no evidence that this explained the lack of support for a group-size effect on vigilance in primates, instead concluding that the absence of a group-size effect may be partially accounted for by within-group vigilance. Certainly, vigilance has been reported to be important in mate and competitor detection in male chacma baboons (*Papio ursinus*) (Cowlishaw, 1998), in social monitoring for within-group threats in chimpanzees (*Pan troglodytes schweinfurthii*) (Kutsukake, 2006), and monitoring both within-group and extra-group threats in blue monkeys (*Cercopithecus mitis*) (Gaynor & Cords, 2012). Furthermore, group size may hold a low predictive value for individual predation risk, since groups contain a mix of age-sex classes and vulnerable and non-vulnerable individuals (Treves, 2000). Indeed, with a plethora of confounding variables influencing individual risk of predation, the group-size effect on vigilance is unlikely to be explained by risk-dilution in larger groups (Roberts, 1996).

At the end of his influential review, Treves (2000) concluded that several functional differences in vigilance behavior and safety in groups accounted for primates deviating from the group-size effect. Nearly two decades on, however, what emerges is that the group-size effect is just one area where the literature of primate vigilance paints a picture of inconsistent or variable results. Over the same period, it has become evident that a variety of other social, demographic and ecological factors could also play a role in shaping primate vigilance patterns. To bring things up to date, therefore, we first review the factors influencing primate vigilance. This highlights an important finding; the primate vigilance literature is characterized by a large number of apparently contradictory studies. While some of this may be expected given the diversity of visual systems, social systems and ecological pressures across species, contradictory results are also apparent within species. We propose that part of this variation may be explained by the considerable methodological inconsistencies that have emerged between studies. Interestingly, primate studies were significantly under-represented in the theoretical chapters in a recent comprehensive review of the vigilance literature (Beauchamp, 2015), despite representing a significant proportion of the available studies. To some extent this is likely to reflect the factors we identify to account for the variation in primate vigilance research that undermines the comparability of studies. Nevertheless, the importance of primate study systems for addressing questions relating to social threats is probably underappreciated. We thus present a framework for future studies of primate vigilance behavior.

2 | VARIATION IN PRIMATE VIGILANCE STUDIES

We conducted an extensive literature review that identified 59 studies exploring vigilance in (non-human) primates (Appendix 1 – study list), 27 of which have been conducted since Treves' (2000) review. Studies span the wild and captivity, although understandably focus on haplorrhines given the inherent challenges of studying vigilance in nocturnal species (Beauchamp, 2015). Within the haplorrhines, New World monkeys, Old World monkeys and apes were all well represented. Studies have explored vigilance in relation to a broad range of topics including group size, nearest neighbors, social dynamics, spatial position and vegetation structure or density (Table 1). Studies of many of these factors have led to inconsistent findings.

[Table 1 here]

Group size effects remain a significant area of focus. Although some studies have reported evidence for vigilance declining with group size (de Ruiter, 1986; Isbell & Young, 1993), many find no effect (Treves, 2000). For example, Treves et al (2001) failed to detect a group-size effect on vigilance in black howler monkeys (*Alouatta pigra*). Some studies, however, have isolated a group-size effect by exploring specific behavioral and socio-ecological conditions. Hill & Cowlishaw (2002) reported that adult female chacma baboons in smaller groups spent more of their foraging time vigilant, once refuge proximity, habitat type and neighbor proximity had been controlled for. Stojan-Dolar & Heymann (2010) initially found no evidence of a group-size effect in single species groups of moustached tamarins (*Saguinus mystax*), likely due to unusually large study groups. Nevertheless, a negative group-size effect was present when *S. mystax* formed mixed species groups with saddleback tamarins (*Saguinus fuscicollis*), although this effect was only apparent during resting behaviors. When Gosselin-Ildari & Koenig (2012) defined "antipredatory vigilance" and "social monitoring" as separate behaviors, they subsequently detected a negative group-size effect on "antipredatory vigilance" in common marmosets (*Callithrix jacchus*). Similarly, when vigilance of this species was categorized as either "induced" or "routine", the frequency of "induced vigilance" (scans longer than 1 second) increased with group size (Teichroeb & Sicotte, 2012).

Alongside these group size phenomena, factors such as distance to nearest neighbors and number of neighbors in close proximity have been shown to influence primate vigilance patterns. Studies have consistently reported vigilance to decrease when focal animals had at least one neighbor(Steenbeek, Piek, van Buul, & van Hooff, 1999; Stojan-Dolar & Heymann, 2010; Treves, 1998; Treves et al., 2001; van Shaik & van Noordwijk, 1989), whilst increased time spent alone (Rose & Fedigan, 1995) and decreased density of nearby neighbors (relative to distant neighbors) (Treves, 1999b) increase individual vigilance use. Despite both Kutsukake (2006) and Watson et al. (2015) reporting that number of neighbors did not significantly affect vigilance in chimpanzees and rhesus macaques (*Macaca mulatta*) respectively, a host of other studies have shown vigilance use to decrease with increasing number of neighbors (Busia, Schaffner, & Aureli, 2016; Cowlishaw, 1998; Stojan-Dolar & Heymann, 2010), although sometimes only for specific behaviors (Stojan-Dolar & Heymann, 2010; Teichroeb & Sicotte, 2012). Robinson (1981) found that wedge-capped capuchins (*Cebus olivaceus*) increased vigilance with increasing distance to nearest neighbor; conversely, Suzuki & Sugiura (2011) reported vigilance increased as distance to nearest group member decreased in Japanese macaque (*Macaca fuscata*) adult females.

Age-sex class, identity and rank of neighbors are also key determinants of vigilance use in a range of primate species. When one or more neighbors were adult, male vigilance was lower in both white-fronted capuchins (*Cebus albifrons*) and tufted capuchins (*C. apella*) (van Shaik & van Noordwijk, 1989) whilst similar effects were reported for Thomas's langurs (*Presbytis thomasi*), but only in adult females with infants (Steenbeek et al., 1999). Opposite effects were found for white-faced capuchins (*Cebus capucinus*), however, with vigilance increasing with increasing number of male neighbors (Rose & Fedigan, 1995). Vigilance has also been shown to increase based on the relationship between focal individuals and neighbors. For example, vigilance increased in adult female blue monkeys when either of the two highest-ranking females were nearby (Gaynor & Cords, 2012), when individual mountain gorilla (*Gorilla gorilla beringei*) who share agonistic relationships were in proximity (Watts, 1998), and when non-affiliates were in proximity (Kutsukake, 2006). Vigilance in ursine colobus (*Colobus vellerosus*) was lower in presence of familiar versus unfamiliar neighbors (MacIntosh & Sicotte, 2009).

Factors relating to focal animals, such as their age-sex class and dominance status also influence vigilance patterns (Chance, 1967), with numerous studies reporting males to be more vigilant than other age-sex classes (Baldellou & Henzi, 1992; de Ruiter, 1986; Fragaszy, 1990; Gould, Fedigan, & Rose, 1997; Isbell & Young, 1993; Rose & Fedigan, 1995; Steenbeek et al., 1999; Treves, 1998, 1999c; van Shaik & van Noordwijk, 1989; Watson et al., 2015). Nevertheless, a number of other studies report no difference between sexes (Cowlishaw, 1998; Gould, 1996; Gould et al., 1997; MacIntosh & Sicotte, 2009; Teichroeb & Sicotte, 2012; Treves, 1998). Subordinate individuals have been reported as being more vigilant than dominants in several species (Chance, 1967; Caine & Marra, 1988; Gaynor & Cords, 2012; Keverne, Leonard, Scruton, & Young, 1978; Pannozzo, Phillips, Haas, & Mintz, 2007); conversely, however, high-ranking individuals are found to be more vigilant in other species (Gould et al., 1997; Isbell & Young, 1993; Watson et al., 2015). Alberts (1994) found daughters of low-ranking yellow baboon (*Papio cynocephalus*) mothers glanced more often than daughters of high-ranking mothers, whilst sons of high-ranking mothers glanced more often than their low-ranking counterparts. Rose & Fedigan (1995) found that alpha male white-faced capuchins tended to be the most vigilant individual in each group, whilst Gould (1996) reported a similar result for alpha female ring tailed lemurs (*Lemur catta*), but found no relationship between vigilance behavior and dominance rank among adult males. Interestingly, two studies on rhesus macaques have produced opposite results, with Haude et al (1976) reporting that subordinates are more vigilant than dominants, whilst Watson et al. (2015) reported that high-ranking individuals were more vigilant, although Haude et al (1976) also notes that intermediates in the dominance hierarchy were the most vigilant individuals.

