JOURNAL OF ANIMAL BEHAVIOUR AND BIOMETEOROLOGY

RESEARCH ARTICLE
Published Online: August 1, 2023
https://doi.org/10.31893/jabb.23024

# Analyzing White-rumped Vulture breeding behavior using Markovian modeling

**Ramji Gautam**[ab] | **Bishnu Prasad Gautam**[c] | **Yusuke Noda**[d] | **Jerrold L. Belant**[e] | **Hari Prasad Sharma**[af]

[a]Central Department of Zoology, Tribhuvan University, Kathmandu, Nepal.
[b]Department of Zoology, Prithvi Narayan Campus, Pokhara, Nepal.
[c]Department of Economic Informatics, Kanazawa Gakuin University, Kanazawa, Japan.
[d]Department of Information and Communication Engineering, Okayama Prefectural University, Soja, Okayama, 719-1197, Japan.
[e]Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, USA.
[f]Nepal Zoological Society, Kirtipur, Kathmandu, Nepal.

**Abstract** Understanding wildlife behavior, including accurate identification, processing, and interpretation of activities or cues, is important to behavioral biology and corresponding conservation strategies. We characterized the breeding activities of the critically endangered White-rumped Vulture *Gyps bengalensis* following a sequential pattern from courtship to fledging. We recorded 4,160 visual observations of 20 behaviors of eight pairs of White-rumped Vultures from September 2021–April 2022 and constructed Markov chain models to model three composite behaviors (i.e., breeding, foraging, and roosting). We found that vultures at four nests displayed >70% of the time in breeding behavior, and each nest produced offspring, indicating a potential correlation between breeding behavior and successful reproductive outcomes. Our model explained each composite behavior with high accuracy. Identifying behaviors White-rumped Vulture have practical applications for developing management plans for their conservation, including the timing of critical reproductive events. Our findings and approach can improve our understanding of White-rumped Vulture behavioral ecology and conservation and have applications for other species.

**Keywords:** behavior, markov, modeling, simulation, White-rumped vultures

## 1. Introduction

The White-rumped Vulture *Gyps bengalensis* is endemic to Southeast Asia (Ali and Ripley 1968). In Nepal, the species is resident and inhabits tropical and subtropical areas <1500 m above sea level (Dhakal et al 2023; BLI 2021; Grimmett et al 2016). White-rumped Vultures were the most common vulture species throughout its geographical range. Still, following rapid population declines during the mid-1990s (Prakash 1999), it is currently listed as Critically Endangered on the IUCN Red List of Threatened Species and Appendix II list of CITES (BLI 2021). A dominant cause of this population decline is the veterinary use of diclofenac (Oaks et al 2004; Shultz et al 2004), where White-rumped Vultures die of kidney failure after consuming the drug in treated livestock carcasses (Oaks et al 2004; Shultz et al 2004). Other causes of population decline include habitat loss and human persecution (Baral et al 2005; BLI 2021; Loveridge et al 2019).

Knowledge of White-rumped Vulture behavior can provide insights into their behavioral biology to improve conservation actions. Correct identification, processing, and interpretation of activities or cues are important aspects of behavioral biology (Kappeler 2021*).* The behavior of White-rumped Vultures varies within and among individuals and in response to environmental conditions (Bell et al 2009; Dingemanse et al 2010; Gautam et al 2022). Also, White-rumped Vulture behavior can be grouped into breeding and non-breeding seasons (Ali and Ripley 1968; Baral et al 2005), and breeding activities are sequential from courtship to nest-building, egg laying, incubation, nestling, and fledgling. Such complex behaviors require accurately characterizing activities concerning surrounding environmental factors and interaction with conspecifics and other species (Pimm et al 2015). These complex behavior activities of White-rumped Vultures can also be categorized broadly as feeding, breeding, and roosting activities, each with intermediate and more specialized behaviors.

Knowledge of species' behavior is essential to predict the likelihood of future behavioral states, which can be enhanced using mathematical models (Atherton and Kerbyson 1999; Baltrusaitis et al 2016; Crall et al 2015; Taha et al 2014). Such methods may reveal information crucial for conserving threatened species (Gautam et al 2020; Noldus et al 2002). Relying on mathematical models for ethological studies should be used cautiously, and field observations can provide information to validate behaviors (Knopff et al 2009). Previous studies of White-rumped Vultures in Nepal have included their distribution, population status, and breeding (Baral et al 2005; Baral et al 2013; Chaudhary et al 2012); however, protection of nesting and roosting sites and understanding their behavior has not yet been investigated. We collected data from field observations to construct Markov chain models (MCMs), to estimate the behavior states of White-rumped Vultures in Nepal. Specifically, we used *Gyps* breeding futures, an enhanced Markov chain

 Received: May 23, 2023 | Accepted: July 6, 2023

analysis that can predict the different dynamics of individuals. As reproduction's success affects species' population viability (Anthony and Blumstein 2000), knowledge of reproductive behavior is important for conserving threatened species like White-rumped Vultures.

The application of MCMs offers a novel insight into species behavior. Our goal was to use MCMs to estimate transition probabilities between different states of vulture behavior and predict the likelihood of vultures being in a particular state at a given time based on their previous state. To our knowledge, no previous studies have used this mathematical model to study White-rumped Vulture behavior. Therefore, we aimed to identify behavioral patterns and their relationship to each other to assess vultures' breeding behaviors accurately and offer a consistent and standard observational framework for future vulture behavioral studies.

## 2. Materials and Methods

### *2.1. Study area and data collection*

We conducted the study in Gaukha (N 28° 2̀ 3.1̀, E 83° 52̀ 31.8̀), Syangja District, Nepal (Figure 1). Gaukha has subtropical forests including Chestnut *Castanopsis indica*, Coromandel Ebony Persimmon *Diospyros melanoxylon*, Hill Sal *Shorea robusta*, Needle Wood *Schima wallichii*, and Kapok *Bombax ceiba*. White-rumped Vultures roosted and nested in Coromandel Ebony Persimmon and Kapok trees in a sacred grove and private lands in the study area.

