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Watch out!

Insecure relationships affect vigilance in wild spider monkeys (*Ateles geoffroyi*)

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Abstract

Vigilance is used to monitor extra-group threats as well as risky group members. We examined whether relationship quality affects vigilance patterns of spider monkeys. We used focal animal sampling to collect data on social interactions and individual vigilance of all adults and subadults (N=22) in a community of well-habituated Geoffroy's spider monkeys living in the protected area of Otoch Ma'ax Yetel Kooh, Yucatan, Mexico. Through a principal component analysis of seven indices of social interactions, we previously obtained three components of relationship quality, reflecting the levels of compatibility, value and security. Such components could differentially affect vigilance depending on whether vigilance is directed to extra-group threats or risky group members. We tested whether an individual's vigilance was affected by 1) the mean level of compatibility, the mean level of value and the mean level of security across subgroup members, 2) the lowest level of compatibility, the lowest level of value and the lowest level of security with any subgroup member, and 3) the mean level of compatibility, the mean level of value and the mean level of security with neighbors (i.e., subgroup members within 5 m). We did not find evidence for any effect of compatibility and value; however, security did affect vigilance, as individuals were more vigilant when they had a less secure relationship with the subgroup member with the lowest level of security or with the average neighbor.

Key words: vigilance, social monitoring, relationship quality, spider monkeys, fission-fusion dynamics

Significance Statement

Vigilance for monitoring group members is common in primate species. We examined whether the quality of social relationships with subgroup members and neighbors modulates vigilance in wild spider monkeys. We used three components of relationship quality (reflecting the levels of compatibility, value and security) and predicted each component would affect vigilance depending on whether vigilance was directed to extra-group threats or risky group members. We found no evidence that compatibility and value affected vigilance. However, an increase in vigilance occurred when spider monkeys had a less secure relationship with 1) the subgroup member with the lowest level of security and 2) the average neighbor. Our results show monitoring risky group members is an important component of vigilance, especially in species facing low predation pressure.

Introduction

The majority of studies focusing on vigilance in group-living species tested the "many-eyes hypothesis" (Powell 1974; van Schaik and van Hooff 1983) and the "dilution effect" (Dehl 1990), examining the relationship between group size and the time individuals spent vigilant (Lima 1995; Beauchamp 2008, 2015). Many birds and mammals showed a negative group-size effect on vigilance (Pulliam 1973; Elgar 1989; but see Beauchamp 2008). Although some researchers found the same negative relationship in primate species (e.g., chacma baboons, *Papio cynocephalus ursinus*, Hill and Cowlishaw 2002, Japanese macaques, *Macaca fuscata,* Kazahari and Agetzuma 2010, common marmosets, *Callithrix jacchus*, Gosselin-Ildari and Koenig 2012), other studies found no group-size effect (e.g., chacma baboons, Cowlishaw 1998; black howler monkeys, *Alouatta pigra,* Treves et al. 2001) or a positive group-size effect on vigilance (e.g., mustached tamarins, *Saguinus mystax*, and saddleback tamarins, *S. fuscicollis*, Stojan-Dolar and Heymann 2010; ursine colobus monkeys, *Colobus vellerosus,* Teichroeb and Sicotte 2012).

The inconsistency in the relationship between group size and vigilance in primate species may be due to two main reasons. First, anti-predator vigilance might be shared among specific individuals and not among all group members. For example, neighbors can be considered as another scale of individual association (Treves 2000) and several studies showed a decrease in vigilance when the number of neighbors increases (e.g. redtail monkeys, *Cercopithecus ascanius schmidtii,* and red colobus monkeys, *Procolobus badius tephrosceles,* Treves 1998; black howler monkeys, Treves et al. 2001; blue monkeys, *Cercopithecus mitis*, Gaynor and Cords 2012; Geoffroy's spider monkeys, *Ateles geoffroyi*, Busia et al. 2016). Second, the decrease of anti-predator vigilance due to large group size might be counterbalanced by an increase of vigilance to monitor other group members (e.g. redtail and red colobus monkeys, Treves 1999). The need to monitor other group members could also be a reason why in some primate species there is a positive relationship between number of neighbors and vigilance (e.g., brown capuchin monkeys, *Cebus* *apella*, Hirsch 2002; chimpanzees, *Pan troglodytes*, Kutsukake 2006, 2007). Furthermore, biases due to different definitions and methods used to study vigilance in primate species (see Allan and Hill 2018 for a detailed discussion) may play a role in the inconsistency in the relationship between group size and vigilance. There are differences in vigilance targets (focus on anti-predator vigilance only, excluding vigilance towards conspecifics e.g. white-faced capuchin monkeys, *Cebus capucinus*, Campos and Fedigan, 2014) and vigilance time requirements across studies (e.g. Gosselin-Ildari and Koenig 2012). In addition, some researchers collected vigilance data using focal sampling (of different length, see Table 6 of Allan and Hill 2018), whereas others used instantaneous sampling (e.g. Hill and Cowlishaw 2002) or one-zero sampling (e.g. Gosselin-Ildari and Koenig 2012). It is not clear, however, whether and how differences in definitions and methods may affect the relationship between group size and vigilance in primate species. In the only study on primates that compared different sampling methods no differences in vigilance were found (Rose 2000, but see Hirschler et al., 2016 for the same comparison in a non-primate species).

