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Avian Behavior, Ecology, and Evolution

Keeping a watch on neighbors: social vigilance in Painted Stork (*Mycteria leucocephala*) nesting colonies

Vigilando a los vecinos: vigilancia social en colonias de nidificación de *Mycteria leucocephala*

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ABSTRACT. Social vigilance, the act of monitoring conspecifics, is a critical behavior in group-living species, balancing the demands of threat detection, resource acquisition, and social interactions. We measured social vigilance in Painted Storks (*Mycteria leucocephala*) nesting in colonies at Keoladeo National Park, India, using high-resolution video observations. We measured three different parameters of social vigilance: number of vigilance bouts, duration of vigilance, and proportion of time spent in vigilance. We aimed to investigate the relationship between social vigilance and various habitat variables related to coloniality such as colony size and number of neighbors. Other objectives included examining the effect of activity intensity on the levels of social vigilance and comparing vigilance levels between the sexes. Our results revealed that the number of neighboring conspecifics significantly influenced social vigilance, which increased with an increasing number of neighbors. Different neighbor activities led to variation in the duration of vigilance in focal individuals. However, we found no significant differences in vigilance parameters between females and males. Our findings highlight the importance of immediate social interactions within colonies for the need to defend nesting resources, assess threats, or gather social information from neighbors.

RESUMEN. La vigilancia social, el acto de vigilar a los congéneres, es un comportamiento crítico en las especies que viven en grupo, equilibrando las demandas de detección de amenazas, adquisición de recursos e interacciones sociales. Medimos la vigilancia social en cigüeñas pintadas (*Mycteria leucocephala*) que anidan en colonias en el Parque Nacional de Keoladeo, India, utilizando observaciones de vídeo de alta resolución. Se midieron tres parámetros diferentes de vigilancia social: número de episodios de vigilancia, duración de la vigilancia y proporción de tiempo dedicado a la vigilancia. Nuestro objetivo fue investigar la relación entre la vigilancia social y diversas variables del hábitat relacionadas con la colonialidad, como el tamaño de la colonia y el número de vecinos. Otros objetivos fueron examinar el efecto de la intensidad de la actividad sobre los niveles de vigilancia social y comparar los niveles de vigilancia entre sexos. Nuestros resultados revelaron que el número de congéneres vecinos influía significativamente en la vigilancia social, que aumentaba con el incremento del número de vecinos. Las diferentes actividades de los vecinos provocaron variaciones en la duración de la vigilancia en los individuos focales. Sin embargo, no encontramos diferencias significativas en los parámetros de vigilancia entre hembras y machos. Nuestros resultados destacan la importancia de las interacciones sociales inmediatas dentro de las colonias por la necesidad de defender los recursos de nidificación, evaluar las amenazas o recabar información social de los vecinos.

Key Words: *avian coloniality; colony size; nesting; number of neighbors; Painted Stork; social vigilance*

INTRODUCTION

Social vigilance, the act of monitoring conspecifics, is crucial in acquiring information about predation risk, food abundance, and quality, or potential competition within groups (Fernández-Juricic et al. 2005, Favreau et al. 2015, Beauchamp 2016, Zhao et al. 2019, Cheng et al. 2020). It allows individuals to make decisions based on social cues, compensating for reduced anti-predator vigilance (Danchin et al. 2004, Zhao et al. 2019). Social vigilance is influenced by many factors such as group size, social dynamics, and individual characteristics (Beauchamp 2015). However, the primary factor influencing vigilance is group size, with studies showing that as group size increases, the individual anti-predator vigilance decreases (Beauchamp 2001, 2010, Fernandez et al. 2003, Watson et al. 2007). However, social vigilance increases in order to gain information about resource quality and the level of threat from predators and to avoid competition (Beauchamp 2009, 2010). This trend has been observed in many mammals such as primates (Hirsch 2002, Kutsukake 2007), giraffes (Cameron and du Toit 2005), and bats (Klose et al. 2009). In birds, monitoring neighbors provides key benefits for assessing resource quality and predation risk (Beauchamp 2001). For example, starlings (*Sturnus vulgaris*) use scanning behavior to gather social information, optimizing foraging and coordination (Fernández-Juricic et al. 2005). Similarly, gulls (*Larus* spp.) observe their neighbors to assess the levels of threat, and adjust their behavior accordingly (Beauchamp 2009).

