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Estimating the population and related dynamics of the cave-dwelling Edible-nest Swiftlet in the Andaman Islands, India

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Apodids (Swifts and Swiftlets) are among the under-studied bird species. They are hard to identify, and their breeding habitats are inaccessible, making studying their population estimation and related dynamics challenging. In this study, we aimed to estimate the populations using the capture-mark-recapture (CMR) and nest count methods. Conducted at the Baratang cave complex in the Andaman Islands, our study used stratified sampling to choose 12 study caves based on the breeding population for capture and recapture in all possible caves occupied by Edible-nest Swiftlet (*Aerodramus fuciphagus*). The use of the Lincoln Index to estimate the populations of the Edible-nest Swiftlet in each cave by analyzing the capture-mark-recapture data and using the program MARK with the Live Recaptures. The Lincoln Index and total population count estimated 486 and 505 birds, respectively, with no significant difference ($p > 0.05$). The best-fit model indicates that the annual survival rate was consistent throughout the study period (0.97–1.00), and the capture probability was 0.35 ± 0.02. The study evidently showed that using only one method is inadequate for accurately estimating the Edible-nest Swiftlet populations. The CMR method is recommended as an alternative when it is necessary to understand related population dynamics, and the nest and roost count methods are not feasible. The study confirms the effectiveness of the CMR method when used in combination with other traditional methods.

1. Introduction

Fluctuations in animal populations can significantly influence conservation action and planning (Gregory *et al*. 2004). Therefore, estimating and monitoring populations is crucial for prioritizing species, research design, policy making, conservation practice, and wildlife management (Sankaran, 2001, Brouwer *et al*. 2003, Taylor & Pollard, 2008, Moussy *et al*. 2021). It is essential to have robust population monitoring to conserve cave-dwelling birds, as they are crucial in providing energy for subterranean habitats (Manchi *et al*. 2022). Numerous survey methods have been developed to estimate the population of terrestrial birds (Sutherland *et al*. 2004, Bibby *et al*. 2000). However, estimating the cave-dwelling bird populations is difficult due to the inaccessibility and limited knowledge of the subterranean habitat, including caves (Wynne *et al*. 2021). Echolocating cave-dwelling birds are observed to enter and exit their roosting caves during twilight (dawn and dusk) and dark hours (Mane & Manchi 2019). Estimating population and understanding factors like annual survival rates is difficult due to the inaccessibility or unknown nature of their roosting and nesting places in caves.

The Edible-nest Swiftlet (*Aerodramus fuciphagus*) is a cave-dwelling species belonging to the Order Apodiformes and Family Apodidae. The species is of ecological and economic importance (Medway 1963, Lau & Melville 1994, Sankaran 2001). It builds nest wholly of the mucilaginous secretion of the paired sublingual glands (Marshall & Folley 1956), which enlarge during the breeding season (Medway 1962a). Since the species uses saliva as nest material, which gets degraded because of the percolated water and high humidity in the limestone caves after every breeding season, the birds need to make new nests every year. The species has an adaptation wherein their salivary glands enlarge every breeding season which helps them to produce more saliva to build their nest (Manchi 2009). The Andaman and Nicobar Islands mark the easternmost limit of the Edible-nest Swiftlet, which is occasionally considered a subspecies, the Andaman Edible-nest Swiftlet (*Aerodramus fuciphagus inexpectatus*), which is endemic to the Andaman and Nicobar Islands (Cranbrook *et al*. 2013). According to Sankaran (2001), > 80% population was lost between mid-1980s and mid-1990s (Sankaran 2001) in Andaman and Nicobar Islands. It is because of the two-decade long conservation efforts the Edible-nest Swiftlet populations have recovered across the islands at Chalis-Ek, Interview and Baratang Islands (Manchi & Sankaran 2014).

