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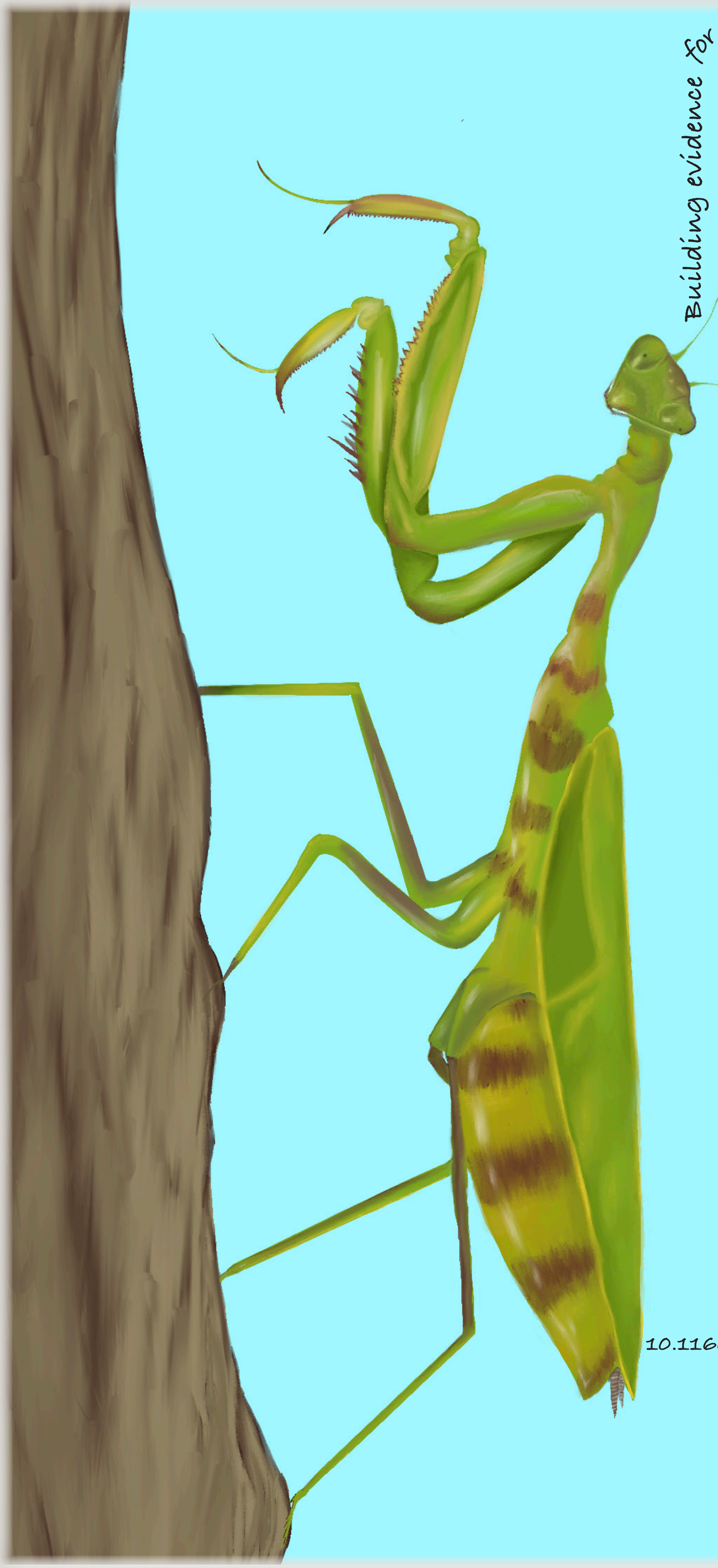

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Cover: A gravid praying mantis just before she laid her ootheca—digital art on procreate. © Aakanksha Komanduri.

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ARTICLE

The population trend of the largest breeding colony of the Indian Swiftlet *Aerodramus unicolor*: is it on the verge of extinction?

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Abstract: Fluctuations in animal populations are indicators of environmental change. Populations of the Indian Swiftlet *Aerodramus unicolor* on the Burnt and Old Lighthouse islands of Vengurla rocks, Sindhudurg district, Maharashtra were assessed using the logistic growth model. The study used secondary literature and primary surveys to estimate breeding population sizes on both islands. To understand population dynamics, we calculated the carrying capacity (K) using the Verhulst population growth model, and the percent rate of change in populations. Swiftlet populations on both islands are considered to be the maximum size their habitat can sustain, not exceeding 5,000 and 246 birds on Burnt and Old Lighthouse islands, respectively. These populations were observed to fluctuate between 2020 and 2023, with change rates of 5.5% on Burnt Island, and -53% on Old Lighthouse Island. The logistic growth model indicates that these Indian Swiftlet populations are fluctuating near the carrying capacities of their habitats, which could gradually lead to extinction. This highlights the urgent need for conservation and regular monitoring of these populations in Vengurla rocks.