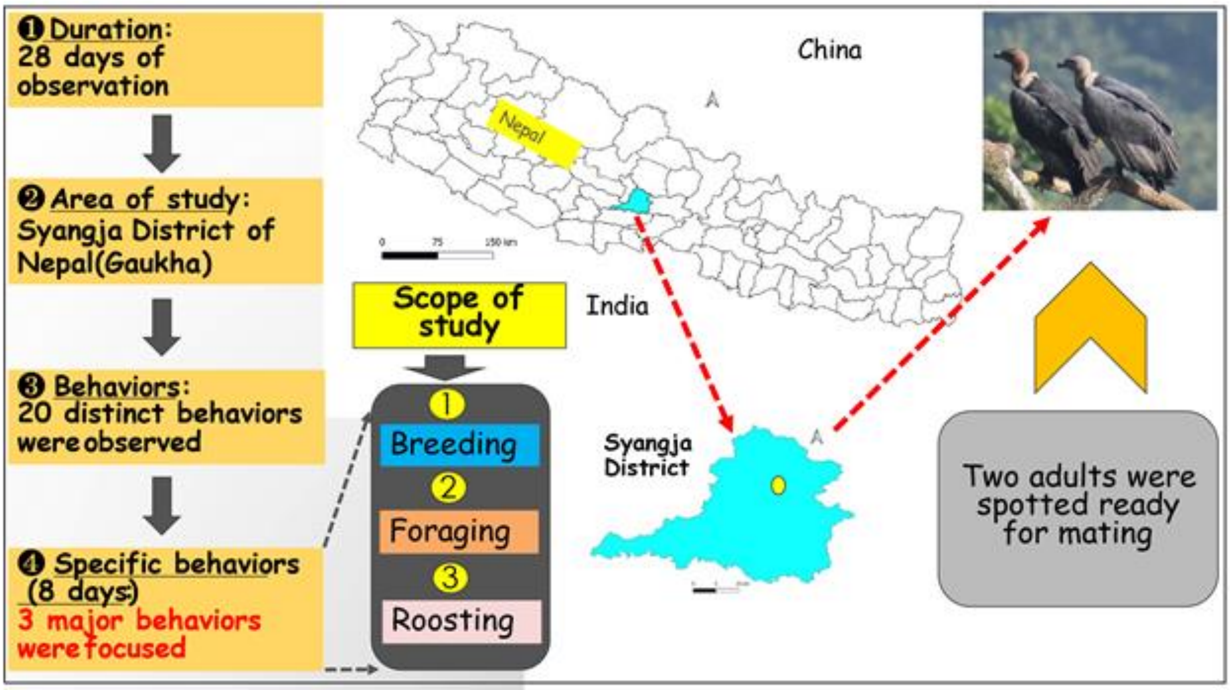


**Figure 1** Study area and duration of White-rumped Vulture behavior study.

During the 2021–2022 breeding season, we monitored eight breeding pairs of White-rumped Vultures using augmented focal sampling (AFS), a modification of a focal sample (Altmann 1974) in which a pair of White-rumped Vultures were observed as opposed to an individual. This method was appropriate to our study because individuals shared nesting activities, behaved as a pair, and we could not discern individuals of a nesting pair.

To apply AFS, we first established recording rules which were continuous recording for a discrete-time and defined the appropriate time interval for recorded observations. These rules were to normalize minor behaviors (i.e., behaviors with low frequency and effect) and later combine these into broader categories of behavior. We collected data on these eight pairs from nest building to fledgling phases. We observed vultures from 9:00 to 17:30 for two days in each stage, monitoring each pair for 10-minute intervals. Observations occurred from September 2021 to April 2022. We defined breeding activities as a stepwise process of pairing, nest construction, egg laying, incubation, and rearing young to a fledgling stage. At least two people collected frequency and transition behavioral data using binoculars and a video camera for observations. Five of the nests observed were constructed in a single Coromandel Ebony Persimmon, two nests in a single Kapok, and one in an adjacent Coromandel Ebony Persimmon tree. We observed White-rumped Vultures 100 m from nesting and roosting trees to reduce disturbances. We recorded 20 readily discernible minor behaviors (see Supplementary material).

We used R programming language to graph the MCMs visually and conducted cohort simulations in Excel to perform MCMs. Furthermore, we performed MCMs simulations using observational data and evaluated our approach using post hoc analyses.

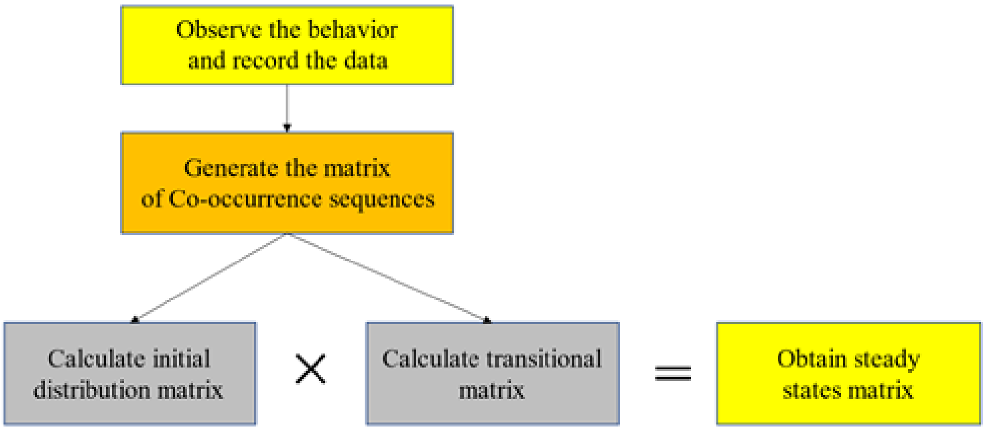


**Figure 2** Conceptual model of White-rumped vulture behavioral model development.

**Table 1** List of major and minor behaviors of White-rumped Vultures.

| Foraging (F) (Sub-classifications) | Roosting (R) (Sub-classifications) | Breeding (B) (Sub-classifications) |
|---|---|---|
| S = Soaring | R = Resting | PR = Pairing |
| L = Landing | B = Basking | NB = Nest Building |
| W = Walking | P = Preening | I = Incubation |
| J = Jumping | PP = Pooping | N = Nourishing |
| T =Take Off | A = Aggression | M = Mating |
| E = Eating | | ND = Nest Defending |
| | | SN = Standing on Nest |
| | | PN = Preening on Nest |
| | | BN = Basking on Nest |

*2.2. Markovian approach and model setup*

The MCMs is a discrete-time probabilistic model that can predict the current state's probability depending on the previous state. We used MCMs to build statistical models to investigate the breeding behaviors of White-rumped Vultures (Figure 2). The MCMs are stochastic and operate within a specific set of states that satisfy the Markov property and consider the prior probabilities of the specific state, and predict the future probabilities of that state (Geyer 1992; Grewal et al 2019; la Torre-Torres et al 2020). We considered three major behaviors (foraging, roosting, and breeding) of White-rumped Vultures for MCMs analysis. To analyze White-rumped Vulture behavior through MCMs, we first identified three key behaviors: the behavioral state space with possible values or states for a process. We then recorded transition operators, noting the probability of occurring from one behavioral state to another. Finally, we identified the probability distribution of the current behavioral state with the probability of being in any state.