Although vigilance of group members may serve to monitor potential breeding partners (e.g., chacma baboons, Cowlishaw 1998), competitors (e.g., Beauchamp 2001) or update social knowledge (e.g., mandrills, *Mandrillus sphinx,* Schino and Sciarretta 2016), it is often associated with the risk posed by group members (Treves 2000). Three main elements, potentially associated with risk, could possibly affect vigilance. The first element is dominance rank, as proximity with higher-ranking individuals is associated with an increase in vigilance (e.g., Kutsukake 2006; Gaynor and Cords 2012). The second element is familiarity, given that vigilance increases when in proximity to less familiar individuals (e.g., ursine black and white colobus monkeys, *Colobus vellerosus*, Macintosh and Sicotte 2009). The third element can be relationship quality, as individuals are more vigilant when they are in proximity with group members with whom they exchange more aggressive interactions (e.g., mountain gorillas, *Gorilla gorilla beringei,* Watts 1998; brown capuchin monkeys, C. *apella,* Pannozzo et al. 2007).

Although a single interaction type is often used to measure the quality of the relationship between two individuals, social relationships depend on the interchange of multiple types of interactions over time (Hinde 1979; Aureli et al. 2012). While quantifying social interactions is relatively simple, inferring the quality of a social relationship is not as straightforward. According to Cords and Aureli (2000), there are at least three components of relationship quality: value, compatibility and security. Value is a measure of benefits that an individual gains from the relationship with the partner. Compatibility refers to the general tenor of social interactions and reflects overall degree of tolerance between two individuals. Security is a measure of the consistency of partners' responses during social interactions over time. Several studies identified these or similar components when evaluating the quality of social relationship between group members (chimpanzees, Fraser et al. 2008; ravens, *Corvus corax*, Fraser and Bugnyar 2010; Japanese macaques, Majolo et al. 2010; Barbary macaques, *M. sylvanus,* McFarland and Majolo 2011; bonobos, *P. paniscus*, Stevens et al. 2015; Geoffroy's spider monkeys, Rebecchini et al. 2011, Busia et al. 2017). These three components may affect individual vigilance. If so, compatibility and value with group members are expected to have a negative effect on vigilance, as more compatible and more valuable individuals are the ideal partners with whom to share vigilance of any threat (Treves 1998). We can also expect a negative effect of security on vigilance but for a different reason, i.e. because security reflects the degree of predictability and risk posed by others.

Spider monkeys (*Ateles* spp.) represent an excellent model to study the effect of relationship quality on an individual's vigilance behavior for several reasons. First, spider monkeys' high degree of fission-fusion dynamics results in social environment (i.e., subgroup composition) changing several times a day (Aureli and Schaffner 2008). Thus, it is possible to evaluate potential changes in individual vigilance depending on subgroup composition. Second, spider monkeys are known to have low predation pressure (black spider monkeys, *A. chamek,* Symington 1987; Di Fiore 2002), based in part on their large body size, arboreal nature and having a low likelihood of predator encounters (Hill and Dunbar 1998), making it an excellent species to better understand vigilance directed to monitor group members. Third, although dominance is not a prominent feature because competition is reduced through fission (Asensio et al. 2008; Aureli and Schaffner 2008), spider monkeys have differentiated social relationships depending on sex (e.g. relationships between males are stronger than relationships between females: Fedigan and Baxter 1984; Chapman et al. 1989; Aureli and Schaffner 2008; Slater et al. 2009) and individual identity (e.g. Rebecchini et al. 2011; Busia et al. 2017). Thus, it is possible to test whether differences in individual vigilance may be due to differences in social relationships with subgroup members and neighbors. Fourth, we carried out a previous study in which we identified three components of social relationships (Busia et al. 2017) that fit the components hypothesized by Cords and Aureli (2000). We can then evaluate which components may affect vigilance.