Keywords: Apodid, carrying capacity, cave habitat, conservation, extinction, logistic growth, sindhudurg, swiftlet populations, tropical cyclone, vengurla rocks.

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Author contributions: DK—conceptualization, data curation, formal analysis, methodology, software, writing-original draft; MSS—conceptualization, funding acquisition, investigation, methodology, project administration, validation, supervision, writing–original draft, review & editing.

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INTRODUCTION

The population and distribution of animals are attributed to various aspects of their environment (Morrison 1986). Birds are frequently regarded as markers of environmental change (Temple & Wiens 1989; Gregory et al. 2009). When there is a rapid decrease in a population (>25%), conservation action is triggered, and influences policy decisions (Dunn 2002; Gregory et al. 2002, 2009; Luther et al. 2016). There are several reasons for bird declines, which include habitat loss (Rolstad 1991; Dolman & Sutherland 1995), predation (Cresswell 2011), unsustainable farmland practices (Rigal et al. 2023), overall range decline (Rodríguez 2002), environmental and climate change (Morrison 1986; Wilson & Fuller 2001; Pearce-Higgins et al. 2015). Birds' response to environmental changes at behavioral and physiological levels affects the population trend; which, in turn, affects the geographic range, population density, age structure, sex ratios, and habitat occupancy (Temple & Wiens 1989). Moreover, it may further lead to population extinction (Sæther et al. 2005).

According to Sæther et al. (2005), the extinction of animal populations has been studied using five approaches: (i) estimates of the loss of species in a specific area over time (Pimm et al. 1988; Ferraz et al. 2003; Schoener et al. 2003), (2) species–area relationships (Simberloff 1992), (3) assigning several species to different risk categories (Sæther et al. 2005), (4) patterns in time series of population fluctuations (Inchausti & Halley 2003), and (5) population viability analysis using given a set of preconditions (Morris & Doak 2002). A few empirical studies have been conducted on the theories, highlighting that more variability in population abundance would mean a higher probability of extinction (Inchausti & Halley 2003). Additionally, there are still few studies conducted on the populations and other aspects such as habitat occupancy and carrying capacity for the terrestrial bird species (Chamberlain & Fuller 1999; Sæther et al. 2005; Ramírez-Cruz et al. 2020; Campos-Cerqueira et al. 2021). Even though few such attempts have been made for the wild populations of cave-dwelling birds in their natural habitats (Sankaran 2001; Nguyên et al. 2002; Manchi & Sankaran 2011; Roark et al. 2022) and in the ex situ conditions (Thorburn 2014; Mursidah et al. 2020), none have attempted studying swiftlets' inter-relatedness of the populations, its variability (trends), long-term survival or probability of extinction.

Swiftlets, the members of Genus *Aerodramus*, *Collocalia*, and *Hydrochous*, are among the least-studied bird groups. These paleo-tropical cave-dwelling birds are colonial (Chantler & Driessens 1999). They breed and roost in colonies varying in size from millions, as in the Gomantong Cave, North Borneo (Stimpson 2013), to a few dozen, as in some caves in the Andaman Islands (Sankaran 1998; Gurjarpadhye et al. 2021). Global demand for the edible nest of one swiftlet resulted in uncontrolled nest harvesting, leading to population declines and local extinctions (Sankaran 2001; Manchi & Sankaran 2010; Mursidah et al. 2020).

India is home to four species of swiftlets, including the Indian Swiftlet *Aerodramus unicolor,* with populations from the Western Ghats (Mahabal et al. 2007; Chantler & Kirwan 2020) and Sri Lanka (Chantler & Kirwan 2020). This species is under illegal nest harvesting pressure in different regions in India and Sri Lanka (Sankaran 2001). The largest known colony is located at Vengurla Rocks in Maharashtra, and it was documented to be under illegal nest harvesting pressure until 2002 (Mahabal et al. 2007). A small breeding colony was discovered recently on Old Lighthouse Island of Vengurla Rocks. After 2002, there is no record of these colonies being raided for the swiftlet's nest.

According to the available literature, the Indian Swiftlet population on Burnt Island has been fluctuating within a specific range since 2001 (Mahabal et al. 2007), possibly due to pressure from illegal nest harvesting. Therefore, it is crucial to understand the dynamics of the world's largest population of Indian Swiftlet in the absence of nest collection pressure. In this study, we attempted to understand the status and trends of populations on the Burnt and Old Lighthouse Islands of Vengurla Rocks and predict population trends at both locations.

METHODS

Study area: Vengurla Rocks Archipelago, Maharashtra, India

According to the Integrated Coastal and Marine Area Management (ICMAM-PD 2001) through IRS LISS-III satellite imagery, Malwan Bay is a submerged and exposed rocky island chain extending straight towards the south. The Malwan coast forms part of the Western Ghats, where the Sahyadri ranges gradually meet the Arabian Sea. Several islands exist in this chain, including 20 islets of the Vengurla Rocks Archipelago at the southern tip, and Sindhudurg Fort at the northern end. The archipelago extends approximately 5 km north-south and 1.6 km east-west, and consists of rocks rising 20–50 m above sea level (Bhanti 2000). Three islands are of significant size: Burnt, New Lighthouse, and Old Lighthouse Islands. Among the remaining, nine are small islands, and eight are submerged rocks (Mahabal et al. 2007; Image 1a). The base rock of these islands is submerged towards the deeper waters and lies below the exposed sediments (Raju et al. 1991), containing ferruginous quartzite of the Dharwar group (Raju et al. 1991).