Avian colonies exhibit substantial differences in group size or colony size across different species and within the same species, ranging over multiple orders of magnitude in many taxonomic groups (Jovani et al. 2008, Brown 2016, Minias et al. 2020). Although avian coloniality has attracted considerable interest, theories attempting to explain its evolution are incomplete, and no finality has been reached (Danchin and Wagner 1997, Wagner et al. 2000, Brown and Brown 2001). The evolution of avian coloniality is traditionally understood through a cost-benefit framework in which factors such as predation risk, energetic trade-offs, mating opportunities, and interference from

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conspecifics in nesting colonies are important (Wittenberger and Hunt 1985). Colonies serve as vital sources of social information; its transfer among individuals enhances predator avoidance through conspecific-derived cues such as using alarm signals from others to detect predators early (Evans et al. 2016). Coloniality has also been linked to changes in vigilance behavior, particularly, reduced predator-scanning time. Wittenberger and Hunt (1985) suggest that flocking behavior in animals provides improved vigilance with reduced time expenditure per individual, and that mutual vigilance in breeding colonies provides protection from predators, allowing for early predator detection. Similarly, Brown and Brown (2001) suggest that nesting in larger colonies offers birds a greater likelihood of predator detection, i.e., the 'many eyes' hypothesis, which proposes that larger vertebrate social groups facilitate more efficient predator scanning, reducing individual vigilance and enhancing feeding, assuming that predator detection by many individuals prompts a coordinated vigilance response that further enhances group safety (Pulliam 1973, Lima 1995). Despite the benefits, coloniality also carries costs such as increased competition for resources, risk of disease transmission, and stealing of nest contents (kleptoparasitism) by neighboring conspecifics (Brown and Brown 2001). In such cases, there are chances that an individual directs vigilance toward neighboring conspecifics; e.g., in large colonies, heightened competition for limited resources often leads to increased scanning directed toward group members because of the possibility of neighboring individuals intruding into nests, attempting nest parasitism, theft, cannibalism, or nest-site usurpation (Burger 1981, Brown and Brown 2001, Roche and Brown 2013). In such cost-benefit situations, vigilance for the acquisition of social information presents animals with complex trade-offs in group settings, highlighting the intricate dynamics of the social and ecological pressures faced by group-living species (Treves 2000, Hammer et al. 2023).

Though studies conducted on social vigilance in birds have been primarily done on the foraging grounds (Beauchamp 2010), literature on social vigilance in nesting colonies is fairly limited, especially in the context of large colonial waterbirds such as storks (Aves: Ciconiiformes). Vigilance directed toward neighbors within stork nesting colonies remains poorly understood. To address this gap, we conducted a study of Painted Stork (*Mycteria leucocephala*), which nests in colonies located on tall trees or clumps of trees located in the middle of waterbodies across large parts of South Asia and Southeast Asia. Its colonies are located amid human habitations such as villages and agricultural fields, along with colonies in wetlands in both protected and unprotected areas as well as urban premises (Urfi 2024). This colonial system serves as a convenient model to investigate the concepts of coloniality and the functional role of vigilance. In Painted Storks, colony size varies from a minimum of 2 nests to a large colony consisting of > 80 nests (Tiwary and Urfi 2016). Previous attempts to study vigilance in Painted Storks have emphasized the significant role of environmental variables such as visitor presence and proximity of the visitors to the nesting colony in driving anti-predator vigilance, also known as environmental vigilance (Ahmed and Urfi 2024). Regarding colony size (i.e., number of neighbors), our previous study showed that as the number of neighbors near the focal individual increases, environmental vigilance decreases (Ahmed and Urfi 2024). In continuation of our studies, we attempt to explore social vigilance, where individuals monitor conspecifics within the colony. Understanding this behavior is crucial for understanding how social dynamics affect vigilance behavior, as highlighted in studies of other taxa (Hirsch 2002, Fernandez-Juricic et al. 2005, Klose et al. 2009, Beauchamp 2016, Zhao et al. 2019, Das et al. 2023).

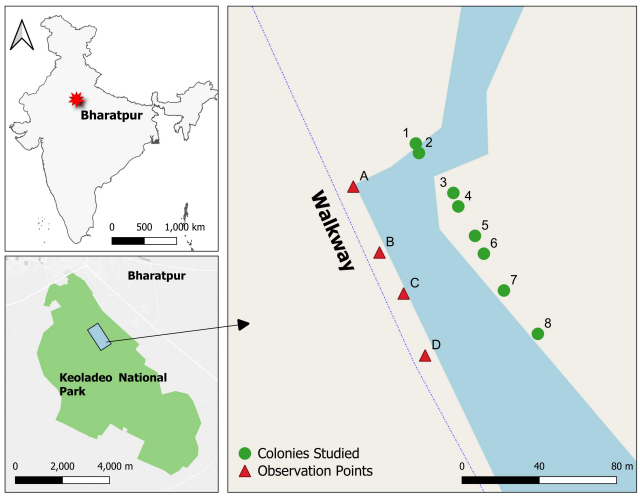
Here, we examine the influence of coloniality-related variables on social vigilance and the patterns of social vigilance in colonies of Painted Storks located within a protected marsh in North India. Our main objectives were: (1) to examine how social vigilance in nesting storks is influenced by factors related to group size, (2) to identify which behaviors of neighboring conspecifics trigger vigilance in focal individuals, and (3) to compare social vigilance rates between male and female storks at the nest, building on previous research that established that males show more environmental vigilance than females (Ahmed and Urfi 2024).