In the unique ecological setting of the Andaman and Nicobar Islands, previous studies (Sankaran 2001, Manchi 2009, Mane & Manchi 2017a, 2017b, 2019) have used the nest count and roost count (arrival and departure surveys) methods for the Edible-nest Swiftlet's population estimation. Engbring *et al*. (1986) used the Variable Circular-Plot (VCP) method in 1982 to estimate the Mariana Swiftlet's (*Aerodramus bartschi*) population on Saipan in the Northern Mariana Islands (Cruz *et al*. 2008). A more appropriate method could be the nest count and evening arrival survey (roost count) using night vision technology, as suggested by Johnson (2015) and Johnson *et al*. (2018). A study by McFarlane *et al*. (2015) in the Gomantong, Sabah, and Borneo caves used high-resolution terrestrial laser scanning to assess swiftlet nest densities on high cave roofs, even in complete darkness. To enhance our understanding of cave-dwelling bird population trends, the taxonomic scope of monitoring should be broadened to include a wider range of species, life histories, environments, and ecologies (Borges *et al*. 2018).

Early researchers have highlighted the unsuitability of a single method for population estimation that is universally applicable in avian studies (Berthold 1976, Shields 1979). However, Nichols *et al*. (1981) suggest that the capture-mark-recapture method can provide valuable estimates for evaluating other population estimation methods and may be the most suitable way to estimate population size in certain circumstances. A few researchers used the capture-mark-recapture method in studying the Apodids (Swifts and Swiftlets) such as Alpine Swift (*Tachymarptis melba*; Hammersley 1953), Biscutate Swift (*Streptoprocne biscutata*; Pichorim & Monteiro-Filho 2010), Pallid Swift (*Apus pallidus*; Boano *et al*. 2020), Common Swift (*Apus apus*; Boano *et al*. 2020), White-rumped Swiftlet (*Aerodramus spodiopygius*; Tarburton 1987), Edible-nest Swiftlet in the Andaman Islands (Gurjarpadhye *et al*. 2021). The capture-mark-recapture was scarcely used for population estimation and annual survival rate of the Apodids across their entire distribution range. Hence, we attempted the capture-mark-recapture method for the Edible-nest Swiftlet in the Andaman Islands.

2. Materials and methods

2.1. Study area

From the Arakan-Yoma mountains of Western Myanmar (Burma) in the north to Sumatra in the south, the Andaman and Nicobar Island arc is located between 06°45'9" N to 13°41'9" N and 92°12'9" E to 93°57'9" E (Fig. 1). The Andaman and Nicobar Islands comprise 572 islands. The archipelago borders the Bay of Bengal in the West and the Andaman Sea in the East. Andaman and Nicobar Islands experience tropical to subtropical climate with 79–89% humidity, 21–33 °C temperature, and 3100 mm rainfall from May to December. The region is predominantly covered by a dense tropical forest (Champion & Seth 2005). The Andaman group comprises 394 limestone caves identified in the Andaman and Nicobar Islands (Manchi & Sankaran 2014, Mane & Manchi 2017b). We conducted the study at the cave complex on Baratang Island (12° 05′ N, 92° 45′ E), situated between Wraffter's Creek and Naya Dera, which contains over 175 caves within an area of 0.77 km² (Sankaran 2001, Manchi & Sankaran 2014, Mane & Manchi 2017a, Mane *et al*. 2019).