The main goal of our study was to examine whether the quality of the relationships with subgroup members and close neighbors (i.e., subgroup members within 5 m; hereafter "neighbors") affects vigilance in wild Geoffroy's spider monkeys. Using compatibility, value and security as components of relationship quality (Busia et al. 2017; c.f. Cords and Aureli 2000), we tested three predictions. As the subgroup is the basic association unit for species with a high degree of fission-fusion dynamics, our first prediction was that individuals are likely to spend more time vigilant when they have, on average, a relationship characterized by lower levels of a) compatibility, b) value and c) security with subgroup members (Predictions 1a, 1b and 1c, respectively). Predictions 1a and 1b are based on the concept that individuals would share vigilance with compatible and valuable subgroup members (Treves 1998), whereas Prediction 1c focuses on monitoring risky group members. Vigilance may however be affected by the presence of specific individuals in the subgroup, rather than the average relationship quality with all subgroup members. Thus, our second prediction was that the time individuals spend vigilant is negatively associated with the lowest level of a) compatibility, b) value and c) security with any subgroup member (Predictions 2a, 2b and 2c). As neighbors can be considered as another association type (Treves, 1998), our third prediction was that individuals are likely to spend more time vigilant when they have, on average, a relationship characterized by lower levels of a) compatibility, b) value and c) security with their neighbors (Predictions 3a, 3b and 3c). We summarized our predictions in Table 1.

Methods

Field site and study subjects

The field site is located in the forest surrounding the Punta Laguna lake, within the natural protected area of Otoch Ma'ax Yetel Kooh, Yucatan Peninsula, Mexico (20°38' N, 87°38' W). The natural protected area covers 5367 ha and includes a mosaic of old-growth, semi-evergreen medium forest, with trees up to 25 m in height, and 30–50-year-old successional forest (Ramos-Fernandez and Ayala-Orozco 2003).

We studied 22 adult and subadult individuals of a community of Geoffroy's spider monkeys living in the protected area (6 adult males, 10 adult females, 1 subadult male, 5 subadult females). During the study period, community size varied between 34 and 37 individuals, due to birth, immigration and emigration events. The study community is part of a continuous long-term project since 1997 (Ramos-Fernandez et al. 2018) and all community monkeys are fully habituated to human presence (i.e. researchers are completely ignored). We therefore assumed researcher presence had no influence on monkey vigilance. We recognized each monkey individually by facial features and differences in fur coloration. We classified individuals as adults if they were more than 8 years of age and as subadults if they were 5-8 years old. As the age was not known for immigrant females, we classified them as subadults until they gave birth for the first time (Shimooka et al. 2008).

Data Collection

We collected data using focal animal sampling (Altmann, 1974) from January 2013 to September 2014 by using a digital voice recorder. The first author and a well-trained field assistant collected 1001 15-minute focal samples (mean ± SE: 45.1 ± 18.9 per subject; inter-observer reliability was high: intra-class correlation coefficients >0.9, see Supplementary information). Focal animals were chosen based on an *a priori* list in order to have a similar number of focal samples across subjects whenever possible. No animal was sampled more than once per hour.

During focal samples, we collected all occurrences and duration of vigilance and social interactions involving the focal animal, recording the identity of the partner. We defined vigilance as the visual monitoring of the surrounding area beyond arm's reach and not in the direction of food while foraging (Treves 2000). Our definition shares the main elements with that of Allan and Hill (2018, p.14), which includes "open eyes and the vision line extended beyond its hand and the substrate, animal or object the individual is in contact with". We also recorded the time when the focal animal was out of view or when the visibility was too poor to reliably observe vigilance. As it is difficult to identify vigilance targets, we made no attempt to distinguish between vigilance of the surroundings and vigilance of other subgroup members. During the focal samples, we recorded the following social interactions: grooming (manipulation of another individual's fur with hands or mouth); co-feeding (feeding on the same fruit species within 1 m from each other); embrace (putting one or two arms around the other's body while facing each other). Every 2 min, we recorded the identity of individuals within 5 m from the focal animal (i.e., neighbors) as neighbors are expected to be more preferred as partners than the other subgroup members. We also recorded aggressive interactions, including conspicuous vocalizations, chases and physical contact, with all-occurrence sampling (Altmann 1974) and whether other individuals provided support to the aggressor (no case of support in favor of the victim was witnessed). Whereas only adults and subadults were subjects of focal samples, juveniles were also considered as subgroup members and neighbors.