In the MCMs, White-rumped Vultures' major behaviors (i.e., foraging, roosting and breeding) entered the model from state F and transitioned to state R at a rate of $\lambda_F$ or to state B with rate $\mu_F$ (Figure 3). However, the activities of the White-rumped Vulture were retained in its current state without transition to form a self-feedback. In these modes of transition and process, we used the following mathematical equation (1) for the MCMs:

$$Pr(X_{t+1}|X_t, X_{t-1}, ......, X_1) = Pr(X_{t+1}|X_t) \quad (1)$$

We used standard notation with slight modification, representing the series of events (Et) from time t = 1 to time point t = T, where the possible events (Ot) values are used in a countable set $O_t \in 1, 2,...,q$. We defined events from the behavioral activities of White-rumped Vultures (Table 1) that served as model inputs and represented the range of potential outcomes for MCMs. For each event to be included in a MCMs, there could be sequences of events for all t = 0,1,2..., for some finite state of m within state space (S) such as $S_0$, $S_1, S_2....S_t$. In our case, the state space was a set of {foraging, roosting, and breeding}. In equation (1), we defined Pr(Xt = j) as the probability of Pr(X) at time t. The left side of the equation can be derived from the chain rule of probability, and based on this equation, we can summarize the future state, which depends only on the current state under the Markov property. Therefore, the system's state at time 't' depends only on the state of the system at time t-1. We note that transitional probabilities can change over time; however, our objective was to estimate the probability of breeding only. Therefore, we used the probability theorem of steady states, assuming the probability of White-rumped Vultures spending time in each state would not change and become the long-term behavior—however, the behavior of White-rumped Vultures before this steady state was considered transient (or short-term).

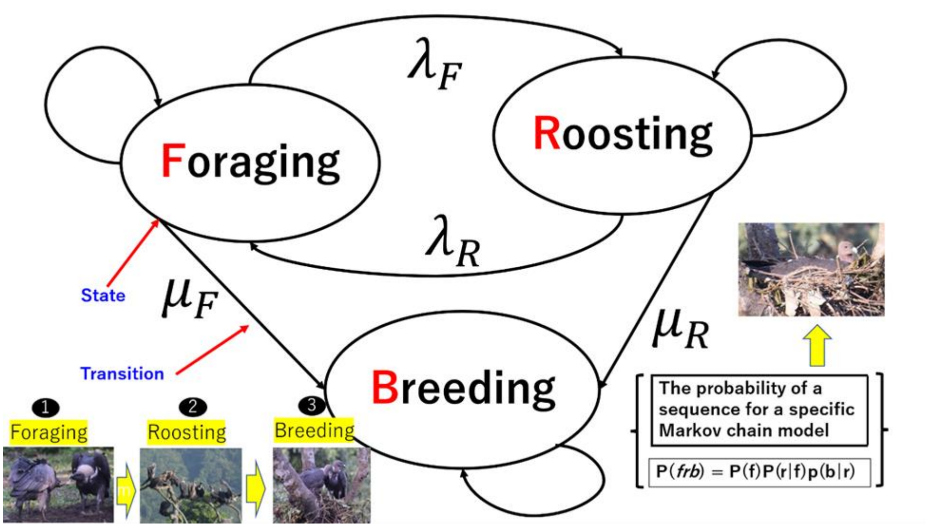


**Figure 3** Markov process for characterizing behavior of White-rumped Vulture.

Let P be the transition matrix for an s-state MCMs for which there exists a vector:

$$\pi = (\pi_1, \pi_2, \pi_3, ..........., \pi_s) \quad (2)$$

which is a steady-state distribution (equation 2). Each element in this vector is the state of White-rumped Vultures after a series of steps reaching the steady state. This steady state can be derived from the following calculations following the steady state theorem (equation 3):

$$\lim_{n\to\infty} p^n = \begin{pmatrix} \pi_1 & \pi_2........ & \pi_s \\ \pi_1 & \pi_2........ & \pi_s \\ \pi_1 & \pi_2........ & \pi_s \end{pmatrix} \quad (3)$$

And

$$\lim_{n\to\infty} p_{ij}(n) = \pi_j \quad (4)$$

In this situation, the steady state distribution is:

$$\pi_1 + \pi_2 + .............\pi_3 = 1 \ and$$
$$\pi(n+1) = \pi(n).P \leftrightarrow \pi = \pi P \quad (5)$$

where "P" refers to the one-step transition matrix. As we had data from vultures at eight nests and behavioral activities were observed in each nest for 10-minute intervals, we estimated the transition matrix for each nest. From this, we assessed each pair of White-rumped Vultures' time spent on breeding activities. The initial state matrix was:

$$(S_0^{n1}, S_0^{n2}, S_0^{n3}, S_0^{n4}, S_0^{n5}, S_0^{n6}, S_0^{n7}, S_0^{n8}) \quad (6)$$

which indicates the initial ratio for each state of foraging, roosting, and breeding of White-rumped Vultures for Nest 1 (equation 7):

$$S_0^{n1} = \begin{bmatrix} 0.019231 & 0.269231 & 0.711538 \end{bmatrix} \quad (7)$$

We also derived initial distribution matrices for all 8 nests from direct observations, then calculated transition matrices from these initial distribution matrices using the formula (equation 8):

$$S_i = S_0^{nj}.P^n \quad (8)$$

where, $S_0$ is the initial state distribution matrix, i is the number of steps from the initial steps to the steady states, and j is limited to 1 to 8 as we considered only eight nests. Similarly, P represented the transitional probability matrix for each nest.