METHODS

Study area and data collection

The study was carried out at Keoladeo National Park, Bharatpur, Rajasthan (27.1596° N, 77.5218° E), where Painted Storks nest in colonies located on the canopies of Gum Arabic (*Acacia nilotica*) trees growing on elevated mounds within an extensive marsh (Urfi 2024). Eight colonies, comprising 37 nests and 74 individuals, were studied from 25 August to 30 November 2023, with visits conducted four times per month at 7-day intervals. Nesting pairs were identified through direct observation, and nest locations were marked on photographs for reference during each field visit. To observe and record the behavior of Painted Storks at their nests, video recordings were made from designated observation points along the park's walkway (Fig. 1). A digital single-lens reflex camera (Canon 200D with a 55–250-mm IS II lens) was mounted on a tripod at each observation point to ensure stable, high-quality recordings. Once the nests of interest were identified, the same nests were consistently recorded during each successive visit. Video recordings were made from 10:00 until 16:00. Each day's footage was divided into six 1-h bins (10:00–11:00, etc.); in each bin, 300 s (5 min) of continuous recording of the nests in the particular recording frame was made from each observation point with a 1-min interval between the two observation points, which ensured that all the nests were covered within a 1-h time bin. From this footage, we calculated the parameters of vigilance during the observation period. All other activities such as preening, nest maintenance, and similar behaviors were classified as non-vigilant activities and hence were not counted. The colonies studied were selected based on their proximity to the observation point, with distances ranging 40–65 m between camera and nesting colony. Due to logistical constraints such as camera placement and lens focal length, nesting colonies that were beyond 65 m away were not included. This approach ensured high-quality, detailed, and clear video recordings of the behavior displayed by the storks. The data collection followed a standardized recording protocol, adapted from the methodology described in our previous study of the environmental vigilance of Painted Storks (Ahmed and Urfi 2024).

Fig. 1. Maps showing the locations of study sites. Keoladeo National Park, Bharatpur, indicating the colonies studied and observation points where the camera was set up. Inset shows the location of Keoladeo National Park in the context of India. The blue box highlights the section in the national park where the colonies were studied. (Map created using QGIS software, version 3.26.3; QGIS Development Team 2023).



Social vigilance

Social vigilance is defined as when the focal individual is looking toward its neighboring conspecific, especially when that individual is performing some activity in its nest or is approaching the focal individual's nest (modified from Klose et al. 2009, Das et al. 2023). Continuous playback of the video data confirmed that the focal individual's act of vigilance was specifically directed toward its neighboring conspecifics, which is different from environmental vigilance, in which the focal individual typically looks upward or its gaze is directed outside the colony (Fig. 2). We measured and quantified three different vigilance parameters (in seconds): the number of vigilance bouts that occurred during the observation bout, duration of vigilance bouts, and the proportion of time spent vigilant (defined as the total duration of vigilance/total observation time; Ahmed and Urfi 2024). Behavioral data for all parameters were extracted by reviewing the videos frame by frame using the latest version of VLC Media Player (version 3.0.18; VideoLan Organization 2006).

Sex identification

Painted Storks exhibit sexual size dimorphism, with males approximately 9–10% larger than females in body measurements such as body length, bill length, and tibia and tarsus length (Urfi and Kalam 2006). While visually distinguishing the sexes of randomly selected birds in the field is not possible, at the nests in the early part of the nesting season, sex identification is possible by observing the position of individuals during copulation. Subsequently, after disengagement, the size difference between the sexes is clearly noticeable. For this study, we determined the sexes using this method, as captured on video recordings. Through repeated review of the footage, we reliably ascertained the sex of the focal individual throughout the study period, even in cases when there was a single individual present at the nest, as in our previous studies (Tiwary and Urfi 2016, Ahmed and Urfi 2024).