A recent study by Manchi et al. (2022) documented the presence of a Swiftlet Cave and a void on Burnt Island, and one void on New Lighthouse Island (Manchi et al. 2022). The Vengurla rocks archipelago bears the Dharwar period of rock formation, fixed mainly between 2,500 and 1,800 million years ago. It is one of the oldest known rock formations in the Indian peninsula (Raju et al. 1991). The Swiftlet Cave is the largest and most accessible cave in the Vengurla Rocks Archipelago (Manchi et al. 2022; Image 1b). The cave is 61 m long with an average height of 18 m (Manchi et al. 2022). It is home to the largest known population of Indian Swiftlet globally.

The Old Lighthouse (Image 1b) is an abandoned structure built in 1876 using laterite and cobblestones (Bhanti 2000). A chamber with a dome inside the structure roughly measures about 5 x 5 m in size and 5 m in height (Mahabal et al. 2007), with five windows and an entrance to the lighthouse. The Indian Swiftlet colony, of 30 breeding pairs nesting on the chamber ceiling, was first documented in 2001 by Mahabal et al. (2007). With continuous and significant deterioration, the structure is not in good condition.

Reviewing the available literature, we compiled Indian Swiftlet population data from Burnt (1940–2006) and Old Lighthouse (2001) Islands. We estimated breeding populations of the Indian Swiftlet by conducting population surveys on both islands using the nest count method between December 2020 and April 2023 (Sankaran 2001; Manchi & Sankaran 2014). After entering the habitat, we meticulously search the cave walls and ceiling. Once located, the nests were counted. These counts are conducted at the end of every month during the breeding season (from December to June) to monitor the breeding populations of the Indian Swiftlet). The highest count obtained usually during the incubation and nestling period (April or May) was taken as the breeding population of that particular cave. The number of nests increases during incubation and nestling periods, as certain nests during the nesting period are camouflaged with the cave wall and are fairly simple to locate once the parents start sitting on eggs for incubation and nestlings hang to or sit in the nests. Since swiftlets are monogamous, each nest is considered to represent a breeding pair (Sankaran & Manchi 2008; Manchi & Sankaran 2014; Gurjarpadhye et al. 2021). Monthly nest counts were done on both islands, and the maximum count in each colony during a season was considered to be the breeding population of each colony for a year.

Data analysis

Following Mujib et al. (2019), we calculated the carrying capacity (K) for both colonies using the Verhulst (Logistic) Population Model. This logistic model assumes that "at some point, the population will be close to the equilibrium point, i.e., carrying capacity" (Timeneno & Utomo 2008). We used the following formula of the Verhulst (Logistic) Population Model to calculate the carrying capacity:

$K = P_1 (P_1P_0 – 2P_0P + P_1P_2)/ P_1^2 - P_0P_2$ .... (Equation 1)

Where, K = Carrying capacity, P_0 = swiftlet population in 2020, P_1 = population in 2021, P_2 = population in 2022

The population growth rate was calculated using the following:

$K = P_0 (P_2 - P_1) / P_1 - P_0$ .... (Equation 2)

We also independently calculated the change in the percent rate of the populations by using the following equation:

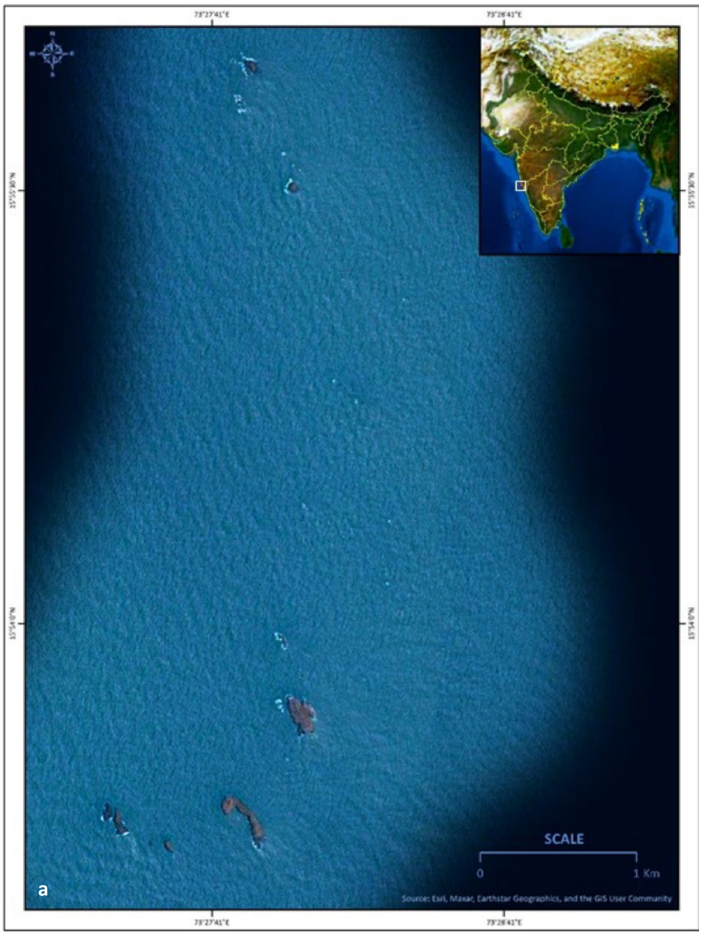
Percent change in population = $100 \times ((P_f - P_i))/ (P_i)$.... (Equation 3)