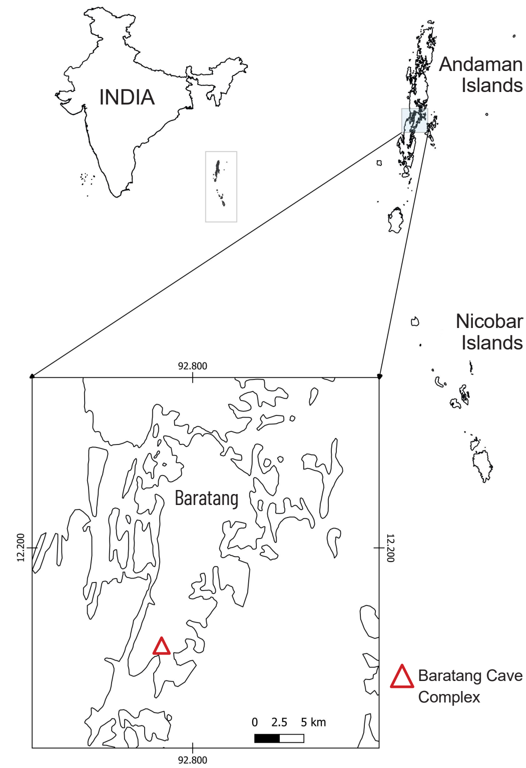

Fig. 1. The geographic location of the study area (Baratang Cave Complex) in the Andaman Islands.

2.2. Data collection

We determined the breeding population of the Edible-nest Swiftlet using the nest count method (Medway 1962b, Manchi & Mane 2012, Manchi & Sankaran 2014, Mane & Manchi 2017a). The breeding season (2 broods) of the species begins in December and continues till September (Medway 1962a, Sankaran 2001, Manchi & Sankaran 2014, Manchi & Mane 2012). However, we sampled only during the first brood because of the accessibility and feasibility issues. The highest count recorded was considered as the breeding population of that specific cave. The Edible-nest Swiftlet is monogamous (Koon & Cranbrook 2002, Winkler *et al*. 2020), with each nest representing a pair of birds (Sankaran 2001, Manchi & Sankaran 2014). Mane (2017) documented that the Edible-nest Swiftlet colonies in North and Middle Andaman Islands, including the Baratang cave complex, consist of an average of 8.05% non-breeding and 91.95% breeding individuals. Accordingly, we estimated the non-breeding and total populations using Equations 1 and 2, respectively:

$$NP = (8.05 \times BP) / 91.95 \quad (1)$$

$$TP = BP + NP \quad (2)$$

Where TP = Total Population, BP = Breeding Population and NP = Non-breeding Population.

A survey conducted at the beginning of 2017 helped us know that the Edible-nest Swiftlet inhabited 112 of the 175 caves in the Baratang cave complex. Then, we selected the caves for conducting the CMR based on cave accessibility, mist-netting feasibility, and the practical difficulties of doing CMR. We used a stratified random sampling method and divided 112 caves into various population classes (0–10; 11–20; 21–30; 31–40 pairs, Fig. 2) to select 12 study caves, *i.e.,* little above 10% of 112 (Fig. 3). It helped us

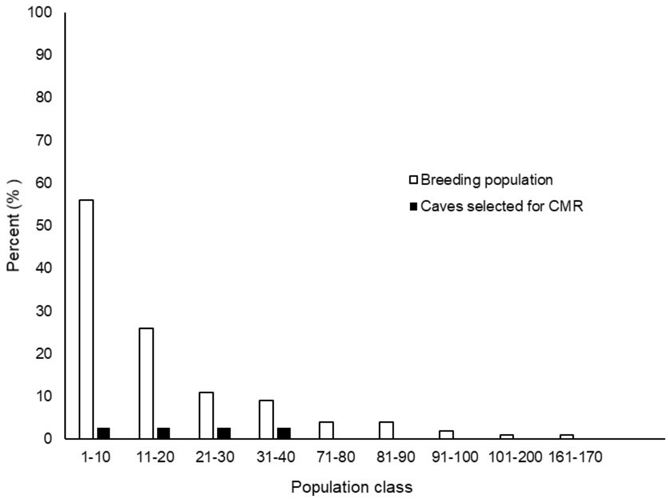

Fig. 2. Caves in Baratang classified based on breeding population, with three caves from each class (0–10, 11–20, 21–30, and 31–40 pairs) selected for Capture-Mark-Recapture.

avoid the risk of losing birds while capturing and errors in population estimation.