*2.2.1. Generating transition matrices*

We used state sequences to generate transition matrices of the MCMs. We first established the number of transition probabilities between two states based on direct behavioral observations, using the 20 minor behaviors (Table 1). We combined these behaviors into three composite behaviors, including Foraging (F), Roosting (R), and Breeding (B) (Table 1), to simplify calculations during model development:

$$X = (x(S_i, S_j)) = \begin{pmatrix} x(S_1,S_1) & x(S_1,S_2) & x(S_1,S_3) \\ x(S_2,S_1) & x(S_2,S_2) & x(S_2,S_3) \\ x(S_3,S_1) & x(S_3,S_2) & x(S_3,S_3) \end{pmatrix} \quad (9)$$

If i, j = 1, 2, 3, and $s_1$ = F, $s_2$ = R, $s_3$ = B, then let x ($s_i$, $s_j$) be the number of pairs of states si, sj. The associated transition matrix X was obtained as below, and the transition matrix (1) can be written as:

$$X_{ij} = (X_{11}..............X_{ij}) \quad (10)$$

$$X = (x_{ij}) \quad (11)$$

Next, we calculated one-step transition probabilities ($p_{ij}$), where $p_{ij}$ is defined by:

$$i, j \in S = \{1, 2, 3\} \quad (12)$$

which represents one-step transition probabilities from i to j given that each previous state is independent and each White-rumped Vulture must advance to one of the three states, with the sum of the row probabilities equal to one. The diagonal represents the likelihood of remaining in the same state. In a MCMs, a state k is considered absorbing if $p_{kk} = 1$, or all $p_{kj} = 0$ for j is not equal to k. The breeding state leading to offspring generation serves as the absorbing state.

$$p_{ij} = x_{ij} / \sum_{j=1}^{3} x_{ij} \tag{13}$$

## 3. Results

We made 4,160 observations of vultures at the eight nests during the eight days of observation. White-rumped Vultures, on average, spent 2.71 ± 3.04 hrs (31.20%) foraging, 1.68 ± 1.76 hrs (19.66%) roosting, and 4.25 ± 3.40 hrs (49.13%) for breeding activities (Figure 4). White-rumped Vultures engaged most often in nest-building activities (n = 57.50 hrs; 71.08%), followed by roosting activities (n = 31.00 hrs; 22.60%), and foraging activities (n = 8.87 hrs; 6.31%) during the nest building phase. Similarly, White-rumped Vultures spent more time in breeding activities (n = 116.00 hrs; 83.67%), followed by roosting (n = 15.50hrs; 11.16%), and foraging (n = 7.17 hrs; 5.17%) during the incubation phase. In contrast, White-rumped Vultures spent more time in foraging activities (n = 200.50 hrs; 48.20%), followed by breeding (n = 127.17 hrs; 30.57%), and roosting (n = 88.33 hrs; 21.23%) during the chick-rearing phase. During the breeding season, vultures at nests 1, 2, 6, and 7 spent more time in breeding activities, whereas nests 3, 4, 5, and 8 were engaged more in foraging (Figure 4). We noticed eggs in nests 2, 6, and 7, but chicks were raised only from nests 2 and 6.

**Table 2** Initial distribution estimated during the White-rumped Vulture nest building phase from direct observations.

| Nest ID | Foraging | Roosting | Breeding |
|---|---|---|---|
| Nest 1 | 0.000 | 0.212 | 0.789 |
| Nest 2 | 0.000 | 0.192 | 0.808 |
| Nest 3 | 0.038 | 0.135 | 0.827 |
| Nest 4 | 0.000 | 0.231 | 0.769 |
| Nest 5 | 0.000 | 0.192 | 0.808 |
| Nest 6 | 0.000 | 0.058 | 0.942 |
| Nest 7 | 0.000 | 0.173 | 0.827 |
| Nest 8 | 0.003 | 0.016 | 0.019 |

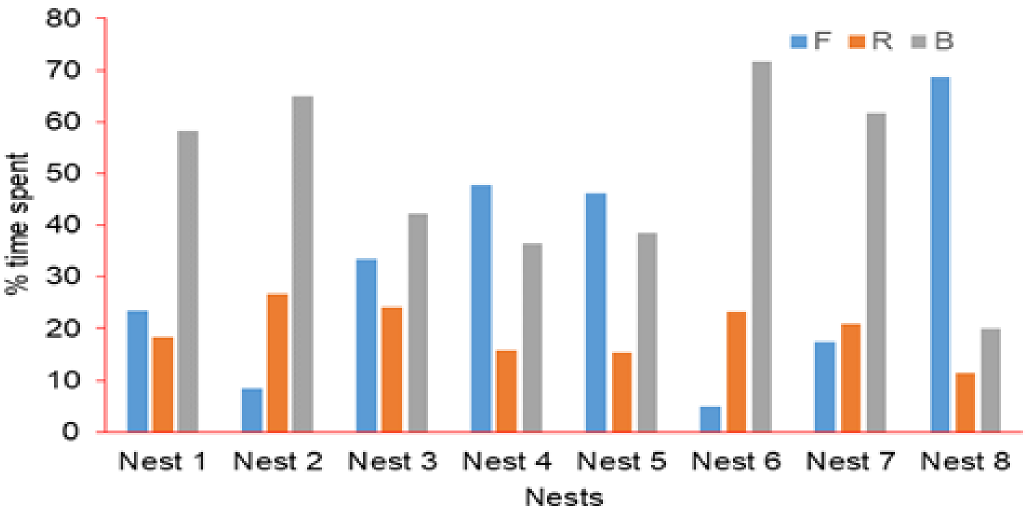


**Figure 4** Total time spent by White-rumped Vultures during foraging (F), roosting (R) and breeding (B) activities during the breeding season.

### *3.1. Transitional matrix via direct observation*

From the MCMs, we developed final transitional probability matrices for eight nests using state sequences of state transitions (List 1: see Supplementary material). We calculated the steady state transitions using matrix multiplication for any n-step transitions from these transition probabilities. All transitional matrices were multiplied by the corresponding initial state distribution (Table 2) derived from the pair of White-rumped Vultures at each nest. Finally, each nest's steady state of White-rumped Vultures was estimated using matrix multiplication until we obtained the steady state vector (Table 3).

Our results during nest building suggested that nests 1, 2, 3, and 6 had the greatest potential for success. During fledging, we conducted direct observation again to determine the initial distribution (Table 4) of White-rumped

Vultures to calculate transitional probabilities (List 1: see Supplementary material).

*3.2. Model evaluation*

We plotted observed behaviors of vultures and arranged them sequentially to create a matrix of co-occurrence sequence (Nests 1 and 8; Figure 5) from which we obtained transition probabilities. We plotted and assessed each nest's initial and transitional probabilities (Figure 6). All nests except Nest 6 followed patterns predicted by the MCMs, and Nest 6 followed absorbing MCMs, suggesting the pair at Nest 6 spent more time engaged in breeding activities (Table 5). The steady states differed among White-rumped Vultures at different nests. They suggested vultures at Nest 1, 2, 6, and 7 were more engaged in breeding activities (>70% of the time) than vultures at remaining nests, in turn suggesting the total duration for nest building by vultures from Nests 1, 2, 6 and 7 was less (see Table 5). We performed a post hoc analysis from these results and found that Nests 1, 2, 6, and 7 produced offspring, which validated our MCM results. We plotted the reoccurrence behavior in each phase for all nests during our observation and mentioned those behavior in heatmap (Figure 7).