Where, P_i = Initial Population, P_f = Final Population

RESULTS

Population status of Indian Swiftlet on Burnt Island

Jerdon (1862) first documented the presence of thousands of birds in the cave on Burnt Island. Considering this as the first record, it is comprehended that the Indian Swiftlet's breeding colony on Burnt Island has been known for the last 161 years. The subsequent documentation of this population was by Abdulali (1940, 1962), who recorded ~5,000 birds, or around 2,500 nests. Later, in 2001, when illegal nest collection was brought to arrest, the population estimate was 3,600 birds (Pande et al. 2001), which increased to 5,000 in 2006 (Mahabal et al. 2007). In 2020, during the beginning of the present study, the Indian Swiftlet population was recorded as ~4,000 birds (2,000 nests), and in subsequent years the counts were 4,674 in 2021, 3,920 in 2022, and 4,220 in 2023 (Figure 1a). The overall population change rates were 39% from 2001 to 2006, and 5.5% between 2020 and 2023.



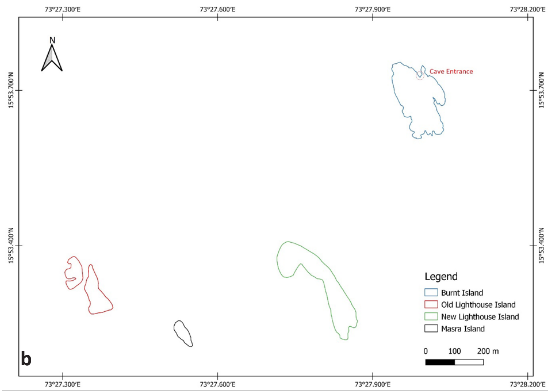


Image 1. a—The geographical location of the Vengurla Rocks in Sindhudurg, Maharashtra | b—The location of the Old Lighthouse Island and Swiftlet cave in the Vengurla rocks.

Population status of Indian Swiftlet in Old Lighthouse Island

The Indian Swiftlet breeding colony on the Old Lighthouse Island is relatively new. The initial population of this colony in 2001 was estimated to be 60 birds, i.e., 30 nests (Mahabal et al. 2007). In 2020 the population was evaluated at 246 birds, and in subsequent years the numbers were 196 in 2021, 92 in 2022, and 116 in 2023 (Figure 1b). The overall population change rate from 2020 to 2023 was -53%.

Logistic population growth model

We considered the three-year population data (2020–2022) to calculate the carrying capacity of both Islands. Considering that the estimated average population size at Burnt Island has never exceeded 5,000 birds and fluctuates within a specific range (between 5,000 and 3,600 individuals), the population is assumed to be '*k*' type. Also, the logistic growth model (Equation 1) suggested that the carrying capacity of the cave at Burnt Island is 4,041 individuals. Based on the estimated