When “social monitoring” has been recorded as a distinct behavior, varied results have emerged with Gosselin-ildari & Koenig (2012) reporting social monitoring to increase with group size, whilst Kazahari & Agetsuma (2010) found social monitoring frequency was higher in small feeding groups of Japanese macaques. The subject of gaze may also be important. Female gelada (*Theropithecus gelada*) were found to glance significantly more at males than other females in their unit and also tended to glance more frequently at regular grooming partners than other females, regardless of rank. In addition, glance rates of males towards females was most strongly correlated with female rank, although the result was not significant (Dunbar, 1983). In captive talapoin monkeys (*Miopithecus* talapoin), dominants paid more attention to the opposite sex compared to subordinates. Adult female eastern gorillas were more likely to cease feeding and focus on males than females (Watts, 1998), whilst lower ranking patas monkeys (*Erythrocebus patas*) gazed toward higher-ranking animals more often than vice versa (McNelis & Boatright-Horowitz, 1998). These studies serve to highlight the importance of social vigilance in primates, despite the inconsistent patterns reported, supporting to some extent the classic predictions of Chance (1967) on “attention” in primate groups.

The effect may extend to extra-group social monitoring. Vigilance was found to increase in areas of range overlap with other groups in both ursine colobus (MacIntosh & Sicotte 2009) and Thomas’s langurs, although this latter effect was not consistent across all conditions (Steenbeek et al. 1999). Rose & Fedigan (1995) reported that male white-faced capuchins in two of the three groups with overlapping ranges were more vigilant in areas of overlap. Similarly, higher vigilance in areas close to the boundary of the home range has been reported in black-handed spider monkeys (*Ateles geoffroyi*) (Busia et al. 2016).

Investigations into the influence of reproductive state of adult females on vigilance have also yielded variable results. Despite Treves (1998) reporting that there was no difference in vigilance use between adult females with or without infants in both redtail monkeys (*Cercopithecus ascanius schidtii*) and red colobus (*Procolobus badius tephroceles*), several subsequent studies reported that mothers with dependent infants more vigilant than those with independent young or females without infants (Boinski et al., 2003; Steenbeek et al., 1999; Treves, 1999c; Treves, Drescher, & Snowdon, 2003). It has also been reported that all adult individuals increased vigilance after birth of infants in black howler monkeys (Treves et al., 2001), and vigilance increased during infant-carrying in moustached tamarins (Stojan-Dolar & Heymann, 2010). When infants are separated from their mothers, mothers increase vigilance if the infants are out of their mother’s reach, but not when moving alone (Onishi & Nakamichi, 2011). Treves (1999c) also found that females glance towards other conspecifics more frequently when infants are younger or out of contact. Treves et al (2003) highlighted that the greatest increase in vigilance was found when immatures were conspicuous; however, allogrooming has been shown to reduce maternal vigilance towards infants in several species (Kutsukake, 2006, 2007; Maestripieri, 1993; Treves, 1999c). Finally, Gosselin-Ildari & Koenig (2012) reported that “antipredatory” vigilance was higher for breeding than non-breeding individuals, whilst “social monitoring” was mostly unaffected by breeding status.

Beyond exploring social, reproductive and demographic determinants of vigilance, the effect of a range of ecological factors has also been investigated. Vigilance rate has been shown to reduce with increasing foliage density in redtail monkeys and blue monkeys (Cords, 1990; Gaynor & Cords, 2012), but habitat structure and visibility had no effect on vigilance in yellow baboons (Alberts, 1994), chacma baboons (Hill & Cowlishaw, 2002), and moustached tamarins (Stojan-Dolar & Heymann, 2010). However, Stojan-Dolar & Heymann (2010) found that vigilance was highest in medium density vegetation during passive grooming, whilst male vigilance was reportedly higher in open than closed habitats in chacma baboons (Cowlishaw, 1998). Vigilance is consistently reported to decrease with height in canopy for a number of species (de Ruiter, 1986; Gaynor & Cords, 2012; Kutsukake, 2006; MacIntosh & Sicotte, 2009; Smith, Kelez, & Buchanan-Smith, 2004; Steenbeek et al., 1999; Teichroeb & Sicotte, 2012; van Shaik & van Noordwijk, 1989) although de Ruiter (1986) noted that vigilance was lowest on the ground for wedge-capped capuchins. Conversely, Kutsukake (2006) reported vigilance was highest at 0-1 meters in chimpanzees while white-faced capuchins which were also reportedly most vigilant near the ground (Campos & Fedigan, 2014). Stojan-Dolar & Heymann (2010) found that vigilance initially decreased within increasing height in *S. mystax* but increased again at higher canopy levels.

Higher levels of vigilance have been reported in animals occupying exposed positions (Baldellou & Henzi, 1992; van Shaik & van Noordwijk, 1989). Josephs et al (2016) reported the same effect when using spatial position as a proxy for exposure in vervet monkeys (*Chlorocebus pygerythrus*) but white-faced capuchins were reported to exhibit lower vigilance when exposed (van Shaik & van Noordwijk, 1989). Cowlishaw (1998) reported that chacma baboons in Namibia increased vigilance with distance from refuge; when data from this population was combined with those of a single group from a South African population, the same effect was found but only during foraging behaviors (Hill & Cowlishaw, 2002). Increased vigilance has also been reported in spatially peripheral individuals (Robinson, 1981; Steenbeek et al., 1999; A Treves, 1998; van Shaik & van Noordwijk, 1989), although no effect of spatial position on vigilance has been reported in other species (Carolyn L Hall & Fedigan, 1997; A Treves, 1998). White-faced capuchin vigilance behavior was heightened in higher risk areas in the absence of actual threats (Campos and Fedigan, 2014).

2.1 | Variation in primate vigilance studies: What's the problem?

Considerable variation exists across and within primate species in the relationships between vigilance and its social, demographic and ecological drivers. Of course, many of these results could reflect the actual differences that exist within and across different primate groups. Nevertheless, whilst several potential determinants of primate vigilance have received widespread investigation (e.g., age-sex class, number of neighbors), there is considerable variation in approaches and the environmental and social factors explored as predictor variables. Indeed, this variation is indicative of more fundamental variation that exists within the methodological approaches used in primate vigilance. Interestingly, this was a topic briefly touched on by Treves (2000), who highlighted that many primate studies use idiosyncratic sampling rules and definitions of vigilance. He concluded, however, that methodological differences could not account for the absence of a group-size effect on vigilance and instead focused on functional explanations for why we expect a group-size effect on vigilance (Treves, 2000). Nevertheless, given the greater diversity of primate vigilance research now available it seems pertinent to revisit this vital area, since the variation in methodological approaches appears to be of much greater significance that envisaged at that time. In particular, the two key methodological levels in which primate vigilance studies show inconsistency appear to have been critically important:

1) Variation in how vigilance is defined.
2) Variation in sampling methodology.

While both facets are clearly important for interpreting research into primate vigilance, a key issue is that variation at one level directly feeds into all other aspects of the study. As a result, variation at either level could make it challenging to compare studies, and so make it difficult to determine whether new or inconsistent findings are specific to primates in general, species, or study groups. Robust sampling methodologies are critical of course, but we initially explore the historical use of the term vigilance in animal studies, as this may help to understand the variation that exists within primate vigilance literature.

3 | VIGILANCE TERMINOLOGY AND INTERPRETATIONS OF BEHAVIORS

Although Belt (1874) suggested that animals benefit from being in groups because it is unlikely an approaching threat would go undetected by all group members, the first published work that discusses the idea of predator detection in terms of sensory capacity appears to be Galton's (1871) study of Damara cattle. Even so, while the terms “glance” and “alert” appear, “vigilance” isn’t explicitly mentioned. Galton instead describes that Damara cattle can use the senses associated with eyes, ears and nose to monitor the environment for threats.

Over a decade later, Oswald (1885) discussed the notion that as monkeys face predation risk during dark hours, they can alleviate risk via the increased vigilance use of group members acting as sentries. This appears to be the first use of the term vigilance in this context, although Holder (1885) used the terms “vigilance”, “vigilant”, and “watchfulness” when describing the aggressive nest guarding behavior of male four-spined sticklebacks (*Apeltes quadracus*). Moving forward, further studies began to use the term vigilance in a range of contexts, although a formal definition was lacking (Cameron, 1908; Davis, 1941; Hartley, 1947; Williams, 1903), whilst other studies continued to discuss vigilance with regards to threat or predator detection without making reference to the actual term vigilance (Jenkins, 1944; Leopold, 1951; Marler, 1956).

Much early research used a range of terms that are generally considered anthropomorphic now, such as guarding or sentry, and their use is now generally avoided (Beauchamp, 2015). Hall (1960) was critical of terms such as “sentinel” when used to describe the behaviors of male chacma baboons, suggesting they were presumptive and should be discarded in favor of more objective observations. Nevertheless, he used the term “watchfulness” to describe lengthy periods where individuals appeared to have elevated vigilance, suggesting that during these periods the individuals were either “nervous”, “restless” or “irritable”. Thus, despite the valid call for greater objectivity, Hall (1960) appears to have drawn conclusions based on subjective assessments of the state of the animals.