Between 2017 and 2019, we used the mist net (6 m × 2.6 m; 30 mm mesh) at the cave entrance to capture and recapture the adult birds at the cave openings during early nest-building, specifically between December and January (Dunn & Ralph 2004, Gurjarpadhye *et al*. 2021, Manchi 2009, Manchi & Mane 2012). The capture was conducted once in the 12 selected caves during the peak roosting hours, *i.e.,* between 17:00 hrs and 20:00 hrs (IST), when most adult birds return to caves for roosting (Mane & Manchi 2017a) during sunset which is mostly between 17:30 hrs to 17:45 hrs. Each bird captured for the first time was marked using aluminum Z-rings with a unique identification code number and then released. We attempted to recapture the marked birds after the capture during the first brood (*i.e.,* June 2018–June 2019). According to Ryan & Collins (2020), there is inter-colonial dispersal in Apodids however, Gurjarpadhye *et al*. (2021), documented no inter-colonial dispersal in adult Edible-nest Swiftlet individuals in the Andaman Islands. As findings from both studies are contradictory we conducted the recapture (two effort night per cave; 58 effort nights) in 29 caves in the study area, including those initially selected for capture. Each captured individual was monitored for the ring and its unique code number. After collecting the required information, all the individuals were promptly released to their respective caves. Thus, period 1 (January–March 2017) was when we captured the individuals in 12 caves and marked them, period 2 (December 2017–June 2018) and period 3 (December 2018–June 2019) when we re-captured the birds in all the Edible-nest Swiftlet 29 caves (including the original 12 caves). Hence, we could also estimate the survival rate between period 2 to period 3.

We used the Lincoln Index also known as Lincoln-Peterson estimator (Cooch & White 2001) to estimate the populations of the Edible-nest Swiftlet in each cave based on the capture-recapture data (Eq. 3). The index is based on some assumptions:

1. Individuals with marks have the same probability of survival as other members of the population.
2. Births and deaths do not occur in significant numbers between the time of release and the time of recapture.
3. Immigration and emigration do not occur in significant numbers between the time of release and the time of recapture.
4. Marked individuals mix randomly with the population at large.
5. Marked animals are neither easier, nor harder, to capture a second time.
6. Recapture rates are high enough to support an accurate estimate (Cooch & White 2001).

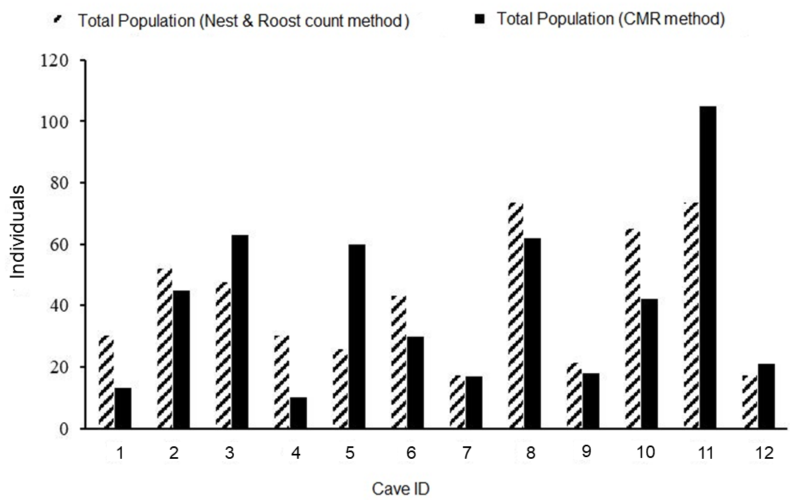

Fig. 3. Population estimation using total population (Nest & Roost Count Method) and Total population (CMR method) in the study caves.

The Lincoln-Peterson calculation tends to overestimate the population size, especially if the number of recaptures is small. We performed a goodness of fit test (Student's *t*-test) to determine the significance of the difference between the population counts from using CMR and total count method.

The formula of the Lincoln Index is as follows:

$$N = (M \times T) / R \quad (3)$$

Where, N = Total population size, M = Initially marked birds, T = Total in the second sample, R = Marked recaptures.