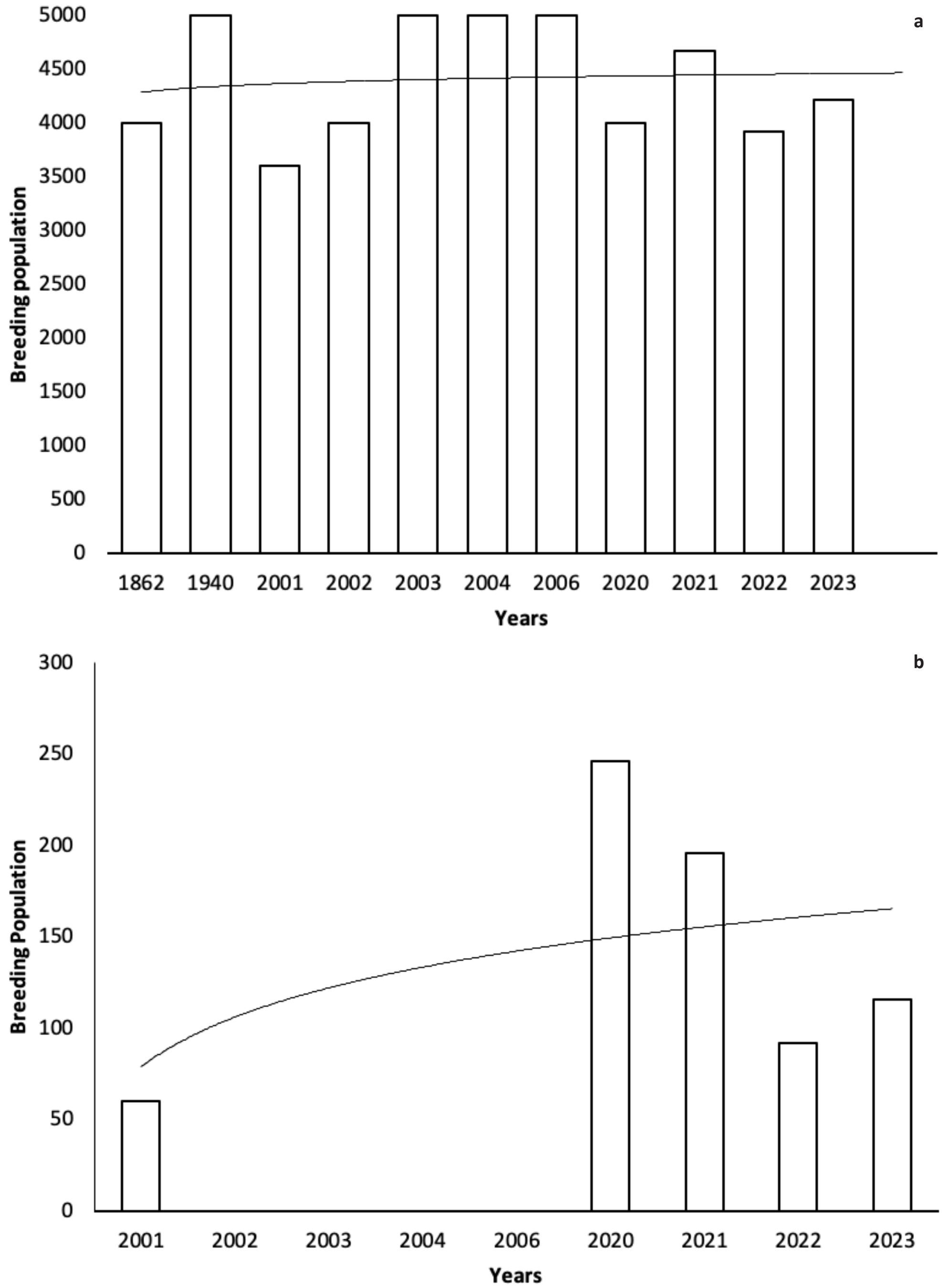


Figure 1. The population of the Indian Swiftlet from: a—1862 to 2023 in Burnt Island | b—2001 to 2023 in Old Lighthouse Island, Sindhudurg district. Note – the trend line is logarithmic.

carrying capacity, the following formulae were made using Mujib et al. (2019), to estimate the population of the Indian Swiftlet for the next 50 years.

$P(t) = 4041.79 / 0.010e^{-1.12t} + 1$ (Equation 4)

$P(50) = 4041.79 / 0.010e^{-1.12*50} + 1$

$P(50) = 3473$ birds

Using this formula, we could predict the swiftlet populations for the next 50 years (Figure 2a), which depicts that this population will have a declining trend over the next 50 years. Similarly, the Indian Swiftlet population on Old Lighthouse Island fluctuated between 246 in 2020 and 116 in 2023. However, as per the logistic growth model, this population is predicted to remain more or less steady for the next 50 years (Figure 2b).

$P(t) = 260.57 / 0.059e^{5.56t} + 1$ (Equation 5)