The next major leap forward appears to center on Pulliam's (1973) model exploring how the probability of detecting a predator increases with group size. Pulliam assumed that “head-cocks” were used by birds to detect predators, and that individual birds could diminish investment in this behavior as group size increased without succumbing to increased predation risk. Despite being widely cited in studies of animal vigilance, the term “vigilance” wasn’t used a single time in the article, instead “head cocks” by flock members were assumed to place the individual group members in a posture allowing them to collect information on predation threats. This highlights some of the underlying assumptions of this model; that certain behaviors or postures adopted by an animal completely close off other information acquisition pathways, assuming incompatibility between the head-down posture (i.e., foraging) and predator detection.

Postural terms that simply document the behavior of an animal, such as “looking-up” (Jenkins, 1944), “head-cocks” (Pulliam, 1973), “raising-head” or “head-turning” (Marler, 1956) seem on the surface to be an adequate method for recording animal vigilance. However, definitions of the term vigilance suggest more precise requirements: “The action or state of keeping careful watch for possible danger or difficulties” (Oxford Dictionary, 2017). Beauchamp (2015), in a large-scale review of animal vigilance literature, put forward a definition from a biological perspective, viewing vigilance as the behavior or state of “monitoring the surroundings for potential threats”. Interestingly, both definitions suggest the sole function of vigilance is to detect threats or difficulties; such requirements are unlikely to be captured by postural definitions alone. The key problem, therefore, is how to detect when an animal is actually in a vigilant state? Researchers typically attempt to identify a postural change or behavioral response made by a study animal that shows they are in a vigilant state. Beauchamp (2015) refers to these outward behavioral signs as ‘markers’ for vigilance. The aim when identifying a good marker for vigilance is that it should be consistently performed concurrent to an animal being in a vigilant state, and be almost never observed when not in a vigilant state. Such conditions are challenging to fulfil.

Most markers of vigilance cannot claim to be the true “markers” Beauchamp (2015) describes, since animals could use “head cocks” (Pulliam, 1973) or “head-up” (Cowlishaw, 1998) to collect multiple forms of visual information that are not all related to threats. For example, “raising of the head” or “scanning the environment” could also be used in personal food search (Giraldeau & Caraco, 2000; Treves, 2000), monitoring of threatening group-members (Hall, 1960; Kutsukake, 2006), intra- and inter-sexual competition (Burger & Gochfeld, 1988; Jenkins, 1944), gestures between individuals (Hall, 1962; Hausfater & Takacs, 1987), movement and navigation (Mueller, Fagan, & Grimm, 2011; Treves, 2000), and scanning for prey (Cameron, 1908; Hartley, 1947).

Dimond and Lazarus (1974) presented an alternative definition of vigilance from an operations research perspective, with vigilance being “a measure of the probability that an animal will detect a given stimulus at a given instant in time”. More vigilant individuals then have a higher probability of detecting a stimulus or event. This seems to be the first use of the term vigilance to describe the collection of multiple types of information; in this sense vigilance is not exclusively linked to detecting predators but instead, as the behavior of ‘looking’, allowing an individual to be attentive to multiple sources of information. This definition enables the consideration of intraspecific competition as a function of vigilance, whilst also allowing for vigilance to be used to collect information on other non-threatening stimulus, such as resources. However, this definition would require the term vigilance to be redefined to incorporate all forms of visual information acquisition, regardless of whether the visual stimuli is threatening or not.

Although it is possible that an animal in a vigilant state can also collect a range of additional information simultaneously, vigilance is rarely considered a multifunctional looking behavior. Instead definitions typically present vigilance as a subset of looking behaviors associated with threat detection. This does not, however, reduce the problems associated with identifying true ‘markers’ for vigilance in animals. In fact, it seems likely that sampling vigilance is a challenging goal for certain taxa, particularly primate species. Indeed, several studies have now gone a step further and subcategorized their study species looking behaviors into different types of vigilance (e.g., routine or induced vigilance: Blanchard & Fritz (2007)). Such classifications also have important implications for how we design our studies.

3.1 | Types of vigilance

Definitions of vigilance tend to identify it as a precautionary or preventative behavior, functioning to assess risk at given moment in time, allowing for early detection of threats. Once a threat has been detected, however, an animal could also use vigilance to monitor that threat, and so inform an animal’s evasive behaviors and decision to flee (Beauchamp 2015). Such distinctions are evident in studies that have separated vigilance into “routine” and “induced” components (Blanchard & Fritz, 2007; Teichroeb & Sicotte, 2012). Routine vigilance concerns an animal’s visual monitoring behaviors during its “spare time”, suggesting that no threatening stimuli is present. In contrast, induced vigilance concerns the active response to a stimulus. Vigilance has also been subdivided into “preemptive” and “reactionary” terms (Boinski et al., 2003); preemptive vigilance requires active visual search of the environment by an animal in the absence of threatening stimuli. Reactionary vigilance on the other hand is the visual response of an animal to the detection of a threatening stimulus. Similar classifications have been used to define “anti-predator” vigilance (Hirsch, 2002) and vigilance “towards a potential predator” (Gould, 1996).

Although the terminology used by these studies varies, they point to similar distinctions within vigilance behavior. One important implication is that “reactive” vigilance is recorded whenever an observer detects a threatening stimuli (Blanchard & Fritz, 2007; Boinski et al., 2003; Gould, 1996; Hirsch, 2002; Teichroeb & Sicotte, 2012), or alternatively when an observer notices a behavioral change in members of the study group that betrays the presence of a threat (e.g., blatant evasive behaviors: Boinski et al., 2003). While the distinction between preemptive and reactionary vigilance is intuitive with regards to predation threats, monitoring social threats is likely to be more nuanced and the distinction between preemptive and reactionary vigilance therefore more challenging. Although reactive vigilance should be possible to record during encounters between rival conspecific groups (Gaynor & Cords, 2012; Gould, 1996; MacIntosh & Sicotte, 2009), within-group vigilance is unlikely to produce behavioral changes that are as simple to detect. As a consequence it may be challenging to robustly separate these forms of vigilance in primate groups where social threats are also prevalent. To counteract this, authors have tried to tease apart antipredatory vigilance and social vigilance, although the distinction between "social vigilance" (Jack, 2001) or "within-group surveillance" (Treves, 1999c) and antipredator vigilance is challenging (Beauchamp 2015). Identifying true markers for these distinct vigilance behaviors may be unachievable. Perhaps unsurprisingly, therefore, primate studies have adopted a diversity of vigilance definitions. Few, however, have formally noted whether they are exploring preemptive or reactionary vigilance, however, and this issue has generally been overlooked in most studies.

3.2 | Primate vigilance definitions

All primate vigilance studies have provided vigilance definitions in describing their methods and this reveals significant variation in how the behavior of vigilance is defined. Some definitions require an interpretation of an animal's 'state', others utilize visual terminology (e.g., looking, gazing, staring etc.), or require a head or eye movement, while operational definitions that treat vigilance as a multifunctional behavior have also been proposed. Many definitions incorporate a number of these facets. This diversity is encapsulated by the plethora of interchangeable terms used within primate vigilance studies (Table 2; Appendix 1).

[Table 2 here]

Some definitions require an interpretation of an animal's state (Table 2). For example, Campos and Fedigan's (2014) definition of "scanning intently at long range while alert and stationary" imposes a requirement of an animal being "alert" so constraining when vigilance can be recorded, whilst "scanning intently" necessitates an interpretation the behavior of the focal animal. This type of definition appears to be a clear attempt to identify a 'marker' for vigilance, but the need for observers to interpret an animal's state from a postural or behavior change may not be objective, particularly when they are not naïve to the questions of study. Terms such as "cautiously observing" (de Ruiter, 1986) or scanning/staring "intently" (Gould et al., 1997; Rose & Fedigan, 1995) add a further complexity to similar definitions in the literature; both contain adverbs that ask observers to make an interpretation of an animal's current behavior.

The use of a visual term to define a vigilance term is common practice in primate vigilance literature (Table 2). Terms such as 'gaze', 'attention', 'scanning' or even 'looking' carry similar problems to the definitions based on an individual's state; they do not necessarily infer a state of vigilance but instead ask observers to interpret when an animal is collecting visual information. The key problem in this instance is that each term is open to interpretation. Several different observers could potentially converge on a similar theoretical understanding of what 'gaze' means, but could interpret the act of 'gazing' differently to one another when recording data in their study. Objective definitions of this sort are challenging.