We used the program MARK (Ver. 9.0, Build 9200) with the Live Recaptures (CJS) option (Cooch & White 2001) for survival estimates and capture probability. We used the four predefined models to check the dependence of survival and capture probabilities as the function of time:

1. $\phi(t)p(t)$ (standard Cormack-Jolly-Seber model; Cormack 1964, Jolly 1965, Seber 1965, 1982, Cormack 1989) with time-dependent survival and capture probability
2. $\phi(.)p(t)$, with constant survival and time-dependent capture probability
3. $\phi(t)p(.)$, with time-dependent survival and constant capture probability
4. $\phi(.)p(.)$, with constant survival and capture probability

The best model fit was selected based on the lowest Akaike's Information Criterion (AICc), Delta AICc > 2 (difference in AICc between models), and superiority of the Akaike's Information Criterion Weight (AICc weight). We used the Likelihood Ratio Test (LRT) to assess the goodness of fit of two competing statistical models based on the ratio of their likelihoods (Seber & Schofield 2019, Boano *et al*. 1993).

3. Results

In 2019, we counted in total 230 nests in the 12 study caves, so using the nest count method, the breeding population (BP) was 460 birds. Using Eqs.1 and 2, the estimated Non-Breeding Population (NP) and total population were 40.64 ~41 birds and 501 birds, respectively. The Lincoln Index (Eq. 3), using CMR data, estimated a total population of 486 ± 28 (estimate ± SE), *i.e.*, 486 birds (Fig. 3). We did not encounter any inter-colonial dispersal in adult Edible-nest Swiftlet. The goodness of fit test between the total populations estimated using nest count and CMR methods revealed no significant difference between the population estimates from both

Table 1. Outputs of the pre-defined Capture-Mark-Recapture (CMR) models. AIC: Akaike Information Criterion; No. Par: Number of parameters; SE: standard error.

Model no.	Candidate models	AICc	Delta AICc	AICc weight	Model Likelihood	No. Par.	Deviance	-2Log(L)	(ϕ) ± SE (Annual survival)	p (capture probability)
1	{ϕt pt} Both survival and encounter probability time dependent	621.90	0.00	0.50	1.00	3	615.83	615.83	0.97 ± 0.10	0.21 ± 0.03
2	{$\phi.pt$} Survival constant over time, encounter probability time dependent	621.90	0.00	0.50	1.00	3	615.83	615.83	0.97 ± 0.10	0.21 ± 0.03
3	{ϕt $p.$} Survival time dependent, encounter probability constant over time	664.81	42.90	0.00	0.00	3	44.10	658.73	1.00 ± 0.00	0.35 ± 0.02
4	{$\phi.p.$} Both survival and encounter probabilities constant over time	662.77	40.86	0.00	0.00	2	44.10	658.73	1.00 ± 0.00	0.35 ± 0.02

methods ($p > 0.05$). Around 3.76% less population was estimated by the Lincoln index compared to the population estimated by the nest count method.

Out of the estimated population of 501 birds, 75.64%, *i.e.,* 379 adult individuals, were captured and marked between December 2017 and June 2018. Around 31.5% ± 17.1% of birds were captured from every study cave. During December 2018 and June 2019 we recaptured 160 individuals which is equivalent to a 42.2% recapture rate. The CMR models (Table 1), along with the LRT (Table 2), indicated that the two models {$\phi_t p_t$} and {$\phi.p.$} are statistically competing based on the goodness of fit ($p < 0.0001$). The first model's time-dependent predicted annual survival rate is 0.97, with a capture probability of 0.21 ± 0.03. The other competing model states that the annual survival rate remains constant at 1.00 for the Edible-nest Swiftlet; the capture probability is 0.35 ± 0.02.