$P(50) = 260.57 / 0.059e^{5.56*50} + 1$

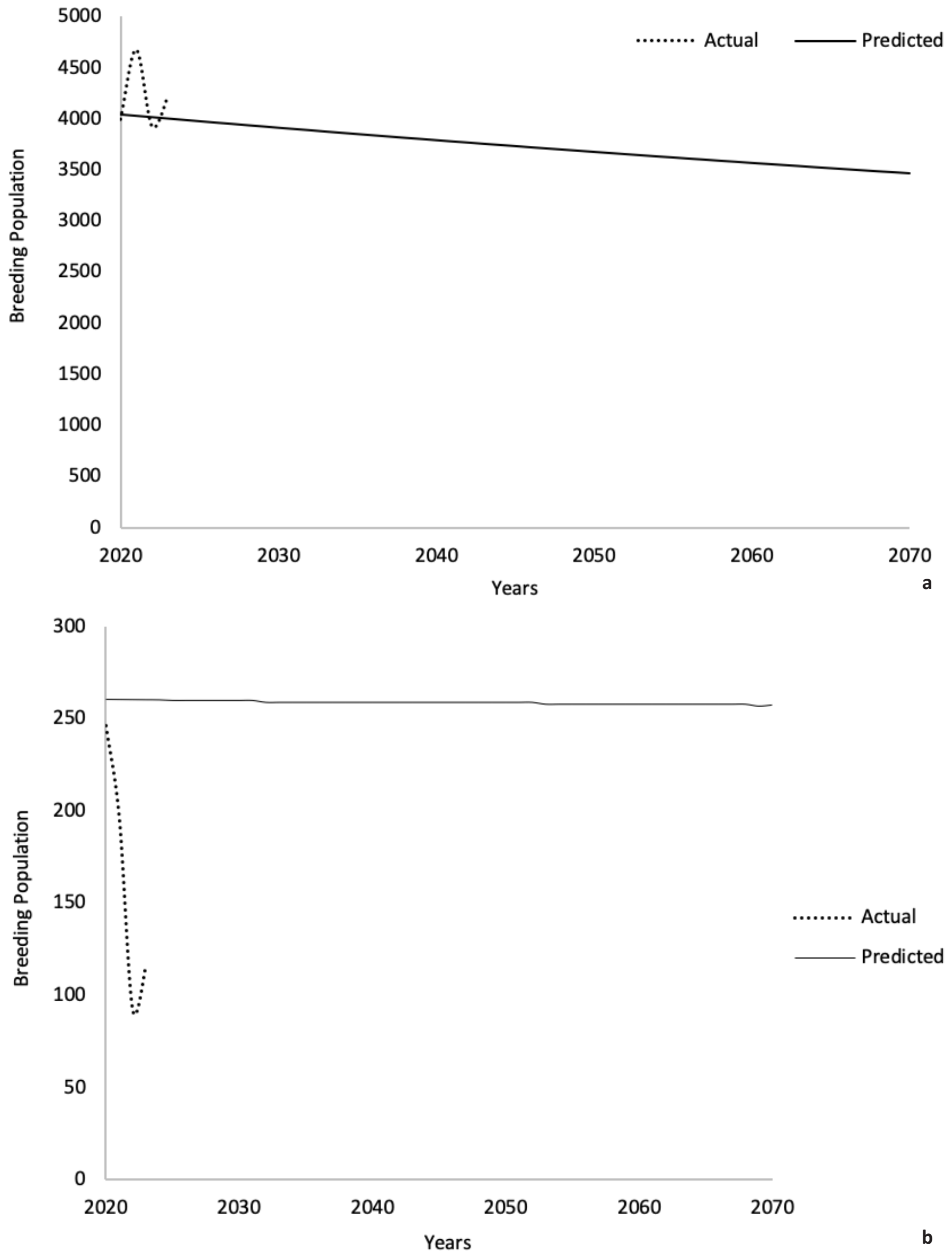


Figure 2. The actual and predicted populations 2020 to 2070: a—Burnt Island | b—Old Lighthouse Island in the Vengurla rocks, Sindhudurg district.

P(50) = 257.59 birds

DISCUSSION

Our estimates for populations of Indian Swiftlet on Burnt and Old Lighthouse Islands of Vengurla rocks indicate fluctuations, as were also observed in the counts between 2000 and 2006 (Mahabal et al. 2007). Similarly, the Indian Swiftlet breeding colony of 60 birds, discovered in 2001 on Old Lighthouse Island (Pande et al. 2001), depicted significant growth. During the present study in 2020, we recorded more than four times increase in the initial population to 246 birds, which later depicted a continuous decline between years 196 (2021), 92 (2022), and 116 (2023). Based on the documented knowledge from other parts of the world, we assume the recent decline of the Indian Swiftlet populations in the Vengurla Rocks Archipelago resulted from the tropical cyclone Tauktae in May 2021. Tarburton & Tarburton (2013)