Numerous studies appear to try and tackle this problem by using postural changes or eye movement in elements of their vigilance definitions (Table 2). Some of these definitions take a very concise multifunctional form such as "head up, eyes open" (Cowlishaw, 1998) or "movement of the head and/or eyes" (Gaynor & Cords, 2012), whilst other authors have added postural requirements to vigilance definitions such as "lifting of the head" (Caine & Marra, 1988) or "turning the head" (Suzuki & Sugiura, 2011). Some are more precise such as "Raising and lowering of the line of vision by at least 30 degrees relative to the horizontal plane" (Bshary & Noe, 1997), or "Head movement of at least 45°, in any direction" (Steenbeek et al., 1999). While these definitions could potentially alleviate issues concerning interpreting the internal state an animal or the objectivity of visual terms, consistently estimating these angles of movement accurately may be difficult for animals that regularly change orientation in the horizontal and vertical planes. It has also been highlighted by Treves (2000) that primates often feed in an upright sitting position, or alternatively can feed in a range of tripedal and bipedal postures, each of which would have their own sensory limitations. Cowlishaw et al. (2004) have shown that upright posture use concurrent to food handling can allow animals to use vigilance; head movement may thus not be necessary to adopt a vigilant state.

Because primate vigilance studies have shown continued interest in the supposed trade-offs between foraging and vigilance this has led to vigilance only being recorded during foraging and stationary behaviors (Table 3). Recording vigilance in moving animals is challenging, and several studies have excluded sampling vigilance use during travel activities, or when focal animals move beyond a certain distance during observations (Gaynor & Cords, 2012; Smith et al., 2004; Stojan-Dolar & Heymann, 2010; Treves, 1998, 1999a; Treves et al., 2001). While such definitions can help methodologically by restricting the focus of data collection it nevertheless limits the understanding of vigilance and questions that can be addressed with the data.

[Table 3 here]

Problems surrounding postural definitions appear to have been circumnavigated via the development of multifunctional vigilance definitions, which operationalize vigilance based on excluding behaviors that are likely inhibit its use. In a series of articles on several different primate species, Treves consistently defined vigilance as any visual search or scanning “directed beyond an arm's reach” (see Treves, 1998, 1999a, 1999b, 1999c, 2000, Treves et al., 2001, 2003). This definition highlighted that “Scanning serves many purposes (food search, travel-path planning, etc.), but an animal searching for food may incidentally spot a predator” (Treves 1999b). This bears direct resemblance to the operational definition of vigilance provided by Dimond and Lazarus (1974). Despite not explicitly stating that the definitions utilized are concerned with either preemptive or reactionary vigilance, Treves consistently made it clear that he was recording vigilance as a multifunctional looking behavior, suggesting that any form of looking would be recorded, without forming a prior expectation of the information an animal was collecting. The work of Treves (Treves, 1998, 1999a, 1999b, 1999c, 2000, Treves et al., 2001, 2003) appeared to popularize these ideas, with several recent studies citing this work as justification for a multifunctional vigilance definition (Busia et al., 2016; Gaynor & Cords, 2012; Stojan-Dolar & Heymann, 2010). Earlier authors had also arrived at similar definitions. Chapman & Chapman (1996) required the animal “looked up, away from the substrate it was on, or away from the food item it was processing”, while van Schaik & van Noordwijk (1989) defined vigilance as "Looked around, providing it was not inspecting vegetation or partners at close range". Hall & Fedigan (1997) defined vigilance as scanning areas and substrates not in an animal’s immediate proximity (within 3 m), while definitions requiring animals to look outside their immediate vicinity or substrate have appeared in a number of studies (Baldellou & Henzi, 1992; Gould et al., 1997; Hirsch, 2002; Jack, 2001; Josephs et al., 2016; Rose & Fedigan, 1995). Provided the immediate vicinity is objective and defined, these definitions should be easier to replicate across studies. In doing so it may obviate many of the problems of using a ‘marker’ approach to recording vigilance.

Although multifunctional definitions remove many of the problems associated with inferring the state of vigilance in an animal or defining the significance of head movements, one implication is that researchers are technically no longer studying vigilance per se, but are instead focused on the behavior of ‘looking’. As a result, a divergence has emerged within the literature, with the most recent work suggesting authors are trending towards the use of multifunctional definitions. This is likely a robust course of action to take provided researchers bear in mind that multifunctional approaches do not explicitly explore vigilance patterns.

One final important element of the definitions of vigilance concerns the lack of consistency in the use of terminology. For example, what constitutes a ‘glance’ in one study may not constitute a glance’ in another. Understandably, many authors have attempted to record the very brief head movements that primates’ make, and in defining these glances have included a time requirement for the behavior. Interestingly, the time requirements for glances in some studies exceed the time requirements for ‘scans’ in others (Table 4). Such inconsistencies in definition have massive implications for the comparability of results across studies.

[Table 4 here]

3.3 | A call for consistency: The behavior of ‘looking’

Despite there being over 50 published studies of primate vigilance, a general review of methodological approaches has been lacking. Treves’ (2000) review stands out as the main attempt to do this thus far, but stops short of exploring methodological differences in great deal and focuses mainly on phenomena related to group size. Nevertheless, it appears that a significant outcome of Treves’ work has been the adoption of operational multifunctional definitions. We advocate that this should be standard practice going forward. Attempts to measure ‘markers’ of vigilance have the embedded assumption that an animal needs to be vigilant in order to detect a predator. In contrast it seems reasonable to suggest that an animal looking in the correct direction will have an equal chance of detecting a predator regardless of their intended gaze focus or motivation (Treves, 1998, 1999a, 1999b, 1999c, Treves et al., 2001, 2003). Instead, therefore, we should move away from studying vigilance per se, and instead focus attention on studying the behavior of looking. In this context, we define an individual as looking if:

“Its eyes are open, and its line of vision extends beyond its hands and the substrate, animal or object that they are in contact with”

This definition is tied to a key prediction however, that any form of looking behavior (in which the focal animal essentially focuses beyond an arm’s reach) should reveal a predator or other threat if it is present. In essence it suggests that animals can collect multiple types of information concurrently and that different information acquisition pathways are compatible. If, as seems likely, animals are under consistent pressure to be attentive to numerous different visual stimuli (food, mates, threats etc.) then pre-emptive vigilance is essentially just one facet of this broader looking activity. Analytically, the behavior can be explored in conjunction with the same sorts of predictor variables used in existing vigilance studies (e.g. number of near neighbors, height above ground, habitat visibility etc.). In doing so it opens up the potential for hypotheses not related to threat detection to be investigated. Intriguingly, if the behavior of looking beyond an arm’s reach will likely detect a predator with reasonable probability regardless of the intended function of looking, it raises the question of whether these animals need to actively search their environment for predators. Will looking for other fitness enhancing tasks (foraging, avoidance of intraspecific competition, mating opportunities) provide adequate predator detection without dedicated ‘vigilance’?

Determining the answer to this question will require carefully planned studies, but should be a highly profitable avenue for future research. This likely goes beyond what can be done with observational studies, therefore experimental approaches, such as through simulated predator attacks (Kaby & Lind, 2003; Lima & Bednekoff, 1999) will undoubtedly be needed. The key is to design ingenious experiments that constrain individuals to certain behaviors or postures, and test predator detection capabilities. There will be a necessary level of variation across these studies as experiments must focus on the unique attributes of the local predator guilds. This variation shouldn't necessarily be a problem as the outcome should reflect accurate detection probabilities for each study group. Going forward, any study of vigilance behavior (on a given species or group) will benefit from robust and complimentary empirical data defining the informational capacities of the body postures of the relevant study species.

Related to our recommendations, we advise that future work moves away from attempts to tease apart any of the subtypes of looking behavior, such as 'antipredator vigilance' or 'social monitoring', during data collection since an unambiguous assessment of what an animal is looking at is unachievable at all times. Although the outcome from statistical analysis can shed light on which components contribute to individual or group looking behaviors when assessed alongside appropriate socio-ecological variables that effectively capture their animals' perception of fear, attempts to ascribe definitions of subtypes of looking will likely re-establish the inconsistencies highlighted earlier. This is not a call for the cessation of studies of vigilance, however. Rather, it is to advocate for variables associated with antipredator vigilance to be assessed within the broader looking framework.