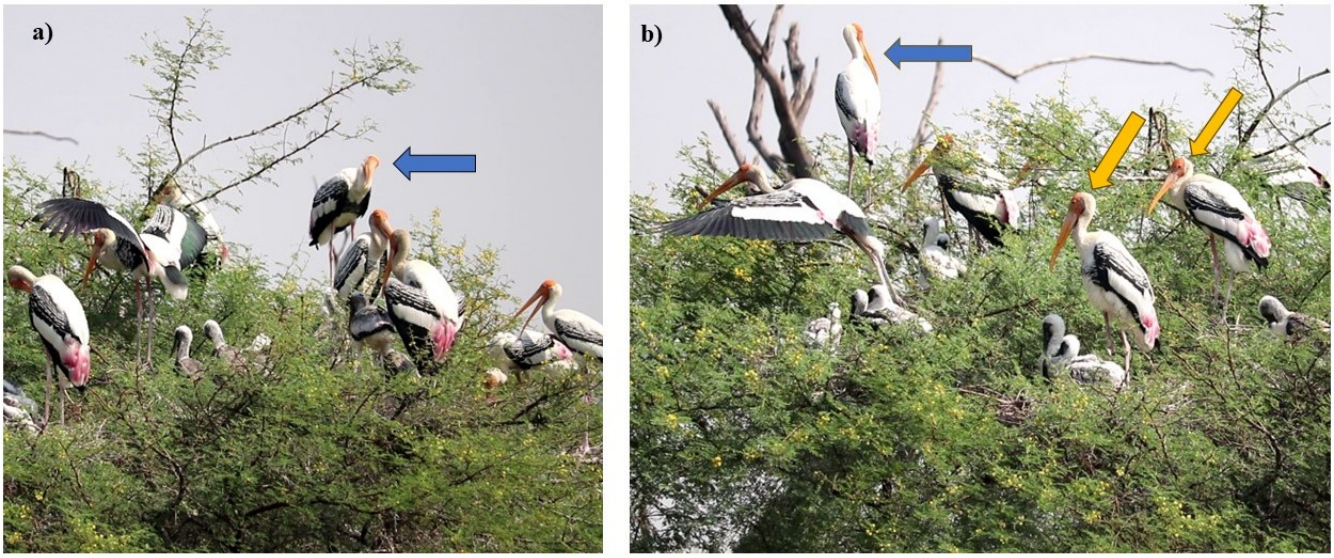
Habitat variables

We estimated "colony size" as the number of nests on the canopies of trees growing on islands (Tiwary and Urfi 2016). During the observation period, we also recorded the "number of neighbors" as the number of neighboring conspecifics visible within the camera frame near the focal nest. This count included both nesting and non-nesting Painted Storks, as the number of individuals in the vicinity of the focal individual varied over time. We measured "nest height" as the height (in meters) of the nest above water level, and the "nearest nest distance" from focal nests using a Leica DISTO Laser Distance Meter. We also measured the "nearest colony distance" as the distance of the nearest neighboring colony to the focal colony using the simple ruler function in Google Earth Pro (Tiwary and Urfi 2016). This variable may play a role in social vigilance, given that Painted Stork colonies are often located on trees with merged canopies (Urfi 2024). We included a variable representing the activity of neighboring conspecifics, termed "activity type", to assess whether social vigilance in the focal individual was influenced by their behavior. Activity type was divided into five categories: (1) stealing, described as instances when the neighbor attempted to steal nesting material from the focal individuals' nest; (2) arrival and (3) departure, corresponding to the neighbor arriving at or leaving its nest, respectively; (4) routine, including movements within the nest such as preening or rearranging nest materials, or moving within the colony substrate; and, (5) no activity, when the neighbor was present but inactive while the focal individual remained vigilant.

Statistical analysis

Normality and homogeneity of variance were evaluated using Shapiro-Wilk and Levene's tests, respectively. Because the data were not normally distributed ($P < 0.05$), we used generalized linear mixed models (GLMMs) to examine the influence of various habitat variables on social vigilance parameters. GLMMs were selected for their ability to handle non-normally distributed data and to incorporate both random and fixed effects (Bolker et al. 2009). Before model building, using Pearson's correlation, we tested for correlation within the parameters (number of vigilance bouts, duration, and proportion of time spent vigilant) and found that the proportion of time spent vigilant was strongly correlated with duration of time spent in vigilance ($r_p = 0.997$, $P < 0.001$). Thus, we used number of vigilance bouts and duration of vigilance in all statistical analyses, including model building. Our data showed overdispersion; hence, we used the "glmmTMB" function in the "glmmTMB" package (Brooks et al. 2017), with a negative binomial distribution and log link function for the count data, i.e., number of vigilance bouts and duration of vigilance bouts (because duration of vigilance was assumed to be discrete, it was measured in whole seconds). Nest ID and individual ID were treated as random effects to control for pseudoreplication. Sex, number of neighbors, colony size, nearest neighbor distance, and nearest colony distance were treated as fixed effects. Before model construction, all fixed effects were standardized (Schielzeth 2010). We used both number of neighbors and colony size as fixed effects because no correlation was detected between them ($r_p = 0.385$). We constructed various

Fig. 2. Photographs showing vigilance behavior in Painted Storks (*Mycteria leucocephala*). (a) An individual exhibits an environmental vigilance posture (i.e., looking up and looking outside the colony. (b) Individuals exhibit a social vigilance posture (i.e., gazing toward a neighbor) in response to activity in a neighboring nest. Blue arrow = environmental vigilance posture, yellow arrow = social vigilance posture. Photo credits: Paritosh Ahmed.



candidate models based on combinations of variables: $N_{(Null)}$, intercept only model; $N_{(PS)}$, variables related to Painted Storks such as sex, colony size, and number of neighbors; $N_{(Habitat)}$, comprising nest height, nearest nest distance, and nearest colony distance; and $N_{(Full)}$, the combination of all model variables. We calculated Akaike information criterion (AIC) values using the "AIC" function in the "stats" package of base R and selected the best model based on the lowest ΔAIC, i.e., ΔAIC < 2 (Burnham et al. 2011). For the analysis of neighbor activity, we first quantified the number of observations when vigilance was triggered by neighbor movement vs. those that occurred without any preceding neighbor activity. Additionally, we categorized vigilance-triggering events based on different neighbor activity types to assess how various situations influenced vigilance duration and used a Kruskal-Wallis test to compare duration of vigilance bouts across all activity types followed by pairwise comparison using post-hoc Dunn's test with Bonferroni correction using the "dunnTest" function in the "FSA" package (Ogle et al. 2023). All statistical analyses and model building were done in RStudio version 4.3.1 (released on 16 June 2023; R Core Team 2023).