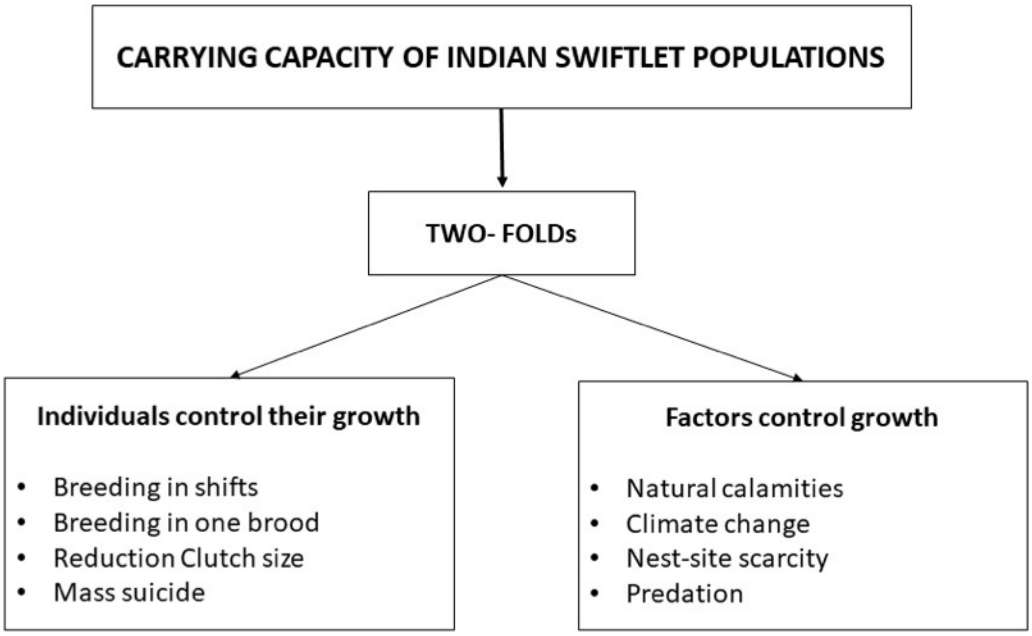


Figure 3. The hypothetical understanding of the factors based on the two-fold carrying capacity described by Del Monte-Luna et al. (2004) of the Indian Swiftlet populations in Vengurla Rocks.

have documented that the cyclones caused a significant decline in the populations of the White-rumped Swiftlet *Aerodramus spodiopygius* by either washing down the rock face on which the nests are anchored or partially dissolving the nests, or by the cave or cracks bed filling up until floodwater drowns the nestlings or causes eggs to fail. According to Tarburton & Tarburton (2013), the offshore and coastal colonies, may also be reduced or destroyed by high waves or heavy rainfall during the cyclonic weather. The cyclonic effect was also observed in the other cave-dwelling animals, such as the Pacific Sheath-tailed Bat *Emballonura semicaudata* in Upolu (South Pacific Ocean). Before cyclones Ofa in 1990, and Val in 1991, the species was known to occur in good numbers in several caves. Some American Samoa caves have reported steep declines over the past 10–20 years, perhaps related to cyclone damage (Hutson et al. 2001). Other natural calamities such as earthquakes also affected swiftlet populations. According to Manchi & Sankaran (2009), the changes (rock fall, closure of cave openings, cracks on the rock surfaces and shifting of rocks) caused in the cave structures and microhabitat because of the mega earthquake of December 2004 in the Andaman & Nicobar Islands, the bats and Edible-nest Swiftlet *Aerodramus fuciphagus* lost their roosting caves or shifting their roosting and nesting sites within the caves. Understanding how natural disasters affect various aspects of the swiftlet populations would be a fascinating scientific exploration. Moreover, detailed studies are also required regarding the cave morphology and behavioural responses of the swiftlets towards strong winds and cyclones.

The Tauktae cyclone hit the Arabian Sea between 14 and 19 May 2021 and passed through the study site (Image 1b; Burnt Island and Old Lighthouse Island). The northeastern direction of the cave opening makes this particular cave on Burnt Island a haven for the swiftlet nesting as the south-west monsoon winds do not directly affect the microhabitat inside the cave. Also, as the nests are on the cave walls at a height of 10–16 m and the sea waves cannot reach that height, the nesting place (walls and ceiling) remains dry. At the same time, the storm and strong cyclonic winds can affect the foraging activity and lead to the mortality of the birds foraging around or returning to the cave. For instance, the population decline seen after Tauktae (220 km/h; northward direction parallel to the western coast of India) might be because of a severe effect on the flying birds.

Furthermore, there may be mortality because the swiftlets, the members of Apodidae, cannot resume flight if pushed onto the ground or any other surface. In another case, during the unusual rains in December 2021, several individuals of the Little Swift *Apus affinis* in urban areas of Mumbai, Maharashtra, were observed in the balconies of the high floored buildings and could not survive post-rescue (Aditya Patil, President, Wildlife

Welfare Association, Mumbai, pers. comm.13 December 2021). The reason for the mortality was suspected to be dehydration and starvation. Studies such as by Porter & Aspinall (2013) recorded the populations of the Himalayan Swiftlet *Aerodramus brevirostris* and the Little Swift following a cyclone in the Indian Ocean in November 2007 in Socotra Island (Middle-east) which is far away from their known distribution range. It indicates that the birds may get disoriented during the cyclones and reach a destination out of their distribution range (Elkins & Johnson 2005). The cyclone Tauktae (2021) took place during May (Swiftlet's peak breeding season and nestling period) and when they made multiple visits to the nest to feed the chicks (Nguyên et al. 2002). Sicurella et al. (2015) documented similar observations in Common Swift *Apus apus*, mentioning that the frequent rains and adverse weather conditions affect their foraging activity and result in the mortality of both adults and chicks.

According to Langham (1980), the cessation of breeding in Edible-nest Swiftlet *Aerodramus fuciphagus* was influenced by the onset of monsoon, where the wet weather affects the prey. The heavy rains and strong winds can cause a low abundance of aerial insects and reduce the foraging activity of Germain's Swiftlet *Aerodramus germani* (Petkliang et al. 2017). Öberg et al. (2015) observed that the fledging success of insectivorous birds is negatively related to rainfall (days >10 mm) during nestling periods. Further, according to Blomqvist & Peterz (1984), birds are known to be sensitive to wind conditions during migration or when foraging at sea, and seabirds are particularly vulnerable to windstorms since they cannot find shelter when facing extreme wind conditions in the open sea. Overall, it is seen that the rainfall affects the breeding success and survival of the swiftlets and indirectly affects the recruitment, ultimately affecting the overall populations. Further studies in this regard would help us understand the related dynamics.