4 | VARIATION IN SAMPLING METHODOLOGY

A host of sampling methodologies are available to behavioral ecologists studying animal vigilance; focal animal sampling and scan sampling (or instantaneous scan sampling) seem to be the most popular (Hirschler, Gedert, Majors, Townsend, & Hoogland, 2016), although one-zero sampling has also been utilized in primate vigilance work (Table 5). Typically, continuous focal sampling is advantageous in vigilance studies as it allows observers to record duration measures for vigilance, in addition to frequency measures. However, there is variation in how these measures are manipulated for analysis and subsequently reported. Frequency measures are typically reported as vigilance rates based on the duration of the focal observations (Alberts, 1994; Chapman & Chapman, 1996; Cords, 1990; MacIntosh & Sicotte, 2009; Maestripieri, 1993; Teichroeb & Sicotte, 2012) but the same information can also be reported simply as a frequency measure (Barros, Alencar, Silva, & Tomaz, 2008; Kazahari & Agetsuma, 2010). When individuals are easily identifiable and subject to repeated observations, a number of authors have chosen to average their frequency measure by individual (Cords, 1995; Keverne et al., 1978) although frequency measures have also been averaged per observation session, grouping data from all individuals instead (Nunes, Gonçalves, Emile, & Barros, 2010). Despite utilizing 60-second continuous focal samples to record within-group surveillance in redtail monkeys and red colobus, Treves (1999c) reported the percentage of focal samples containing at least one glance toward another conspecific. Manipulating vigilance into a binary variable was deemed more reliable than utilizing a frequency measure due to the inherent difficulties in recording within-group surveillance reliably.

[Table 5 here]

Studies recording duration measures for vigilance typically average individual vigilance bout durations, either for each experimental trial (Barros et al., 2008) or each focal observation (Hirsch, 2002; Nunes et al., 2010), although bout lengths can be overlooked with total time spent vigilant instead averaged for each individual across all observations (Caine, 1984). Individual vigilance bouts have also been cumulatively summed across a focal observation, allowing a duration measure to be calculated (Gaynor & Cords, 2012; Gould et al., 1997; Kutsukake, 2007; Treves, 1998, 1999a). Another alternative has divided cumulative duration measures by total observation time, producing either vigilance rates (Gould, 1996; Hall & Fedigan, 1997; Treves, 1999c; Watson et al., 2015) or proportion/percentage of time spent vigilant (Busia et al., 2016; Caine & Marra, 1988; Cowlishaw et al., 2004; Jack, 2001; Onishi & Nakamichi, 2011; Rose & Fedigan, 1995; Stojan-Dolar & Heymann, 2010; Treves et al., 2001, 2003), although vigilance rates per minute (Nowak, Richards, le Roux, & Hill, 2016) and per hour (Gould et al., 1997) have also been used.

Considerable variability exists in sample durations across studies utilizing continuous focal sampling (Table 6). Captive environments appear to have offered some authors the potential to utilize longer durations for focal sampling (Barros et al., 2008; Maestripieri, 1993; Nunes et al., 2010) than would be practically achievable in the wild, where the majority use samples of 5 minutes or less, with many using 60 second samples. Short sampling periods are an effective method to minimize the likelihood of aborted samples, require socio-ecological variables to be updated less frequently, and reduce observer fatigue. It is unclear whether the degree of variation found in focal observation lengths could influence the equivalency of results, and a broad comparative assessment of the consistency of results from different methodologies is needed.

[Table 6 here]

Instantaneous scan sampling and focal point/interval sampling (Altmann, 1974) allow authors to calculate the percentage of samples scored as vigilant. There is variability, however, in how these estimates are calculated. Percentages are typically calculated by dividing the number of vigilant ‘scans’ by the total number of ‘scans’ recorded within a group or age-sex class (de Ruiter, 1986; Isbell & Young, 1993; van Shaik & van Noordwijk, 1989). Vigilance has also been reported as a percentage of total scans collected on a given day (Smith et al., 2004), and percentage of total scans collected across an entire study period, for each categorical level of the conditional variables investigated (Robinson, 1981). Alternatively, these percentages can be calculated for each individual study subject over the study period (Josephs et al., 2016; Kutsukake, 2006), or for each individual within each month (Baldellou & Henzi, 1992), or time period (Caine, 1987). Time spent vigilant may also be broken down for a range of behavioral and habitat categories (Cowlishaw, 1998) and Pannozzo et al (2007) calculated the percentage of “social looks” out of the total of “social” and “non-social” looks. Alternatively, model approaches allow researchers to include vigilance state as binary response variable (Campos & Fedigan, 2014).

One-zero sampling has been used sparingly in primate vigilance literature thus far, and its use is rarely advocated in behavioral studies (Altmann 1974). Where applied, however, the number of intervals containing vigilance can be used directly in subsequent analysis (Bshary & Noe, 1997) but more commonly the frequency of vigilant intervals is expressed as a proportion of total interval frequency, yielding percentage of vigilance. Percentages can be expressed per individual (Tsingalia & Rowell, 1984), experimental condition (Koenig, 1998), age-sex class (Fragaszy, 1990; Gosselin-Ildari & Koenig, 2012), or for each socio-ecological condition under investigation (Gosselin-Ildari & Koenig, 2012; Steenbeek et al., 1999; Suzuki & Sugiura, 2011).

A key factor in one-zero sampling is the choice of interval length, which has proved variable in primate vigilance literature, varying from 5-seconds (Gosselin-Ildari & Koenig, 2012; Koenig, 1998) though 10-seconds (Bshary & Noe, 1997), 30-second (Tsingalia & Rowell, 1984) and 60-second (Steenbeek et al., 1999; Suzuki & Sugiura, 2011) intervals. In addition, Fragaszy (1990) used one-zero sampling to record the predominant activity occurring in the first 5-seconds of consecutive 15-second intervals. Such variability undoubtedly undermines the comparability of results.

All the methods discussed above should in theory produce similar if not identical results, and indeed a number of authors have made this assumption (Hill & Cowlishaw, 2002; Smith et al., 2004). Thus far, however, there has been little research to test this assertion. Hirschler et al (2016) recently compared results from two different sampling methods used to record vigilance patterns in Gunnison’s prairie dogs (*Cynomys gunnisoni*): continuous focal sampling and instantaneous scan sampling. Vigilance estimates produced from scan sampling were found to be consistently and significantly higher than the estimates produced from continuous focal sampling. It also highlighted that the use of alert/non-alert criteria in their vigilance definitions made instantaneous assessments of vigilance more challenging than focal sampling the duration of vigilance. In primates, Rose (2000) compared continuous and point samples within a focal sampling protocol for white-faced capuchins and found that, overall, the two focal sampling methods produced similar activity budgets for most behaviors. However, time spent eating was noticeably higher in datasets collected using a continuous protocol, whilst interval sampling seemed to produce lower estimates for time allocated to foraging and movement behaviors. Most importantly, vigilance estimates were slightly lower for interval sampling versus continuous sampling. These results were attributed to omission of rare behaviors in interval sampling (i.e., behaviors of short duration such as glances), and conditional sampling biases in continuous sampling (i.e., under-representing certain behaviors such as fast movement).

The tendency for authors to analyze average vigilance-bout lengths or convert vigilance information into percentage or proportion measures also highlights another area of interest. Thus far, the temporal organization of vigilance (Beauchamp 2015), or vigilance scheduling (McVean & Haddlesey, 1980) has received little attention, particularly in primates. Vigilance scheduling refers to the different strategies an animal can use to achieve vigilance. For example, an animal can achieve 10 seconds of vigilance in a set length of time through a single 10-second bout, or through 10, brief, 1-second glances. In both cases 10-seconds of vigilance is achieved, but through very different strategies. Equally, the organization of inter-scan interval (periods of non-vigilance) can vary, and should not be overlooked (Figure 1). A key point here is how to approach the coding of datasets, as both recording the frequency of bouts and averaging vigilance information across an observation period clearly removes a lot of important information (Figure 1). This issue has essentially been overlooked in primate vigilance studies, with numerous different approaches found. With a switch in focus to studying looking, we believe there is a now an opportunity to develop a consistent approach to tackling this problem going forward, as there is clearly room for a great degree of behavioral flexibility in looking scheduling.

[Figure 1 here]

4.1 | A call for consistency: Sampling methodology

In addition to researchers adopting a common definition, a convergence of sampling methodologies is also required. While different methodologies should in theory give similar results for specific questions, many preclude the ability to look at vigilance scheduling and the temporal organization of vigilance (Beauchamp 2015). It is thus recommended that studies move towards the use of continuous focal sampling, and where possible, video-recording focal observations. Although, this may be challenging for certain populations, short focal observation lengths (such as less than 1-minute) should be viable across a wide range of contexts. The advantage of video footage is that researchers can extract precise information on the duration of looking bouts, and can additionally extract a host of alternative measures such as frequency of looking, or interval between looking bouts. Multiple measures increase the scope of the questions that can be addressed.