**4. Discussion**

Understanding activities associated with reproductive events is important for further behavioral biology and conserving threatened and endangered species. Although subjective behavior related to reproductive events was frequently reported from field observations, no quantitative assessments applying MCMs have been made. We identified that White-rumped Vultures spent more time in breeding activities than foraging and roosting. We recognized the importance of breeding activities from our informed and validated model using direct observations. Our results suggest that the extent of parental investment (i.e., breeding behavior) corresponded with behaviors observed during nest construction, incubation, and chick rearing.

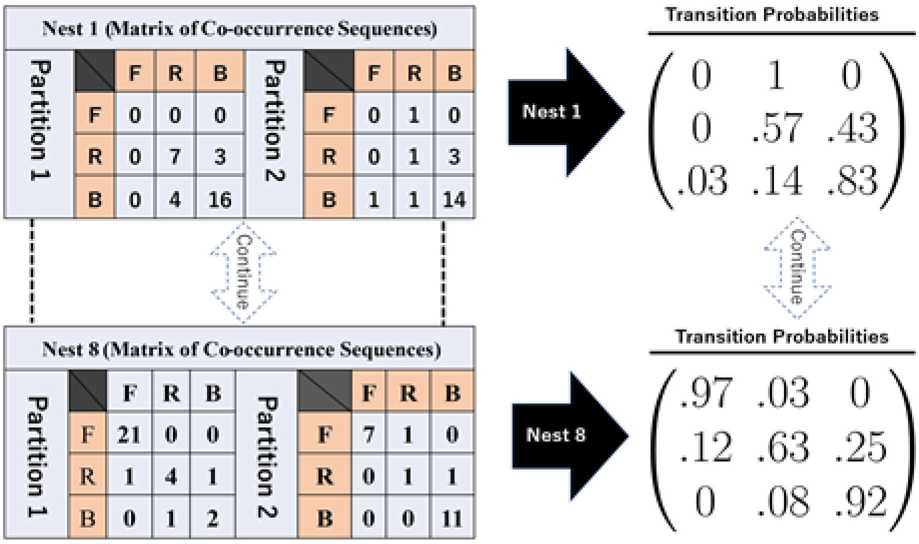


**Figure 5** Matrices for state transitions of White-rumped Vultures.

**Table 3** Final distribution of White-rumped Vulture behaviors estimated during incubation phase from direct observations.

| Nest ID | Foraging | Roosting | Breeding | Steady state |
|---|---|---|---|---|
| Nest 1 | 0.000 | 0.229 | 0.771 | 24 |
| Nest 2 | 0.000 | 0.240 | 0.760 | 9 |
| Nest 3 | 0.047 | 0.041 | 0.912 | 24 |
| Nest 4 | 0.000 | 0.240 | 0.760 | 24 |
| Nest 5 | 0.000 | 0.196 | 0.804 | 28 |
| Nest 6 | 0.000 | 0.059 | 0.941 | 10 |
| Nest 7 | 0.000 | 0.218 | 0.782 | 32 |
| Nest 8 | 0.000 | 0.005 | 0.030 | 4 |

We note that the limited number of nests and individual vultures could reduce the strength of our inference. However, behavior analysis composed of direct observation and MCMs were generally consistent and largely similar to previous studies (Gautam et al 2020; Jiang et al 2020). We suggest that our method can be applied in behavior analyses of species that may otherwise require substantial direct observation. Also, though we could not distinguish males and females during observations, our method allowed for analyses of both members of breeding pairs simultaneously. Finally, we caution that it is not always appropriate to consider the states from MCMs fitted to observational data as biologically significant as MCMs are frequently used in an unsupervised approach with state characteristics data-driven rather than pre-defined. Therefore, the most significant model patterns may not be ecologically relevant. However, the behavioral states we modeled in a supervised approach to predict vulture breeding successfully supported the importance of integrating behavioral data from direct observations.

**Table 4** Final distribution estimated during White-rumped Vulture fledgling phase from direct observations.

| Nest ID | Foraging | Roosting | Breeding | Steady state |
|---|---|---|---|---|
| Nest 1 | 0.000 | 0.361 | 0.428 | 85 |
| Nest 2 | 0.015 | 0.000 | 0.773 | 4 |
| Nest 3 | 0.000 | 0.159 | 0.571 | 25 |
| Nest 4 | 0.000 | 0.060 | 0.729 | 20 |
| Nest 5 | 0.000 | 0.085 | 0.684 | 9 |
| Nest 6 | 0.000 | 0.015 | 0.773 | 5 |
| Nest 7 | 0.031 | 0.015 | 0.742 | 14 |
| Nest 8 | 0.257 | 0.220 | 0.312 | 90 |

**Table 5** Final distribution of behaviors estimated during White-rumped Vulture breeding season from direct observations.

| Nest ID | F (Foraging) | R (Roosting) | B (Breeding) | Steady state |
|---|---|---|---|---|
| Nest 1 | 0.021 | 0.277 | 0.702 | 12 |
| Nest 2 | 0.020 | 0.216 | 0.765 | 9 |
| Nest 3 | 0.059 | 0.373 | 0.569 | 21 |
| Nest 4 | 0.137 | 0.333 | 0.529 | 54 |
| Nest 5 | 0.118 | 0.412 | 0.471 | 48 |
| Nest 6 | 0.000 | 0.176 | 0.824 | 15 |
| Nest 7 | 0.098 | 0.176 | 0.726 | 33 |
| Nest 8 | 0.446 | 0.123 | 0.431 | 211 |