RESULTS

We analyzed 2400 minutes of video data recorded from 74 Painted Stork individuals. Based on AIC values, our best-fit model for number of vigilance bouts was the $N_{(PS)}$ model (Table 1), which revealed a significant effect of number of neighbors ($\chi^2 = 16.09$, $P < 0.001$) only, and no significant effect of sex and colony size ($P > 0.05$; Table 2). Similarly, the best model for the duration of vigilance was also the $N_{(PS)}$ model (Table 1). Only the number of neighbors had a significant effect ($\chi^2 = 3.99$, $P < 0.001$; Table 2), and neither sex nor colony size affected social vigilance. Despite the results of the best model, which only had one significant predictor, we also examined the effects of other variables (interestingly, other variables related to coloniality, i.e., nearest colony distance, nearest nest distance, and nest height, had no significant effect on either of the social vigilance parameters, except that number of neighbors had a significant effect as per the results of the $N_{(Full)}$ model; for details, see Appendix 1). Based on the best-fit model, as the number of neighbors increased, the number of vigilance bouts also increased (Fig. 3a). Similarly, for duration of vigilance, we observed a comparable trend, with duration increasing as the number of neighbors increased (Fig. 3b).

Table 1. Model comparison statistics, including degrees of freedom (df), and the difference in Akaike Information Criterion (ΔAIC) for each model. The model with the lowest AIC is considered the best fit.

Parameter	Model	df	AIC	ΔAIC
Number of vigilance bouts	$N_{(PS)}$	7	2816.17	0
	$N_{(Full)}$	10	2820.13	3.96
	$N_{(Null)}$	4	2837.32	21.15
	$N_{(Habitat)}$	7	2841.92	25.74
Duration of vigilance bouts	$N_{(PS)}$	7	7655.13	0
	$N_{(Null)}$	4	7657.81	2.69
	$N_{(Full)}$	10	7659.73	4.60
	$N_{(Habitat)}$	7	7662.26	7.14

Of 1791 observations collected across 74 Painted Stork individuals, 1326 observations were those where no vigilance was recorded, whereas there were 465 observations in which vigilance was observed. Of these 465 observations, 451 observations were those in which social vigilance was triggered by the activity of the neighboring conspecific, and 14 were those in which vigilance was observed but there was no neighbor activity. Focusing on the activities of neighboring conspecifics that triggered vigilance,

Table 2. Results of the best-fit model (generalized linear mixed model) analyzing the effects of various habitat variables on the social vigilance behavior of Painted Storks nesting at Keoladeo National Park.

Response	Predictor	Estimate	Standard error	*Z*	*P*
Number of vigilance bouts	Intercept	−1.140	0.086	−13.203	< 0.001
	Sex	0.119	0.094	1.264	0.206
	Number of neighbors	0.278	0.056	4.971	< 0.001
	Colony size	−0.149	0.077	−1.939	0.053
Duration of vigilance bouts	Intercept	3.000	0.135	22.274	< 0.001
	Sex	0.091	0.211	0.433	0.665
	Number of neighbors	0.332	0.121	2.757	0.006
	Colony size	−0.086	0.108	−0.792	0.429

routine movements triggered vigilance in 368 observations (~79% of the cases where vigilance was observed), followed by 61 observations (~13.1%) in which vigilance in the focal individual was triggered by the arrival of a neighbor. Similarly, in 18 observations (~3.9%), vigilance was triggered by the departure of a neighbor from the focal individual's vicinity. Instances when vigilance was prompted by the absence of any apparent neighboring activity (no activity) accounted for 14 observations (~3.0%). Additionally, stealing-related behavior by neighbors triggered vigilance in only four observations (~0.9%).