Importantly, such an approach would start to address the fact that numerous studies have included arbitrary time requirements in their vigilance definitions (table 4). It is recommended that researchers report ‘looking distributions’ in future work to enable readers to understand how study groups utilize different lengths of looking bouts. These distributions could be used to identify clusters of bout durations that might represent a functional difference in use. For example, consistent bout durations between say 0.3 seconds and 0.9 seconds could represent animals using quick bouts, or ‘glances’, to rapidly update information on the environment. In contrast, extensive looking bouts of 30 seconds or more might be consistent with a classification of scanning. The key point here is that researchers move away from arbitrary definitions of different aspects of vigilance prior to data collection and instead use their quantified looking distributions to understand whether subcategories might exist and whether there are significant patterns in the temporal scheduling of looking. At the same time these looking distributions will be informative in selecting an ideal focal observation length. If the individual bout durations utilized by a study group consistently exceed the length of the focal observation, then bout durations will be artificially truncated (Treves et al., 2001), leading to biased and unreliable results. For example, if members of a study group consistently utilize looking bouts exceeding 30-seconds in duration, then 30-second focal observation lengths would be inappropriate. Where possible, future work should attempt to use similar focal observation lengths, particularly where working on the same species or at the same study site, although this should never come at the cost of biasing results via systematic sampling errors.

5 | FUTURE OPPORTUNITIES IN THE BEHAVIOUR OF LOOKING

Despite a wealth of factors receiving thorough investigation in studies of primate vigilance thus far, our review found some key areas have received less attention, or have been overlooked entirely. These represent interesting opportunities for future work in the framework of looking. Although Alberts (1994) reported that the glance rates of juvenile female baboons decreased between 6 and 24 months of age, ontogeny effects otherwise appear to have been largely overlooked. Favreau et al.

(2014) explored the possibility that individual variation in vigilance use by eastern grey kangaroos (*Macropus giganteus*) and its trade-off with feeding rates could be governed by age-related factors, such as diminishing body and bite size with age. These factors could lead to older individuals occupying a phenotype that is at greater risk of predation, which could then directly influence the vigilance patterns exhibited by these individuals. Ontogeny effects could drive differences in visual capabilities, with juveniles experiencing underdeveloped systems and lacking knowledge to utilize gaze attention effectively, and older individuals suffering from diminished visual acuity (Davidson & Clayton, 2016; Fernández-Juricic, Erichsen, & Kacelnik, 2004). Some age-related effects have been reported in primate vigilance studies, with juveniles of both sexes typically less vigilant than adults (Boinski et al., 2003; de Ruiter, 1986; Fragaszy, 1990; Gosselin-Ildari & Koenig, 2012), although Watson et al (2015) reported the opposite effect. This was the only paper to investigate the heritability of vigilance, however, in this case estimated at 12% for rhesus macaques (Watson et al 2015). Primate groups often contain numerous non-adult individuals that are consistently excluded from sampling efforts. If these individuals are able to contribute to predator detection then they could be a vital component in collective detection. It is strongly encouraged that future work investigate all individuals within their study groups to understand the impact that different age-sex classes have on threat detection.

Anthropogenic factors have also been largely overlooked in primate vigilance work thus far. Nowak et al (2016) found that cage-trapping and subsequent re-exposure to cage-trap stimulus had no effect on vigilance rates in samango monkeys (*Cercopithecus albogularis schwarzi*). However, factors such as habitat modification or anthropogenic noise pollution have not received investigation. Treves & Brandon (2005) found no evidence for tourism influencing the vigilance use of black howler monkeys but showed that monkeys increased their distances to observers during intense interactions with tourists and increased their height from the ground in response to the size of tourist parties, suggesting tourist presence is far from neutral for these monkeys. Equally, it is unclear whether factors such as habituation level or the human shield-effect (Berger, 2007; Nowak, Le Roux, Richards, Scheijen, & Hill, 2014) are consistent across individuals within groups, or across different groups and species.

In captivity, experimental apparatus could exclude observer effects on vigilance (Barros et al., 2008; Caine, 1984; Nunes et al., 2010), but these are more challenging to control in wild environments. Looks towards observers have been recorded and excluded (Koenig, 1998; Pannozzo et al., 2007), simply not recorded (Suzuki & Sugiura, 2011), or grouped with other forms of reactionary vigilance and classified as ‘anti-predator’ vigilance (Hirsch, 2002). MacIntosh & Sicotte (2009) recorded and retained vigilance data in which study animals directed vigilance towards observers and other humans, leading to human related factors being considered as possible driver of vigilance use in ursine colobus. Despite these studies representing good attempts to account for vigilance directed at observers, they overlook the idea that the presence of an observer or multiple observers could alter an animal's perception of fear, for both predation and social threats, and therefore influence its vigilance patterns as a result. Treves & Brandon (2005) reported that increasing number of observers led to increased distances between monkeys and observers; even though a vigilance response was not detected the behavioral adjustments made by the monkeys suggest observer related effects are worthy of greater attention. Treves et al (2001) likely accounted for some of these elements by including number of observers as a control factor in their analysis.

While technology isn't fully available to allow observers to capture the looking behaviors exhibited by wild primate groups in the absence of observers (but see Nowak et al., 2016), we should not overlook the fact that the presence of observers could also be a key determinant of 'looking'. Just as the influence of an animal's height from the ground or number of neighbors on 'looking' patterns could be subject to variation across different individuals, so too can the degree to which individuals tolerate the presence of observers. The scale of response by individual study subjects to observers could arguably range from a flee-on-sight response, to a tendency for certain individuals to 'observe' observers, in each case these fundamental personality traits could be a key determinant of individual 'looking' behaviors. Future work that explores ways to capture this information and include it within multivariate analysis would be valuable.

Any group-level patterns or trends must be driven by individual group members adapting to different conditions. For example, individual nutmeg mannikins (*Lonchura punctulata*) experimentally placed into groups of different sizes showed that some individuals were consistently more vigilant than others, regardless of group size (Rieucau, Morand-Ferron, & Giraldeau, 2010). Similarly, high inter-individual differences in vigilance use have been reported in eastern grey kangaroos (Edwards, Best, Blomberg, & Goldizen, 2013), to the extent some individual kangaroos can cancel out a group-size effect on vigilance by devoting more effort to social vigilance (Carter, Pays, & Goldizen, 2009). Such issues undoubtedly extend to primates. Inter-individual differences have often been overlooked, or treated as background noise, and numerous multivariate approaches now include individual as a random effect. However, this practice will overlook some of the precise drivers underlying individual vigilance patterns. An interesting avenue would be to explore individual vigilance profiles (Beauchamp 2015), and furthermore utilize these profiles to define strategies that can be factored into future simulation models exploring the behavior of looking and threat detection. Many primates are excellent study species for these questions.

6 | CONCLUSIONS

Studies of vigilance have had a long history in primatology, with research exploring a wide range of potential drivers of vigilance in a diversity of socio-ecological conditions. An emerging feature of this work has been the variability of the relationships reported, something that appears, in part, to relate to fundamental differences in the methods employed across studies and inconsistencies in definitions of vigilance behavior. Greater consistency is therefore needed. In his recent review of animal vigilance Beauchamp (2015) identified a series of unanswered questions: Is vigilance for predators compatible with looking for scrounging opportunities? Are vigilant animals better able to detect a predator sooner? Has the incompatibility between vigilance and other activities been exaggerated? How do animals coordinate their vigilance in groups and does it conform to the assumption of randomness of vigilance that underpins theoretical models? What about nocturnal species? Or animals on islands and so subject to reduced predator pressure? What about humans as predators? Primates should be a good study system for many of these issues. With a consistent approach to defining looking, and a robust methodology that permits the multifaceted dimensions of looking to be addressed, future studies of primate vigilance are likely to be a profitable avenue of enquiry that has the potential to place primatology at the forefront of animal vigilance research.

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Table 1. Sample of reported effects in studies of primate vigilance patterns highlighting variability in published relationships.