4. Discussion

Between December 2017 and June 2019, a total population of 501 birds was estimated based on the nest count method in the 12 study caves, while CMR estimated 486 birds. The present recapture efforts reconfirmed the findings of Gurjarpadhye *et al*. (2021), that the adult Edible-nest Swiftlet individuals do not depict the inter-colonial dispersal. The statistical analysis confirmed that both methods yielded similar population estimates for the species ($p < 0.05$). This can be attributed to the rigorous capture and recapture efforts, which provide reliable estimates that are significantly similar to those given by the total count. Contrastingly, there have been studies such as Rees *et al*. (2011), wherein the population estimation for small mammals was poor because of low number of sampling efforts (n = 5 trapping nights). However, according to Nichols *et al*. (1981), no single population estimation method is universally appropriate for avian studies and that CMR method can provide estimates that are useful in assessing the appropriateness of other estimation methods. It can also provide the most reasonable means of estimating population sizes in some situations.

Table 2. Likelihood-ratio (LR) test between the predefined models of Capture-Mark-Recapture model. PIM: Parameter Index Matrix; NA: signifies that the LR test could not be performed.

Reduced model	General model	Chi-sq	Degrees of freedom (df)	Probability (p)
{ϕ (.) p (.) PIM}	{ϕ (t) p(t) PIM}	42.901	1	< 0.0001
{ϕ (t) p (t) PIM}	{ϕ (.) p (t) PIM}	0.00	0	NA
{ϕ (.) p (.) PIM}	{ϕ (t) p (.) PIM}	0.00	1	NA
{ϕ (.) p (t) PIM}	{ϕ (t) p (.) PIM}	-42.901	0	NA
{ϕ (t) p (t) PIM}	{ϕ (t) p (.) PIM}	-42.901	0	NA

On the other hand, the total count which is a result of roost and nest count method, have been proved non-invasive and suitable for the Edible-nest Swiftlet's population monitoring in Andaman and Nicobar Islands (Sankaran 2001, Manchi 2009, Gurjarpadhye *et al*. 2021). Further, it is important to understand the combination of the methods can always give a better understanding of population dynamics of the species as in the present study.

The Edible-nest Swiftlet shows high annual survival rates ranging between 97–100%, whereas the recapture probability is 42.2%. The Jolly-Seber model using the Capture-Mark-Recapture data suggested that the swifts have high rates of annual survival (34%–100%) and a life span (Collins 1985). However, survival during the first year of life is much lower in most Apodid species (Boano *et al*. 1993, Chantler & Driessens 1995). The Edible-nest Swiftlet shows high annual survival rates similar to the tendency shown by the Biscutate Swift (34%–100%; Pichorim & Monteiro-Filho, 2010). Comparatively, the annual survival rate of the White-rumped Swiftlet is higher (64%–73%), and high annual survival rates are also recorded in the Common (78%; Boano *et al*. 2020) and the Pallid Swifts (71%-76 %; Boano *et al*. 1993).

Swifts are known to be long-lived and the survival in Apodiformes is very high as compared to passerine aerial feeders such as swallows (Hirundinidae; Masoero *et al*. 2016). Pichorim and Monteiro-Filho (2010) proposed that the survival estimate based on capture-recapture data should be considered as a minimum, owing to the dispersal of some individuals to other colonies. Hence, according to Boano *et al*. (1993), the CMR can be useful in the case of birds that show philopatry. Further studies are required to understand philopatric behaviors in swiftlets to get reliable estimates.

Four CMR models were tested for the collected data (Table 1). The best-fit model for the Edible-nest Swiftlet colonies in the caves of Baratang exhibits characteristics of a closed population with constant survival. The capture probability (0.35) remained consistent, independent of time. Thus, in the present study the model could reliably estimate the size of the breeding and non-breeding populations with a recapture rate of 35% between 17:00 and 20:00 (IST), regardless of the capture season.