According to several studies (Cigna 1968; Badino 2010; Borsato et al. 2015; James et al. 2015), the subsurface air flows are controlled by the cave geometry, its connection with the surface, and variations in external weather and climate. Further, as there are two entrances on the cave ceiling, the continuous rains and winds can enter the cave, adversely affecting the bird populations. Also, a study by Jessel et al. (2019) found that the Edible-nest Swiftlet uses a mechanical overdesign strategy for building the edible nest (safety factor 5–10), however, it has been observed that an extremely violent storm could destroy mud nests which has a safety factor (10) similar to the edible nest (Turner 2006). This directly means that the strong winds might affect the nest of the swiftlet and the nestlings' survival.

The population growth rate of the Indian Swiftlet in Burnt Island from 2001–2006 is 39%, and from 2020–2023 is 5.5%. Until the poaching of the swiftlet nests was brought to a halt in 2001, the Indian Swiftlet population was observed to be dwindling (Mahabal et al. 2007). In the Andaman Islands, continuous poaching reduced swiftlet populations by >80% within a decade (Sankaran 2001). After the conservation actions after the year 2000, the population in protected caves increased by 39%, whereas it declined by 74% in unprotected caves from 2000 to 2008 (Manchi & Sankaran 2014). Similar to our observations on Burnt Island, the study by Manchi & Sankaran (2014) on the Andaman Islands, also assessed the growth rate of ~38–39 % after ceasing the nest collection through participatory conservation efforts.

To explore further population dynamics, in the present study, the logistic population growth model is used to calculate the carrying capacity (K) of the Indian Swiftlet populations in both Burnt (4,041 birds) and Old Lighthouse (260 birds) Islands. The exploration also highlights that both these populations have already reached their thresholds and keep fluctuating around their respective *K* values. As per the model's predictions, the population in both colonies will continue to experience slight fluctuations between 2020 and 2070. However, some of the factors responsible are yet unidentified. Based on the understanding of the two-fold carrying capacity described by Del Monte-Luna et al. (2004), we could identify a few factors that can lead to population declines or fluctuations in the swiftlet populations (Figure 3).

Understanding the findings by Sæther & Engen (2003), many populations fluctuate around their carrying capacity for an extended period before they eventually go extinct. However, it is also evident from Lande et al. (1993) that the average time of extinction of a population and the *K* follows different laws in response to demographic stochasticity, environmental stochasticity, or random catastrophes. Mursidah et al. (2020) observed similar fluctuations in the ex-situ populations in a 1,600 m^2 swiftlet house with a productive population of 725 birds in its third year, increasing to 5,500 birds in 23rd year and declining to 400 in the 45th year due to the increased compactness in the breeding colony. According to Stimpson (2013), in the Niah region, Sarawak, Malaysia, the fluctuations in the swiftlet populations since the late Pleistocene result from changes in the environment's carrying capacity and prey resources. Additional efforts are required to understand the factors affecting the decline in swiftlet populations (Caughley 1994).

A few studies have demonstrated the logging and conversion of land to plantations affected on insect diversity and abundance (Koh 2008; Brühl & Eltz 2010), which is a crucial part of the swiftlet diet (Tarburton 1986; Lourie & Tompkins 2000; Nituda & Nuneza 2016). A similar effect of rapid land use change is observed in the northern Western Ghats, India (Munje & Kumar 2022). Hence, comparative studies based on the swiftlet diet and population trend should be conducted to understand the overall effect of these factors to assess the species' extinction risk.

Further, it is of utmost importance that the responses of the population dynamics towards all the factors must be assessed. The Indian Swiftlet populations in the Vengurla Rocks have been known for more than 100 years, and continuous monitoring is required of these populations to understand the population behaviour and variable time before extinction. Also, as the abandoned structure at Old Lighthouse Island has very limited nesting space available for Indian Swiftlet, it is important to create suitable breeding spaces for the species.

Understanding the population status, monitoring trends and predicting their carrying capacity provides a significant opportunity to assess the aspects of the population dynamics (the population growth rates, future population trends, and carrying capacities; Fagan & Holmes 2006) to globally manage the existing and upcoming in situ and ex situ populations of the commercially and ecologically important swiftlets (Manchi et al. 2022). No specific studies have been conducted on the carrying capacity of swiftlets, but many studies have indirectly pointed out the related aspects, such as species habitat requirements and the occupancy of the populations inside caves. Overall, this study provides an interesting perspective on the logistic growth of the Indian Swiftlet populations on Burnt and Old Lighthouse islands and highlights the utmost need to continuously monitor the swiftlet populations worldwide for better conservation action and practice.

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