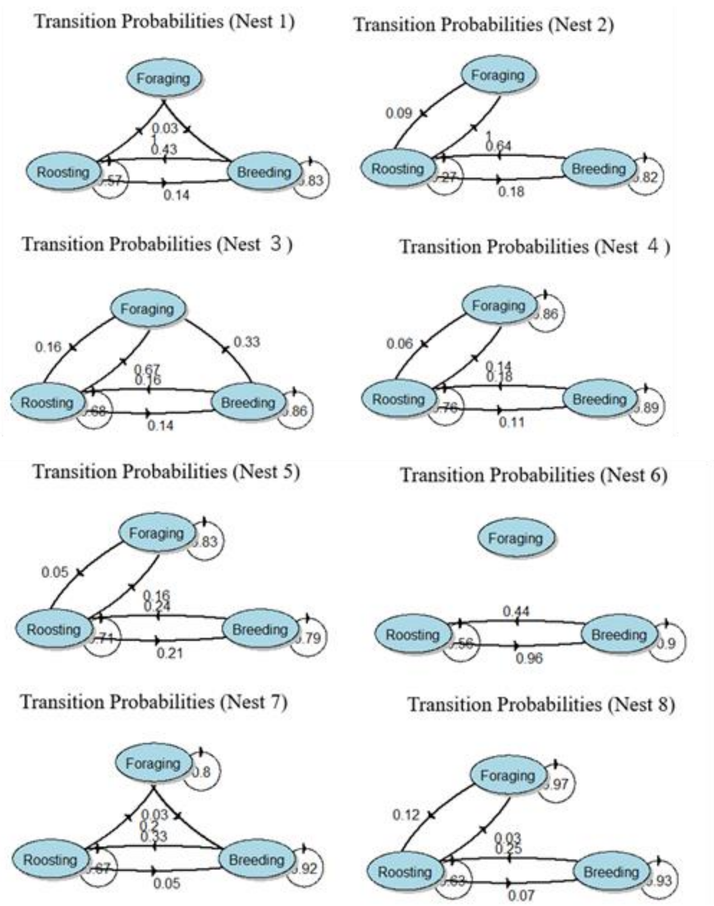


**Figure 6** Transitional probabilities of White-rumped Vultures during breeding season.

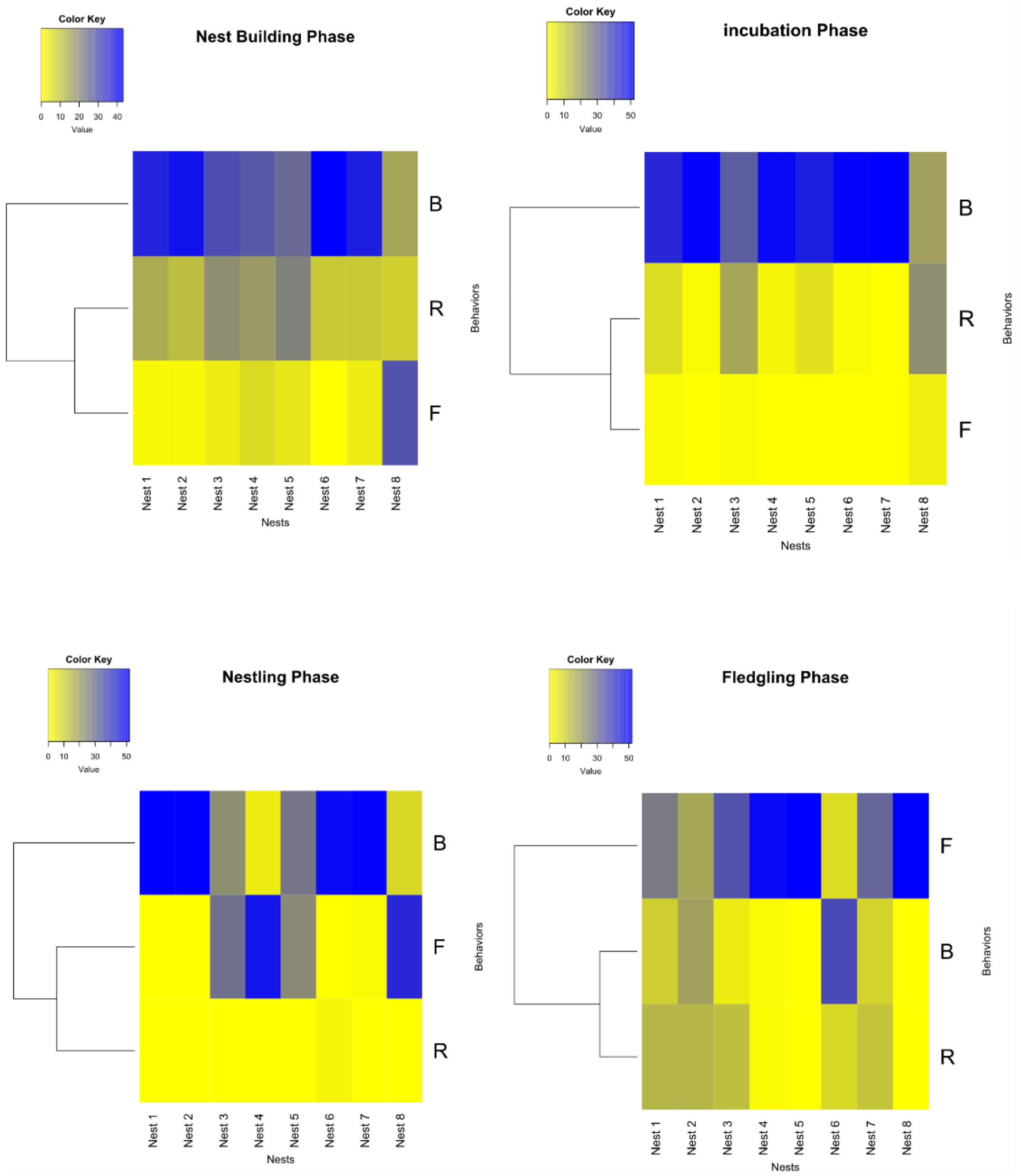


**Figure 7** Behavior activity of White-rumped Vultures during breeding season. The color code yellow to low activity and increasing the color intensity to blue to represent higher occurrence of behavioral activity.

We demonstrated that White-rumped Vulture behavior varied among nesting pairs and breeding phases. This variation in behavior could be influenced by food availability, the presence of predators, or vulture age. However, we acknowledge that further research is needed to support these hypotheses. Further, other factors, such as nest quality and environmental conditions, can influence behaviors and breeding success.

Model development allowed us to draw inferences regarding White-rumped Vulture behavior and comparisons with other studies. For example, four pairs of vultures established nests earlier than the other four pairs, apparently a consequence of the effort required to transport nesting materials to the site (e.g., dense tree canopies) and to construct the nests (e.g., weak support of tree for nest material). Early nesting allows vultures to lay eggs sooner, which could increase offspring survival (Barash 1975). The behavior of Eurasian Vultures was altered due to food scarcity, improved carcass disposal, and European conservation policy changes (Donazar et al 2010).