Subgroup membership was continuously updated as we recorded the identity of every member of the initially encountered subgroup and all changes due to fission and fusion events. An individual was considered part of the followed subgroup if it was <30 m from a subgroup member according to a chain rule established for this study site (Ramos-Fernandez 2005; see Croft et al. 2008 for the concept of the chain rule). Fission was defined as individuals from the followed subgroup separating from one another in different subgroups and was recorded when one or more individuals were not seen within 30 m from any member of the followed subgroup for 30 min. Fusion was defined as individuals from two subgroups joining one another to form a larger subgroup and was recorded when one or more individuals came within 30 m from any member of the followed subgroup (Rebecchini et al. 2011).

Data analyses

In a simultaneous study, we calculated seven indices based on social interactions between individuals (see Busia et al. 2017 for details) and we included them in a principal component analysis. We obtained three components. The first component reflected compatibility as it had high loadings of grooming and proximity. The second component reflected value as it had high loadings of support during aggressive interactions and cofeeding. The third component reflected security as it had high loadings of aggressive interactions and inconsistency in subgroup association over time (Busia et al. 2017). Each dyad was therefore characterized by its own measure of compatibility, its own measure of value and its own measure of security (Busia et al. 2017).

Beta-distribution models were used to examine the effect of relationship quality components on the proportion of time individuals spent vigilant. The dependent variable was the proportion of time the subject spent vigilant in each focal sample. To calculate this proportion, the duration the subject spent vigilant was divided by the duration of the focal sample minus the time the subject was out of view or visibility was too poor to reliably observe vigilance. To test Prediction 1a, 1b and 1c, we used the mean of the compatibility measure, the mean of the value measure and the mean of the security measure the focal animal had with the subgroup members as independent predictor variables. To test Prediction 2a, 2b and 2c, we considered the lowest measure of compatibility, value and security between the focal animal and any subgroup member as independent predictor variables. In 86% of the 1001 focal samples the subgroup composition did not change during the 15-minute sample. In each of the 136 focal samples during which subgroup composition changed due to fission and fusion events, we used the subgroup composition occurring during the majority of the 15-minute sample. As results did not change when we ran the analyses excluding those 136 focals, here we presented results using the whole dataset. To test Prediction 3a, 3b and 3c, we used the mean of the compatibility measure, the mean of the value measure and the mean of the security measure the focal animals had with the neighbors (i.e., individuals that were within 5 m from the focal animal in at least one 2-minute scan during the focal samples) as independent predictor variables. There was no collinearity among the predictor variables because they were derived from the three components obtained through the principal component analysis. In all models, we included the mean number of neighbors as well as the age and the sex of the focal individual as control variables, and the individual ID as random factor. We did not include subgroup size as an additional control variable because we did not find that it affected vigilance in this monkey community (Busia et al. 2016).

We ran the beta-distribution models using the "glmmTMB" package [Magnusson et al. 2019) in R (version 3.6.0, R Core Team, 2019). We compared full models with null models, which included only the control variables (i.e. sex and age of the focal individual, and the mean number of neighbors) and the random factor, using a likelihood ratio test with the function ANOVA (Dobson and Barlett 2008). We set an alpha level of 0.05 for all tests. We checked the model's adequacy through Q-Q plots (normality of the residuals) and residual vs. fitted graphs (homoscedasticity), and the assumptions were satisfied. Plots were created using the "effects" package (Fox and Weisberg 2019), which allows the visual representation of the model results.

Data availability: the datasets generated during and/or analysed during the current study are not publicly available but are available from the corresponding author on reasonable request.

Results

Predictions 1a, 1b and 1c that the time individuals spent vigilant would be higher when they have, on average, a relationship characterized by lower levels of compatibility, value and security with subgroup members were not supported, as the model was not different from the null model (N=838, χ^2=4.7286, p=0.1928). Predictions 2a and 2b, that individual's vigilance is negatively affected by the lowest level of compatibility and value with any subgroup member, were not supported. However, Prediction 2c was supported, as individual's vigilance was negatively affected by the lowest level of security with any subgroup member. (Table 2, Fig. 1).