Upon further analysis, we found that the duration of vigilance bouts varied significantly across activity types (Kruskal-Wallis test, $\chi^2 = 1672.7$, df = 4, $P < 0.001$). Pairwise comparisons of vigilance behavior across activity types revealed significant differences (Fig. 4), particularly between "no activity" and other behaviors. The pairs that were significantly different were: no activity vs. arrival ($Z = 16.08$, $P < 0.001$), no activity vs. departure ($Z = 8.83$, $P < 0.001$), no activity vs. routine ($Z = -38.28$, $P < 0.001$), and no activity vs. stealing ($Z = -4.23$, $P < 0.0001$). In contrast, other comparisons, such as those among arrival, departure, and routine, did not yield statistically significant differences after adjustment ($P > 0.05$ in all cases). Neighboring individuals who were engaged in routine movements led to the longest vigilance durations in focal individuals (mean ± standard error: 89.98 ± 3.34 s), and vigilance bouts associated with arrival (62.26 ± 6.59 s) and departure (62.17 ± 12.13 s) were relatively shorter. Notably, in some instances, focal individuals tended to be vigilant even when the neighboring individual was present but not engaged in any visible activity (59.71 ± 12.80 s). Among the different activity types, stealing-related behaviors were associated with the shortest vigilance duration (54.25 ± 9.83 s).

DISCUSSION

Our study indicates that the number of neighbors, rather than colony size, is the only significant predictor for social vigilance in Painted Storks, with a positive relationship between the two variables. In large groups, animals tend to focus their social vigilance on nearby neighbors rather than individuals farther away (Treves et al. 2001, Beauchamp 2009). As group size increases, individuals face difficulties in monitoring the behavior of all members, making it harder to adjust their actions accordingly. Instead, immediate neighbors, or the closest individuals, play a more significant role in shaping individual

Fig. 3. The relationships between (a) the number of vigilance bouts and number of neighbors and b) the duration of vigilance bouts (s) and number of neighbors among Painted Storks during field studies at Keoladeo National Park between August and November 2023.

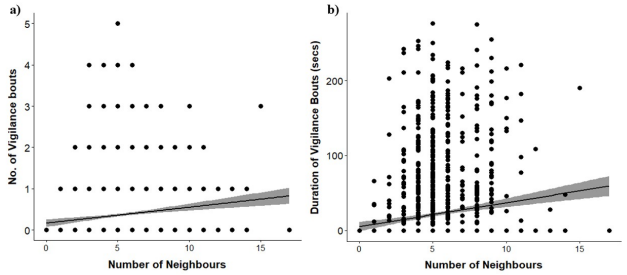
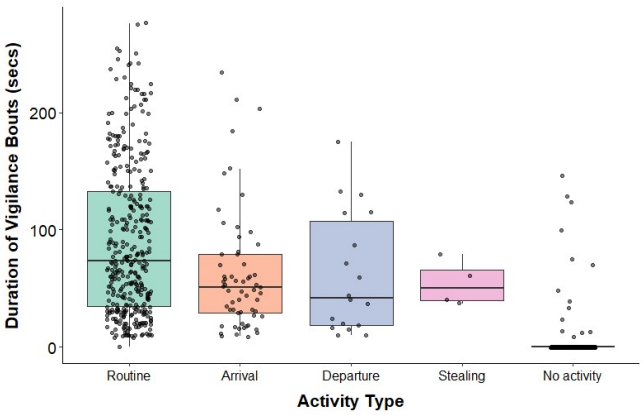


Fig. 4. The duration of vigilance bouts (s) across different activity types in Painted Storks. The boxplots display the median (horizontal line), interquartile range (box), and data distribution (individual points).



vigilance levels, as information transfer is more direct and faster from those within close range (Evans et al. 2016, Zhao et al. 2019, 2020). Moreover, the increasing number of individuals and the complexity of spatial arrangements can make it difficult to assess the overall size of the group or colony accurately (Das et al. 2023). Furthermore, because competition intensity increases with the number of neighbors, focal individuals are more likely to monitor their neighbors' behavior to either engage in or avoid agonistic interactions (Zhao et al. 2019). This effect may explain why colony size (number of nests) is not a significant predictor of social vigilance in Painted Storks. Similarly, other variables such as nest height, nearest nest distance, and nearest colony distance are also inconsequential.

As previous studies have shown, vigilance plays an important role in the detection of threats from predators, human disturbance, and similar activities (Ahmed and Urfi 2024). It has been postulated that the underlying mechanism is the "many eyes" effect that allows individuals to detect threats (Pulliam 1973, Lima 1995, Brown and Brown 2001, Beauchamp 2010). However, in

colonial situations, constant competition for territories, resources, and mates, as well as the need to gather information about these resources and potential mates, leads an individual to exhibit heightened vigilance toward their neighboring conspecifics (Brown and Brown 2001, Beauchamp 2015, Evans et al. 2016, Das et al. 2023), which is a likely explanation for our results.