In contrast to our study, diurnal activities of captive White-rumped Vultures were predominantly roosting (56.3%) (Islam et al 2018); however, the observation periods differed between studies. We also combined sitting and roosting during breeding season as courtship displays which could explain our greater estimates of breeding activities compared to a previous study (i.e., Islam et al 2018). The amount of observed foraging and roosting by White-rumped Vultures was less than the breeding behavior in our study. We included only soaring as foraging behavior in our observations. Furthermore, we did not observe any carcasses during our observations which could influence behavior, and topography in part also limited our observations of soaring, therefore, likely reducing estimated foraging times (see Islam et al 2018). We also did not include behaviors from the entire diel period which could alter overall time spent in various activities. The daily activities of vultures can vary due to internal and external environmental factors (Bjorklund and Kipp 1996) and support that the daily activities of White-rumped Vulture breeding pairs differed in this study. Factors including infertility (Jamieson and Ryan 2000), predation (Feare et al 2017), modification to nesting habitat (Evans 2004), and human disturbances (Bamford et al 2009) can cause nesting failure and alter behaviors. Our model could help understand breeding success in White-rumped Vultures and the factors influencing this success.

Based on our observations and heatmap representation, we can speculate that different nests of vultures have different patterns of behavior during each phase. For example, during the nest building phase, nest 4 and nest 8 had a higher occurrence of foraging activity, which could indicate that they have better access to food sources and therefore a higher likelihood of producing an egg. During the incubation phase, nest 8 had the highest amount of foraging activity, while nest 7 had the highest amount of breeding activity. In the nestling phase, nest 4 had the highest amount of foraging activity, while nest 6 had the highest amount of roosting activity and nest 1 and nest 2 had the highest amount of breeding activity. During the fledgling phase, nest 8 and nest 5 had the highest amount of foraging activity, nest 1 and nest 2 had the highest amount of roosting activity, and nest 6 had the highest amount of breeding activity.

## 5. Conclusions

MCMs can be used to explain complex systems, including animal behavior. We used MCMs to evaluate the probability of three states such as foraging, roosting, and breeding behavior of the critically endangered White-rumped Vulture in Nepal. Comparing behavioral observations with those obtained from computational results revealed our MCMs explained vulture behavior with high accuracy and efficiency. Our results can help to improve our understanding of White-rumped Vulture behavioral ecology in continuous and discrete time and have applications for other wildlife species. We conclude that direct observations of animal behavior are essential to ensure model reliability and appropriately characterize early transition probabilities. However, this process can be labor intensive, and we recommend further automation, including machine learning and computer visualization techniques.

## Acknowledgments

The authors of this manuscript are grateful to their respective university for its technical assistance and valuable support in completing this research. We thank the Government of Nepal, Ministry of Forest and Environment, Department of Forest and Soil Conservation, Babar Mahal, Kathmandu, Nepal, for providing research permission. We thank Aman Sunar and Sushila Adhikari for field assistance.

## Ethical considerations

Data for this research was collected without handling or disturbing animals, so ethical permission for animal handling animals was not required.

## Conflict of interest

We declare no conflict of interest.

## Funding

University Grants Commission, Nepal (ID: PHD-76/77-S&T-3) has provided financial support for this research.

## References

Ali S, Ripley SD (1968) Compact handbook of the birds of India and Pakistan. Oxford: Oxford University press.

Altmann J (1974) Observational study of behavior: sampling methods. Behavior 49:227-266.

Anthony LL, Blumstein DT (2000) Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce $N_e$. Biological Conservation 95:303-315 DOI: 10.1016/S0006-3207(00)00037-9.

Arjmand S, Wegener G, Landau AM, Eskelund A (2022) Tips and traps for behavioral animal experimentation. Acta Neuropsychiatrica 1-39. DOI: 10.1017/ neu.2022.4.

Atherton TJ, Kerbyson DJ (1999) Size invariant circle detection. Image Vision Computing 17:795–803 DOI: 10.1016/S0262-8856(98)00160-7.

Baltrusaitis T, Robinson P, Morency LP (2016) OpenFace: An open source facial behavior analysis toolkit. 2016 IEEE Winter Conference on Applications of Computer Vision (WACV) DOI: 10.1109/wacv.2016.7477553.

Bamford AJ, Monadjem A, Hardy IC (2009) Nesting habitat preference of the African White-backed Vulture *Gyps africanus* and the effects of anthropogenic disturbance. Ibis 151:51-62 DOI: 10.1111/j.1474-919X.2008.00878.x.

Baral N, Gautam R (2007) Population status and breeding success of White-rumped Vulture Gyps bengalensis in Rampur, Syanja and Tanahu, Nepal. The Peregrine Fund, Boise, Idaho, USA and Royal Society for the Protection of Birds, The Lodge, Bedfordshire, UK.

Baral N, Gautam R, Tamang B (2005) Population status and breeding ecology of White Rumped Vulture *Gyps bengalensis* in Rampur Valley, Nepal. Forktail 21: 87–91.

Baral N, Nagy C, Crain BJ, Gautam R (2013) Population viability analysis of Critically Endangered white-rumped vultures *Gyps bengalensis*. Endangered Species Research 21:65–76.

Barash DP (1975) Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. The Wilson Bulletin 367-373.

Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. Animal behaviour 77:771-783. DOI: 10.1016/j.anbehav.2008.12.022

BirdLife International (2021) Gyps bengalensis. The IUCN Red List of Threatened Species 2021:e.T22695194A204618615. DOI: 10.2305/IUCN.UK.2021-3.RLTS.T22695194A204618615.en

Bjorklund DF, Kipp K (1996) Parental investment theory and gender differences in the evolution of inhibition mechanisms. Psychological bulletin 120:163.

Boake CR (Ed.) (1994) Quantitative genetic studies of behavioral evolution. University of Chicago Press.

Chaudhary A, Subedi TR, Giri JB, Baral HS, Bidari B, Subedi H, Cuthbert RJ (2012) Population trends of Critically Endangered *Gyps* vultures in the lowlands of Nepal. Bird Conservation International 22:270–278.

Cho WKT, Liu YY (2018) Sampling from complicated and unknown distributions: Monte Carlo and Markov Chain Monte Carlo methods for redistricting. Physica A: Statistical Mechanics and its Applications 506:170-178 DOI: 10.1016/j.physa.2018.03.096.

Crall JD, Gravish N, Mountcastle AM, Combes SA (2015) BEEtag: a low-cost, image-based tracking system for the study of animal behavior and locomotion. PloS One 10:e0136487 DOI: 10.1371/journal.pone.0136487.

Dhakal H, Sharma HP, McClure CJ, Virani M, Rolek BW, Pradhan NM, Bhusal KP (2022) Vulture distribution and people perception of vultures in Pokhara Valley, Nepal. Ecology and Evolution12:e8528.