Factor	Effect	Reference
Sex	Males more vigilant	Baldellou & Henzi (1992), Busia et al. (2016), de Ruiter (1986), Fragaszy (1990), Gould et al. (1997), Isbell & Young (1993), Rose & Fedigan (1995), Steenbeek et al. (1999), Stojan-Dolar & Heymann (2010)[1], Treves (1998, 1999c), van Schaik & van Noordwijk (1989), Watson et al. (2015)
	No difference between sexes	Cowlishaw (1998), Gould (1996), Gould et al. (1997), Macintosh & Sicotte (2009), Smith, Kelez & Buchanan-Smith (2004), Teichroeb & Sicotte (2012), Treves (1998)
Dominance	Subordinates more vigilant than dominants	Alberts (1994)[2], Caine & Marra (1988), Gaynor & Cords (2012), Haude et al. (1976), Keverne et al. (1978) Pannozzo et al. (2007)
	High-ranking individuals more vigilant	Alberts (1994)[3], Gould (1996), Gould et al. (1997), Isbell & Young (1993), Rose & Fedigan (1995), Watson et al. (2015)
	No effect of rank	Robinson (1981)
Adult females with Infants	Mothers with dependent infants more vigilant than those with independent young or females without infants	Boinski et al. (2003), Treves (1999c), Treves et al. (2003)
	No difference found between adult females with or without infants	Treves (1998)
	All adult individuals increased vigilance after birth of infants	Treves et al. (2001)
	Vigilance increased when infant-carrying	Steenbeek et al. (1999), Stojan-Dolar & Heymann (2010)
Age	Vigilance increases with age in both sexes	Boinski et al. (2003), Busia et al. (2016), de Ruiter (1986), Fragaszy (1990), Gosselin-Ildari & Koenig (2012)
	Vigilance decreased with age in both sexes	Watson et al. (2015)
	No age-related effects	Caine & Marra (1988)
Activity	Vigilance higher during resting and travelling	van Schaik & van Noordwijk (1989)
	Vigilance higher during resting	Cowlishaw (1998), Gaynor & Cords (2012), Stojan-Dolar & Heymann (2010), Suzuki & Sigiura (2011)
	Vigilance lower during grooming than resting or feeding	Cords (1995)
	Routine vigilance higher during feeding	Teichroeb & Sicotte (2012)
	No difference between feeding or resting	Macintosh & Sicotte (2009), Teichroeb & Sicotte (2012)
	Vigilance higher during foraging than resting	Kutsukake (2006)[4]
	Vigilance lower during foraging than resting	Kutsukake (2006)[5]
	Vigilance lowest during grooming	Stojan-Dolar & Heymann (2010)
Group-size	No group-size effect	Cowlishaw (1998), Rose & Fedigan (1995), Stojan-Dolar & Heymann (2010), Treves (1998), Treves et al. (2001)
	Positive group-size effect	Gosselin-Ildari & Koenig (2012)[6], Stojan-Dolar & Heymann (2010)[7], Teichroeb & Sicotte (2012)[7]
	Negative group-size effect	de Ruiter (1986), Gosselin-Ildari & Koenig (2012), Isbell & Young (1993) Kazahari & Agetsuma (2010)[6], Hill & Cowlishaw (2002)[8]
Subgroup size	Vigilance lower with larger subgroup sizes but only in boundary areas	Busia, Schaffner & Aureli (2016)
	No effect of daily party size	Kutsukake (2006)
Group composition	Vigilance rate higher in single-species groups	Chapman & Chapman (1996), Cords (1990)
	Species composition did not influence vigilance	Chapman & Chapman (1996), Treves (1999a,c)
	Individual vigilance rate lower in larger mixed-species groups	Chapman & Chapman (1996), (Hardie & Buchanan-Smith, 1997)
Spatial position in group	Increased vigilance when peripheral	Robinson (1981), Steenbeek et al. (1999), Treves (1998), van Schaik & van Noordwijk (1989)
	No effect of spatial position on vigilance	Hall & Fedigan (1997), Josephs et al. (2016), Treves (1998)

Number of neighbors	Vigilance decreases with increasing neighbors	Busia, Schaffner & Aureli (2016), Cowlishaw (1998), Gaynor & Cords (2012)[9], Rose & Fedigan (1995), Stojan-Dolar & Heymann (2010), Teichroeb & Sicotte (2012)
	Vigilance lower with at least one adult neighbor	Steenbeek et al. (1999), Stojan-Dolar & Heymann (2010), Treves (1998), Treves et al. (2001), van Schaik & van Noordwijk (1989)
	Vigilance increases with increasing neighbors	Kutsukake (2006, 2007)
	No significant effect	Kutsukake (2006), Watson et al. (2015)
Distance to neighbors	Vigilance increased as distance to nearest group member decreased	Suzuki & Sigiura (2011)
	Vigilance increased as distance to nearest conspecific or heterospecific neighbor increased	Robinson (1981), Stojan-Dolar & Heymann (2010)
	Vigilance higher with few neighbors near and many neighbors farther away, and vice versa.	Treves (1999b)
Sex of neighbor	Vigilance lower when one or more adult male neighbors	van Schaik & van Noordwijk (1989)
	Vigilance increases with increasing male neighbors	Rose & Fedigan (1995)
	Adult female’s greater vigilance towards male neighbors	Dunbar (1983), Watts (1998)
	Adult females with infants less vigilant with adult male present	Steenbeek et al. (1999)
	No effect of adult male presence	Steenbeek et al. (1999)
Rank of neighbors	Vigilance greater towards dominant animals	Gaynor & Cords (2012) McNelis & Boatright-Horowitz (1998)
	Proximity of alpha male had no influence on vigilance	de Ruiter (1986)
Relationship to neighbor	Affiliative neighbors increase vigilance	Dunbar (1983), Watts (1998)
	Vigilance increases with non-affiliative individuals	Kutsukake (2006)
	Agonistic neighbors relationships increase vigilance	Keverne et al. (1978), Pannozzo et al. (2007) Watts (1998)
Foliage density	Vigilance declines with increasing foliage density	Cords (1990), Cowlishaw (1998)[5,] Gaynor & Cords (2012)
	No significant effect of habitat visibility	Alberts (1994), Hill & Cowlishaw (2002), Stojan-Dolar & Heymann (2010)
Height in canopy	Decrease with height in canopy	de Ruiter (1986), Gaynor & Cords (2012), Hirsch (2002), Kutsukake (2006), Macintosh & Sicotte (2009), Smith, Kelez & Buchanan-Smith (2004), Teichroeb & Sicotte (2012), van Schaik & van Noordwijk (1989)
	Most vigilant near the ground	Campos & Fedigan (2014)
Distance from refuge/exposed	Lower vigilance when exposed	van Schaik & van Noordwijk (1989)
	Increase vigilance with distance from refuge or when exposed	Baldellou & Henzi (1992)[5], Cowlishaw (1998), Hill & Cowlishaw (2002)[8], Josephs et al. (2016), van Schaik & van Noordwijk (1989)
Landscape of fear	Vigilance increased in higher risk areas	Campos & Fedigan (2014)
Range overlap	More vigilant in areas of range overlap	Macintosh & Sicotte (2009), Steenbeek et al. (1999), Rose & Fedigan (1995)
	No effect	Steenbeek et al. (1999)
Home-range boundary areas	Higher vigilance in areas close to the boundary of the home-range	Busia, Schaffner & Aureli (2016)

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[1] Males more vigilant at one site with higher male to female ratio; [2] Daughters of low vs high ranked mothers; [3] Sons of low vs high ranked mothers; [4] Males only, [5] Females only; [6] Social monitoring only; [7] Resting only; [8] Foraging or feeding only; [9] Only when neighbors are kin.

Table 2. Selection of terms and key behavioral requirements used in vigilance definitions in the primate vigilance literature.

Key behavioral requirements	Term	Reference
Actively searching	Preemptive vigilance	Boinski et al. (2003)
	Vigilance	Smith, Kelez & Buchanan-Smith (2004)
Alert and stationary	Vigilance	Baldellou & Henzi (1992), Campos & Fedigan (2014), Gould et al. (1997), Rose & Fedigan (1995),
	Non-social vigilance	Jack (2001)
Cautiously observing	Scanning	de Ruiter (1986)
Eyes open	Vigilant	Cowlishaw (1998), Hill & Cowlishaw (2002)
Eye movement	Glances	Dunbar (1983), Keverne et al. (1978), Maestripieri (1993)
	Looking up/down	Bshary & Noë (1997)
	Scan	Cowlishaw et al. (2004)
	Vigilance	Smith, Kelez & Buchanan-Smith (2004)
	Vigilant scanning	Gaynor & Cords (2012)
Gazing	Glance and Look	Watts (1998)
	Vigilance	Kutsukake (2006, 2007)
	Scanning	Isbell & Young (1993)
Head up	Vigilant	Cowlishaw (1998), Hardie & Buchanan-Smith (1997), Hill & Cowlishaw (2002), Kutsukake (2006,2007), Robinson (1981), van Schaik & van Noordwijk (1989)
Head movement	Glances	Alberts (1994), Keverne et al. (1978), Maestripieri (1993)
	Looking/Look-up	Bshary & Noë (1997), Caine & Marra (1988), Hardie & Buchanan-Smith (1997), Watson et al. (2015)
	Routine/induced scans	Teichroeb & Sicotte (2012)
	Scanning	Caine (1984), Cowlishaw et al. (2004), de Ruiter (1986), Fragaszy (1990), Hardie & Buchanan-Smith (1997), Koenig (1998), Macintosh & Sicotte (2009), Suzuki & Sigiura (2011)
	Vigilance	Smith, Kelez & Buchanan-Smith (2004), Steenbeek et al. (1999), Stojan-Dolar & Heymann (2010)
	Vigilant scanning	Gaynor & Cords (2012)
Look	Vigilance	Robinson (1981) van Schaik & van Noordwijk (1989)
	Antipredatory vigilance	Gosselin-Ildari & Koenig (2012)
	Social monitoring	Gosselin-Ildari & Koenig (2012)
Scanning/staring intently	Vigilant	Campos & Fedigan (2014) Gould et al. (1997), Rose & Fedigan (1995)
	Look up	Hardie & Buchanan-Smith (1997)
	Preemptive vigilance	Boinski et al. (2003)
Scanning the environment	Vigilant	Baldellou & Henzi (1992), Gould (1996), Gould et al. (1997), Koenig (1998)
	Social monitoring	Kazahari & Agetsuma (2010)
	Scanning	Tsingalia & Rowell (1984)