In the case of Painted Stork colonies, the need to monitor a neighboring conspecific arises from two situations. One possibility is that Painted Storks exhibit vigilance to defend themselves from neighboring individuals because nests are tightly packed in small clusters. During the initial nesting stage, there is intense competition for territories and mates (Urfi 2024). Later on, storks often attempt to steal nest material such as twigs or food items for their own nests, resulting in frequent and intense intraspecific encounters (Urfi 2024). As observed in our recordings, focal individuals became more vigilant when neighboring storks moved around the colony, especially when they approached the area where the focal individual's nest was located or attempted to steal nesting material (Appendix 2 Figs. A1 and A2). These situations often led to heightened alertness and sometimes escalated into aggressive interactions such as forward clattering threats (Kahl 1972). This behavior suggests that Painted Storks may perceive their neighbors as potential threats because of the densely packed nesting arrangement in which even small movements can feel intrusive. Additionally, we observed that when a neighbor left its nest (Appendix 2 Fig. A3), the focal individual became more watchful, possibly seizing the opportunity to steal nest materials from the unattended nest. Roche and Brown's (2013) study of Cliff Swallow (*Petrochelidon pyrrhonota*) colonies found that individuals who exhibited higher vigilance were more likely to attempt intrusions into their neighbors' nests, suggesting that vigilance is partly directed toward monitoring the activities of nearby conspecifics (Roche and Brown 2013). By observing when a neighboring conspecific leaves its nest, a vigilant individual may seize the opportunity to usurp the nest or steal its contents (Roche and Brown 2013).

Other possibilities could be to gather social information about the location of resources such as nesting material or food, or to assess predator risks from neighbors. In our study, Painted Storks were observed closely monitoring their neighboring individuals, particularly during key moments of activity, including instances when a neighbor returned to the colony after a foraging trip, often carrying nesting materials or food in their beak (Appendix 2 Fig. A4). Such behavior likely reflects the storks' need to assess the situation, as these activities could indicate information about resource availability and quality as observed in studies in which social vigilance was associated with resource quality (Beauchamp 2001, Fernández-Juricic et al. 2005). Painted Storks may also monitor their neighbors to gather information about predation risk (in our case, perceived threat from humans). Studies of other bird species have reported similar findings. A study of Egyptian Geese (*Alopochen aegyptiaca*) found that under elevated predation risk, individuals in larger groups showed a positive relationship between vigilance and group size (Atkins et al. 2019). The geese engaged in social vigilance by observing and mimicking conspecifics to gather information about potential threats, suggesting the presence of social information transfer (Atkins et al. 2019). Similarly, Black-headed Gulls (*Chroicocephalus ridibundus*) have been observed to synchronize their vigilance with their nearest neighbors, allowing them to gather additional information about potential threats (Novčić et al. 2023). Other studies have observed a comparable pattern whereby social vigilance becomes more prominent as group size increases, allowing individuals to adjust their behavioral decisions to gather information about food availability and predation risks from their neighbors, suggesting that social interactions enhance information flow and allow individuals to avoid competition from neighbors (Evans et al. 2016, Zhao et al. 2019, Das et al. 2023). Furthermore, enhanced social vigilance contributes to better resource allocation and risk management, ultimately improving survival rates while informing adaptive behaviors such as foraging strategies and group cohesion during threats (Beauchamp 2007, Zhao et al. 2019, Novčić et al. 2023). Focusing on sex-based differences, we did not find any significant differences in rates of social vigilance between male and female Painted Storks, which may suggest that both sexes experience similar pressures to monitor their neighbors. However, this result is in contrast to our previous study in which males were more environmentally vigilant compared to females, possibly because males defend their mates from environmental threats such as predators (Ahmed and Urfi 2024).

CONCLUSION

Our study highlights the importance of social vigilance in Painted Stork colonies, emphasizing that the number of neighbors, rather than overall colony size, plays a key role in shaping vigilance behavior. The tightly packed nesting arrangement and frequent competition for resources create a dynamic social environment where individuals must remain attentive to their immediate neighbors. However, there were a few instances in which the focal individual remained vigilant despite no apparent activity by the neighbor, highlighting that individuals continuously monitor their neighbors regardless of immediate social cues. In a broader sense, increased vigilance serves multiple purposes, including defending against nest intrusions, gathering social information about resources, and assessing potential threats. Interestingly, our results contrast with our previous study of environmental vigilance in which we found a negative trend such that vigilance decreased as the number of neighbors increased, due to shared predator detection (Ahmed and Urfi 2024). These results highlight the different ways in which vigilance functions in varying contexts, suggesting that social and environmental factors may influence vigilance behavior in opposing directions (Zhao et al. 2019). Future research could explore trade-offs with environmental vigilance, as well as other key behaviors such as nesting, to explore the long-term consequences of heightened vigilance on individual fitness and reproductive success. Additionally, future studies could investigate how the spatial position of a focal individual within the colony influences social vigilance.

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Data Availability:

The data and code used in this study are available upon request from the corresponding author.

LITERATURE CITED

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Appendix Table A1

Results of the $N_{(Full)}$ model (GLMM) analyzing the effects of various habitat variables on the social vigilance behavior of Painted Storks nesting at Keoladeo National Park.