Dingemanse NJ, Kazem AJ, Réale D, Wright J (2010) Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology & Evolution 25:81-89 DOI: 10.1016/j.tree.2009.07.013.

Donázar JA, Cortés-Avizanda A, Carrete M (2010) Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation. European Journal of Wildlife Research 56:613-621 DOI: 10.1007/s10344-009-0358-0.

Evans KL. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1-13 DOI: 10.1111/j.1474-919X.2004.00231.x.

Fagen RM, Young DY (1978) Temporal patterns of behaviors. Quantitative Ethology (Colgan, ed.). Wiley.

Feare CJ, van der Woude J, Greenwell P, Edwards HA, Taylor JA, Larose CS, ... de Groene A (2017) Eradication of common mynas Acridotheres tristis from Denis Island, Seychelles. Pest Management Science 73:295-304. DOI: 10.1002/ps.4263.

Fernandes AFA, Dórea JRR, Rosa GJDM (2020) Image analysis and computer vision applications in animal sciences: an overview. Frontiers in Veterinary Science 800. DOI: 10.3389/fvets.2020.551269.

Gagniuc PA (2017) Markov chains: from theory to implementation and experimentation. John Wiley & Sons. 1-235.

Gautam R, Baral N, Sharma HP (2022) Are white-rumped vultures (Gyps bengalensis) scavengers or predators at a vulture safe feeding site of Nepal?. Biodiversitas Journal of Biological Diversity 23:3808-3812.

Gautam BP, Noda Y, Gautam R, Sharma HP, Sato K, Neupane SB (2020) Body Part Localization and Pose Tracking by Using Deepercut Algorithm for King Cobra's BBL (Biting Behavior Learning). In *2020 International Conference on Networking and Network Applications (NaNA)*. IEEE 422-429.

Gautam R, Baral N (2013) Population trends and breeding success of three endangered vulture species in Pokhara Valley, Kaski, Nepal. *Ibisbill Journal of Himalayan Ornithology* Issue 2: 30 years in Bird Conservation. Bird Conservation Nepal.

Gautam R, Baral N (2014) Monitoring the population status of White-rumped vulture *Gyps bengalensis* in Rampur, Syanja and Tanahu, Nepal.

Geyer CJ (1992) Practical markov chain monte carlo. Statistical Science 473-483.

Green RE, Newton I, Shultz S, Cunningham AA, Gilbert M, Pain DJ, Prakash V (2004) Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. Journal of Applied Ecology 41:793-800.

Grewal JK, Krzywinski M, Altman N (2019) Markov models-markov chains. Nature Methods 16:663-664 DOI: 10.1038/s41592-019-0476-x.

Grimmett R, Inskipp C, Inskipp T, Baral, HS (2016) *Helm Field Guides. Birds of Nepal.* Revised edition. Christopher Helm London.

Islam MA, Ahammed R, Aktar M (2018) Diurnal activity pattern of white-rumped vulture, *Gyps bengalensis* (Gmelin, 1788) in captivity during breeding season at Bangladesh National Zoo, Dhaka. Jahangirnagar University Journal of Biological Sciences 7:81-85.

Jamieson IG, Ryan CJ (2000) Increased egg infertility associated with translocating inbred takahe (*Porphyrio hochstetteri*) to island refuges in New Zealand. Biological Conservation 94:107-114.bDOI: 10.1080/03949370.2018.1561523.

Jiang W, Wang K, Lv Y, Guo J, Ni Z, Ni Y (2020) Time series based behavior pattern quantification analysis and prediction—A study on animal behavior. Physica A: Statistical Mechanics and Its Applications. 540:122884 DOI:10.1016/j.physa.2019.122884.

Kappeler PM (2021) Behavioural Biology: Content and History. In *Animal Behaviour* 3-14. Springer, Cham DOI: 10.1007/978-3-030-82879-0_1.

Knopff KH, Knopff AA, Warren MB, Boyce MS (2009) Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Managment 73:586-597 DOI: 10.2193/2008-294.

Koralewski, TE, Westbrook JK, Grant WE, Wang HH (2019) Coupling general physical environmental process models with specific question-driven ecological simulation models. Ecological modelling 405:102-105. DOI:10.1016/j.ecolmodel.2019.02.004.

la Torre-Torres D, Oscar V, Aguilasocho-Montoya D, Álvarez-García J, Simonetti B (2020) Using Markov-switching models with Markov chain Monte Carlo inference methods in agricultural commodities trading. Soft Computing 24:13823-13836. DOI: 10.1007/s00500-019-04629-5.

Loveridge R, Ryan GE, Sum P, Grey-Read O, Mahood SP, Mould A, Harrison S, Crouthers R, Ko S, Clements T, Eames JC, Pruvot M (2019) Poisoning causing the decline in Southeast Asia's largest vulture population. Bird Conservation International 29:41-54.

Noldus LPJ, Spink AJ, Tegelenbosch RA (2002) Computerised video tracking, movement analysis and behaviour recognition in insects. Computers and Electronics in Agriculture 35:201–227. DOI: 10.1016/s0168-1699(02)00019-4.

Oaks JL, Giltbert M, Virani MZ, Watson RT, Meteyer CU, Rldeout BA, Shivaprasad HL, Arshad S, Chaudhry MJI, Arshad M, Mahmood S, All A, Khan AA (2004) Diclofenac residues as the cause of population decline of vultures in Pakistan. Nature 427:630-633.

Pimm SL, Alibhai S, Bergl R, Dehgan A, Giri C, Jewell Z, … Loarie S (2015) Emerging technologies to conserve biodiversity. Trends in Ecology & Evolution 30:685– 696 DOI: 10.1016/j.tree.2015.08.008.

Prakash V (1999) Status of vultures in Keoladeo National Park, Bharatpur, Rajasthan, with special reference to population crash in Gyps species. Journal of Bombay Natural History Society 96:365-378.

Simmons KEL (1955) The nature of the predator-reactions of waders towards humans; with special reference to the role of the aggressive, escape, and brooding drives. Behavior 130-173. https://www.jstor.org/stable/4532827

Shultz S, Baral HS, Charman S, Cunningham AA, Das D, Ghalsasi GR, Goudar MS, Green RE, Jones A, Nighot P, Pain DJ, Parkash V (2004) Diclofenac poisoning is widespread in declining vulture populations across the Indian subcontinent. Proceedings of the Royal Society of London B (Suppl.) 271:458-S460. DOI: 10.1098/rsbl.2004.0223.

Taha A, Zayed HH, Khalifa ME, El-sayed M (2014) Exploring behavior analysis in video surveillance applications. International Journal of Computer Applications 93:22-32.