Table 3. Selection of studies that restrict observations to certain activities or exclude vigilance use during specific behaviors

Behavior required or excluded	Term	Reference
Restricted vigilance records to:		
During water drinking only	Looking bouts	Watson et al. (2015)
Feeding	Vigilance: Scans/Glances	Cords (1990)
	Glances	Dunbar (1983)
Foraging	Looking	Caine & Marra 1988
	Scan	Cowlishaw et al. (2003)
Feeding or foraging	Glance/Look	Watts (1998)
Feeding or resting	Vigilant scanning	Gaynor & Cords (2012)
	Scanning	Treves (1999c)
Feeding or moving	Glances	Alberts (1994)
Feeding, resting, grooming	Look-ups	Cords (1995)
Feeding, travelling, resting, grooming	Vigilant	Cowlishaw (1998)
Slow-moving or stationary	Scanning	Treves et al. (2001), Treves et al. (2003)
Stationary	Antipredatory vigilance	Gosselin-Ildari & Koenig (2012)
	Vigilance toward a potential predator or unknown source	Gould (1996)
	Visual scanning	Koenig (1998)
	Vigilance	Smith, Kelez & Buchanan-Smith (2004) Stojan-Dolar & Heymann (2010)
Stationary sitting posture	Vigilance	Kutsukake (2006, 2007)
Stationary or moving	Scan	Fragaszy (1990)
Excluded observations when:		
Animal moved >10m	Scanning	Treves (1998, 1999a), Treves et al. (2001), Treves et al. (2003)
Grooming	Non-social target (look), Social target (look)	Pannozzo et al. (2007)
Social activities	Vigilant	van Schaik & van Noordwijk (1989)

Table 4. Time requirements attached to terms within vigilance definitions in primate studies

Time requirement	Term	Reference
<1 second	Routine scans	Teichroeb & Sicotte (2012)
"Up to about 1 second"	Glance	Watts (1998)
>1 second	Induced scans	Teichroeb & Sicotte (2012)
	Look	Watts (1998)
	Watch	Watts (1998)
<2 seconds.	Glance	Cords (1990)
≥2 seconds.	Scans	Cords (1990)
>3 seconds	Visual scanning	Suzuki & Sigiura (2011)
5 seconds or less	Glances	Alberts (1994)
"Fast" <5 seconds	Aerial/Terrestrial Glance	Barros et al. (2008), Nunes et al. (2010)
"Long-lasting" ≥5 seconds	Aerial/Terrestrial Scan	Barros et al. (2008), Nunes et al. (2010)
≥10 seconds	Visual scanning	Caine (1984)
	Vigilance	Caine (1987)
"At least for a short period" (an entire 5 second interval)	Visual scanning	Koenig (1998)
Uninterrupted for at least 5 seconds.	Antipredatory vigilance	Gosselin-Ildari & Koenig (2012)
"Any length of time"	Look	McNelis & Boatright-Horowitz (1998)

Table 5. Observation methodology in studies of primate vigilance.

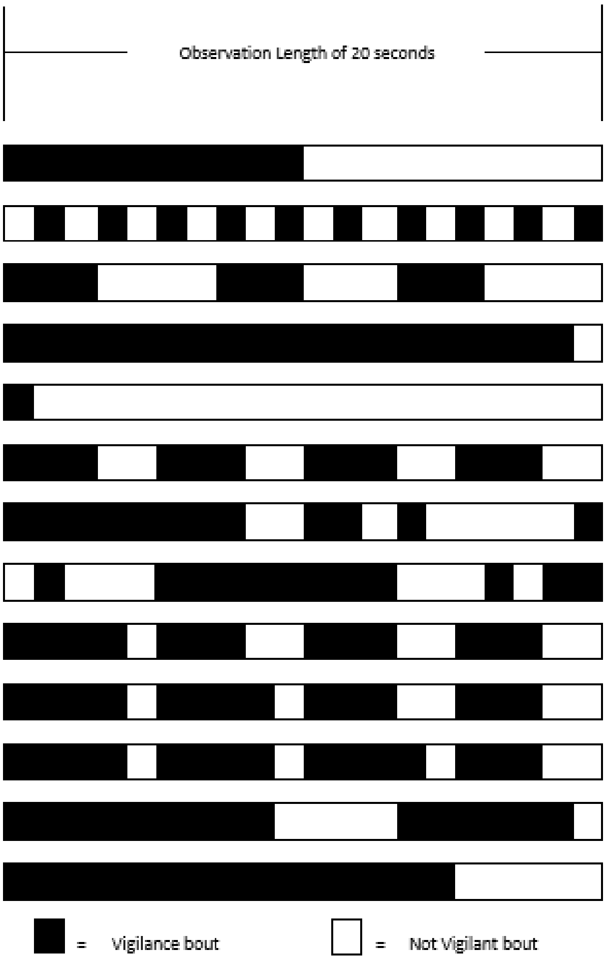
Sampling methodology	Total number of studies	References
Total number of studies utilizing continuous focal observations	37	See Table 6
Total number of studies utilizing instantaneous sampling (focal interval, scan or point samples)	16	Baldellou & Henzi (1992), Boinski et al. (2003), Caine (1987), Campos & Fedigan (2014), Cowlishaw (1998), de Ruiter (1986), Hardie & Buchanan-Smith (1997), Hill & Cowlishaw (2002), Isbell & Young (1993), Josephs et al. (2016), Kutsukake (2006), McNelis & Boatright-Horowitz (1998), Pannozzo et al. (2007), Robinson (1981), Smith, Kelez & Buchanan-Smith (2004) *, van Schaik & van Noordwijk (1989)
Total number of studies utilizing one-zero sampling	7	Bshary & Noë (1997), Fragaszy (1990), Gosselin-Ildari & Koenig (2012), Koenig (1998), Steenbeek et al. (1999), Suzuki & Sigiura (2011), Tsingalia & Rowell (1984)

*Utilized instantaneous scan sampling and continuous focal sampling

Table 6. Continuous focal observation lengths in studies of primate vigilance.

Continuous focal observation length	Number of studies	References
10 seconds	1	Hirsch (2002)
30 seconds minimum	1	Watson et al. (2015)
30 - 120 seconds	2	Onishi & Nakamichi (2011), Stojan-Dolar & Heymann (2010)
60 seconds	8	Chapman & Chapman (1996), Cords (1990, 1995), Smith, Kelez & Buchanan-Smith (2004) *, Treves (1998, 1999a,b,c)
90 seconds	1	Gaynor & Cords (2012)
2 minutes	4	Treves et al. (2001), Treves et al. (2003), Treves & Brandon (2005), Kutsukake (2007)
3 minutes	1	Caine & Marra (1988) †
5 minutes	2	Caine (1984), Keverne et al. (1978) †
8 minutes	1	Kazahari & Agetsuma (2010)
10 minutes	6	Alberts (1994), Gould et al. (1997), Hall & Fedigan (1997), Macintosh & Sicotte (2009), Rose & Fedigan (1995), Teichroeb & Sicotte (2012)
15 minutes	5	Busia, Schaffner & Aureli (2016), Dunbar (1983), Gould (1996), Gould et al. (1997) †, Jack (2001)
20 minutes	1	Nunes et al. (2010) †
30 minutes	2	Barros et al. (2008) †, Maestripieri (1993) †
Unspecified	3	Cowlishaw et al. (2003), Nowak et al. (2016), Watts (1998)

*Utilized instantaneous scan sampling and continuous focal sampling. †Captive studies



Vigilance bouts			Not Vigilant bout (interscan interval)		
Frequency	Total time	Average bout length	Frequency	Total time	Average bout length
1	10	10	1	10	10
10	10	1	10	10	1
3	10	3.33	3	10	3.67
1	19	19	1	1	1
1	1	19	1	19	19
4	12	3	4	8	2
4	12	3	3	8	2.67
4	12	3	4	8	2
4	13	3.25	4	7	1.75
4	14	3.5	4	6	1.5
4	15	3.75	4	5	1.25
2	15	7.5	2	5	2.5
1	15	15	1	5	5

Figure 1. Example vigilance schedules and the information that can be extracted from each strategy, adapted from Beauchamp (2015).