Response	Predictor	Estimate	SE	Z	p
No. of Vigilance Bouts	(Intercept)	-1.141	0.085	-13.459	<0.001
	Sex	0.117	0.095	1.237	0.216
	Number of Neighbors	0.282	0.057	4.987	<0.001
	Colony Size	-0.146	0.105	-1.387	0.165
	Nearest Nest Distance	-0.076	0.079	-0.961	0.337
	Nest Height	0.045	0.095	0.470	0.638
	Nearest Colony Distance	-0.049	0.091	-0.540	0.589
Duration of Vigilance Bouts	(Intercept)	2.993	0.135	22.096	<0.001
	Sex	0.091	0.214	0.426	0.670
	Number of Neighbors	0.355	0.127	2.787	0.005
	Colony Size	-0.076	0.161	-0.474	0.635
	Nearest Nest Distance	0.042	0.153	0.274	0.784
	Nest Height	-0.059	0.105	-0.562	0.574
	Nearest Colony Distance	-0.096	0.124	-0.778	0.436

Appendix

Screenshots from the video data showing different activities displayed by neighbors (red arrow) that triggered vigilance in focal individuals (yellow arrow)

Fig. A1: Screenshot of the recording showing focal individuals (marked by yellow arrows) exhibiting social vigilance towards the neighboring individual (marked by red arrow) as it moves around the nesting colony.

Fig. A2: Screenshot of the recording showing the focal individual and neighboring ones (marked by yellow arrow) exhibiting social vigilance towards an individual (marked by red arrow) as it attempts to steal twigs from the focal individual's nest.

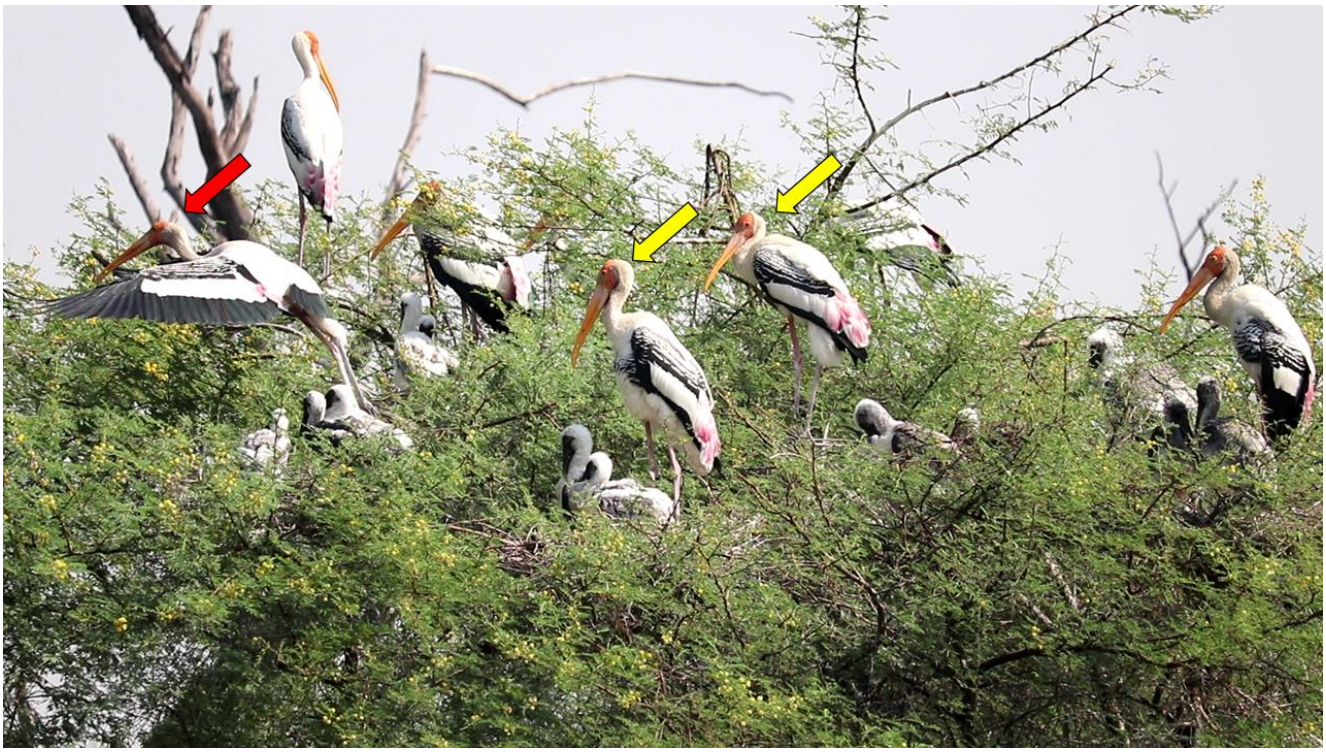

Fig. A3: Screenshot of the recording showing focal individuals' vigilance behavior being triggered (marked by yellow arrow) by the movement of the neighboring individual (marked by red arrow) as it departs from its nest.

Fig. A4: Screenshot of the recording showing the focal individual (marked by yellow arrow) exhibiting social vigilance towards the neighboring individual (marked by red arrow) as it arrives in its nest with nesting material in its beak.