Similarly, Predictions 3a and 3b, that individuals would spend more time vigilant when they have, on average, a relationship characterized by lower levels of compatibility and value with their average neighbor, were not supported. However, Prediction 3c was supported, as individuals were more vigilant when they had a lower level of security with their average neighbor (Table 3, Fig. 2).

Discussion

Our overall findings showed that spider monkeys' vigilance is affected by a component of the relationship with other community members. Indeed, among the three components of relationship quality we considered, only security played a role in influencing the amount of time an individual spent vigilant. Whereas spider monkey vigilance was not affected by relationship quality with the average subgroup member, individuals were more vigilant the lower the level of security with at least one subgroup member (Prediction 2c). In addition, spider monkeys spent more time vigilant when the relationship with the average neighbor was less secure (Prediction 3c).

Despite the high variation in subgroup composition due to the high degree of fission-fusion dynamics of the species, Predictions 1a, 1b and 1c, that individuals would spend more time vigilant when they share lower levels of compatibility, value and security with the average subgroup member, were not supported. At the subgroup level, it may be possible that calculating the mean of each component of the relationship quality the focal animal share with other individuals masked the effect that relationship quality can have on vigilance. This might be due to two main reasons. First, changes in individual's vigilance may depend on the presence of specific individuals. This possibility is supported by our findings that spider monkeys are more vigilant when community members with whom they have a highly insecure relationship were in the same subgroup (Prediction 2c). Similarly, mountain gorilla females monitored approaching males longer than approaching females, especially when males gave a display, and monitored females with whom they had an antagonist relationship for longer than females with whom they had an affiliative relationship (Watts 1998).

Second, the quality of relationship with the average individual may affect vigilance at a different scale of association (e.g. neighbors, Treves 1998) rather than at the subgroup level. This possibility is supported by our findings that spider monkeys spent more time vigilant when they had a less secure relationship with the average neighbor

(Prediction 3c). It is plausible that a more precise measure of proximity (neighbor vs. subgroup membership) was more effective in revealing the role of risk, which characterizes insecure relationships. Further support comes from studies that found an effect of the type of social interactions exchanged with neighbors on vigilance (e.g., mountain gorillas, Watts 1998; chimpanzees, Kutsukake 2006; brown capuchin monkeys, Pannozzo et al. 2007; blue monkeys, Gaynor and Cords 2012). Concerning the role of neighbors, several primate studies focused on the number (e.g., chacma baboons, Cowlishaw 1998; redtail and red colobus monkeys, Treves 1998; black howler monkeys, Treves et al. 2001; chimpanzees, Kutsukake 2006, 2007; ursine colobus monkeys, Teichroeb and Sicotte 2012), the sex (e.g. brown capuchin monkeys and white-fronted capuchin monkeys, *C. albifrons*, van Schaik and van Noordwijk 1989; Thomas's langurs, *Presbytis thomasi,* Steenbeek et al. 1999), and the dominance rank (e.g. blue monkeys, Gaynor and Cords 2012) as neighbor characteristics affecting individual vigilance. As we previously found that spider monkeys decrease the time spent vigilant when they have a higher number of neighbors (Busia et al. 2016), we controlled for the number of neighbors while examining the effect of the quality of social relationships with neighbors on vigilance. Thus, our finding of the effect of the level of security with neighbors on vigilance is independent from any effect the number of neighbors may have.

Despite more compatible and more valuable individuals being the ideal partners with whom to share vigilance of any threat (Treves 2000), we did not find evidence for quality components labeled compatibility and value to play a role in modulating vigilance in our study. This result could be because vigilance may not need to be shared with specific partners in spider monkeys. Although predation events were observed in the study area as part of a long-term project (Busia et al. 2018), spider monkeys experience an overall low predation rate (Di Fiore 2002). It is then plausible that anti-predator behavior does not require specific individuals (e.g., highly compatible and valuable partners) with whom to share vigilance. Whereas sharing vigilance for external threats (e.g. threats from other spider monkey communities) was supported by a previous study on the same monkeys (Busia et al. 2016), the need to share vigilance for within-group threats that are partner-specific (e.g., community members with whom one has highly insecure relationships) may be limited. Thus, there is no reason to share vigilance with community members with specific characteristics (i.e., high compatibility and high value) to monitor within-group threats.