Capture probabilities vary depending on the species, sex, and whether the populations are closed, partially open, or open (Nichols *et al*. 1981). Terrestrial birds' capture probabilities (when using mist nets) are interpreted to understand the adult-sex ratios (Senar *et al*. 1999, Amrhein *et al*. 2012, Lovász *et al*. 2018) and estimate the population size (Whitman *et al*. 1997, Dunn & Ralph 2004, Sutherland *et al*. 2004). Due to a lack of knowledge about cave ecosystems with closed populations and the scarcity of relevant research, it is challenging to draw definitive conclusions about the suitability of the CMR method for estimating population size in cave-dwelling birds, especially Apodids. Studies on seals and dolphins indicate that capture probabilities above 0.3 are reliable and reflect the accuracy of mark-recapture estimates

(Otis *et al*. 1978, Speakman *et al*. 2010). According to the occupancy models, the capture probability of insectivores and frugivorous birds is from 0.43 to 0.60 and is not influenced by habitat types (Hernandez *et al*. 2013). Additional studies using alternative methods and statistical models could potentially corroborate the findings from CMR in the present study.

Conclusion

This study adds to our current understanding of *Aerodramus sp*. Estimating the population of the cave-dwelling colonial birds is challenging due to various factors. Thus, a single method is insufficient for accurately estimating the population of cave-dwelling birds under different conditions; instead, a combination of roost and nest count methods can be relied upon. This information is solely based on our firsthand experiences and knowledge regarding the species, drawn from extensive studies on swiftlets. The CMR method is recommended as an alternative only when the nest and roost count methods are not feasible, despite its ability to estimate the population close to the total count derived from the breeding and non-breeding population. The study validates the use of the CMR method in combination with the nest and roost count methods.

Luolissa pesivän jaavansalangaanin populaation ja dynamiikan arviointi Andamaaneilla, Intiassa

Salangaanit ja kiitäjät (Apodidae) kuuluvat vähiten tutkittuihin lintulajeihin. Ne ovat vaikeasti tunnistettavia, ja niiden pesimäympäristöt ovat usein saavuttamattomia, mikä tekee populaation arvioinnista ja niihin liittyvän dynamiikan tutkimisesta haastavaa. Tässä tutkimuksessa pyrimme arvioimaan populaatioita käyttämällä merkintä–uudelleenpyynti -menetelmää (CMR) sekä pesälaskentaa. Tutkimus toteutettiin Baratangin luolakompleksissa Andamaaneilla, ja siinä käytettiin ositettua otantaa valittaessa 12 tutkimusluolaa pesimäpopulaation perusteella merkintää ja uudelleenpyyntiä varten kaikissa mahdollisissa luolissa, joissa jaavansalangaani (*Aerodramus fuciphagus*) esiintyy.

Populaatioarviot laskettiin Lincolnin indeksin avulla analysoimalla CMR-dataa sekä käyttämällä MARK-ohjelmaa Live Recaptures -mallilla. Lincolnin indeksi ja kokonaispopulaation laskenta arvioivat vastaavasti 486 ja 505 yksilöä, ilman tilastollisesti merkittävää eroa ($p > 0,05$). Parhaiten sopiva malli osoitti, että vuotuinen selviytymisaste pysyi tasaisena koko tutkimusjakson ajan (0,97–1,00), ja pyydystämistodennäköisyys oli $0,35 \pm 0,02$.

Tutkimus osoitti selvästi, että pelkän yhden menetelmän käyttö ei riitä jaavansalangaanin populaatioiden tarkkaan arviointiin. CMR-menetelmää suositellaan vaihtoehtona silloin, kun populaatiodynamiikan ymmärtäminen on välttämätöntä eikä pesä- tai yöpymislaskentaa voida toteuttaa. Tutkimus vahvistaa CMR-menetelmän tehokkuuden, kun sitä käytetään yhdessä perinteisten menetelmien kanssa.

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Ethics statement. All the methods and procedures adhere to the Wildlife Protection Action, 1972 ethical guidelines.

Conflict of interest. The authors report no conflicts of interest.

Author contributions. PG: Data curation, Conceptualization, Investigation, Writing - original draft, DK: Formal analysis, Writing - original draft, Writing – review & editing, Methodology, Software, RPS: Project administration, Writing - review & editing, SM: Conceptualization, Methodology, Funding acquisition, Resources, Validation, Writing – original draft, Writing – review & editing

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