There are many factors affecting vigilance, such as the animal's spatial position within the group, its distance to neighbors, its height in the canopy and the overall visibility (Allan and Hill 2018). Here we focused on social relationships. Overall, our study contributed to the understanding the role relationship quality plays on the time individuals spend being vigilant. Although several studies already showed the influence of single social interactions on vigilance (blue monkeys, Gaynor and Cords 2012; brown capuchin monkeys, Pannozzo et al. 2007; mountain gorillas, Watts 1998; chimpanzees, Kutsukake 2006), our study goes one step further considering multiple interactions to characterize how components of relationship quality affect vigilance. Security modulated the time spider monkeys dedicated to vigilance when considering the relationships with specific subgroup members (Prediction 2c) and the average neighbor (Prediction 3c), whereas compatibility and value had no effect. In a previous paper (Busia et al. 2017), the component of social relationship labeled as “security” had negative loadings with two indexes of social interactions: rate of aggressive interactions and inconsistency of subgroup association. Thus, more time was spent to be vigilant when there were companions that were usually more aggressive and less predictable. Our result on the modulating role of the quality of the relationships with neighbors on vigilance gives insights into the apparent contrasting findings of time spent vigilant decreasing (i.e., sharing vigilance with neighbors: redtail and red colobus monkeys , Treves 1998; Geoffroy’s spider monkeys, Busia et al. 2016) and increasing with a larger number of neighbors (i.e., vigilance to monitor risky neighbors: e.g., chimpanzees, Kutsukake 2006, 2007). Sharing vigilance with neighbors would usually reduce costs, but if an insecure relationship exists with them, spending more time being vigilant may be cost effective.

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Compliance with ethical standards

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Conflict of Interest: The authors declare that they have no conflict of interest.

Ethical approval: this study was conducted with the approval from CONANP and SEMARNAT (SGPA/DGVS/00910/13 and SGPA/DGVS/02716/14).

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Table 1: Details of the relationship components and their measures used to test each prediction of the three hypotheses.

<table>
<tr><th>Component</th><th>Indexes with high loading</th><th>Predictions</th><th>Measure for Hypothesis 1</th><th>Measure for Hypothesis 2</th><th>Measure for Hypothesis 3</th></tr>
<tr><td>Compatibility</td><td>Grooming, Proximity</td><td>a</td><td rowspan="3">Mean of all subgroup members</td><td rowspan="3">Lowest value of all subgroup members</td><td rowspan="3">Mean of all neighbors</td></tr>
<tr><td>Value</td><td>Support during aggression, Cofeeding</td><td>b</td></tr>
<tr><td>Security</td><td>Aggression, Inconsistency in subgroup association</td><td>c</td></tr>
</table>

Table 2. Results of the beta-distribution model showing the association between time spent vigilant and the level of compatibility, value and security the focal individual shared with the subgroup member with the lowest levels.

	Estimate	Std. Error	z	p
(Intercept)	-1.04844	0.08956	-11.707	< 0.0001 ***
Compatibility	-0.02301	0.04235	-0.543	0.587
Value	0.05364	0.04194	1.279	0.2009
Security	-0.09605	0.03756	-2.557	0.0106 *
Neighbors	0.02447	0.03627	0.675	0.5000
Age	0.21103	0.1404	1.503	0.1328
Sex	-0.12263	0.12972	-0.945	0.3445

The model was statistically different from the null model (likelihood ratio test: N=849, χ^2=8.5603, p=0.036).
* = p<0.05; ** = p<0.01; *** = p< 0.001

Table 3. Results of the beta-distribution model showing the association between time spent vigilant and the levels of compatibility, value and security the focal individual shared with the average neighbor.

	Estimate	Std. Error	z	p
(Intercept)	-1.01245	0.114890	-8.820	< 0.0001 ***
Compatibility	-0.05272	0.04894	-1.077	0.2814
Value	0.06133	0.04572	1.341	0.1798
Security	-0.1517	0.05510	-2.753	0.0059 **
Neighbors	0.03357	0.04748	0.707	0.4795
Age	0.29579	0.14084	2.100	0.0357*
Sex	-0.16127	0.12844	-1.256	0.2093

The model was statistically different from the null model (likelihood ratio test: N=485, χ^2=9.353, p=0.025).
* = p<0.05; ** = p<0.01; *** = p< 0.001

Figure legends

Figure 1: Illustration of the proportion of time spent vigilant depending on the lowest level of compatibility, value and security shared with the subgroup members.

Figure 2: Illustration of the proportion of time spent vigilant depending on the average level of compatibility, value and security shared with the neighbors.