EVIDENCE FOR COLONY ATTENDANCE BY IMMATURE STREAKED SHEARWATERS *CALONECTRIS LEUCOMELAS* DURING THE CHICK-REARING PERIOD

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ABSTRACT

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Many seabird species have a long breeding-deferral period, during which individuals mature and spend most of their time at sea, making them particularly difficult to study. In some species, immatures are known to start visiting colonies before reaching adulthood, presumably to learn the behaviours required to secure a nest and mate for future breeding. However, immature colony attendance remains undocumented in many species, particularly those that are difficult to observe, such as nocturnal, cavity-nesting species and species in which immatures are indistinguishable from adults. Here, we studied the attendance patterns and behaviour of Streaked Shearwaters *Calonectris leucomelas* on Awashima Island, Japan, during the chick-rearing period. We logged the number and duration of visits to the colony and assessed the potential influence of moonlight on these metrics. We found a weak effect of moonlight on attendance but identified two types of nocturnal visits: one in which birds spent little time above ground and the other in which birds spent hours sitting on the surface. During the latter, birds often gathered in groups and either rested or engaged in behaviours such as allopreening, fighting, calling, and digging burrows. These longer visits sharply decreased in numbers well before the end of the chick-rearing period, and we suggest these visits are most likely undertaken by immatures, based on behaviours documented in other shearwater species. The presence of immature Streaked Shearwaters at the colony during the breeding period has implications for the population ecology of the species and highlights the potential impact of predators and other at-colony risks on an additional age class of Streaked Shearwaters, beyond adults and chicks.

Key words: *Calonectris leucomelas*, immature behaviour, colony attendance, social behaviour, moonlight avoidance, shearwater

INTRODUCTION

A common feature in the life history of long-lived, K-selected animals (MacArthur & Wilson, 1967) is a period of immaturity, a life cycle phase characterised by the deferral of first breeding for at least one breeding cycle. This delay may be an extended period of physiological maturation, or a time in which to improve skills required for independent adulthood. Its length and characteristics vary among species and species groups. For instance, immature individuals may still be partially dependent on their parents for food and protection, as in the great apes (e.g. Sumatran Orangutans *Pongo abelii*; van Adrichem et al., 2006) and many marine mammals (Noren, 2020), or they may live independently, as in many long-lived avian species such as raptors and seabirds (Blas et al., 2011; Carneiro et al., 2020).

The study of immatures can be challenging, particularly in species in which their distribution differs from that of adults. However, understanding immature behaviour and ecology is important, as these individuals can constitute a significant proportion of the population, especially in species where immaturity lasts several years (e.g. Votier et al., 2008). Immatures are also an important age class because they represent a pool of future breeding individuals, whose rate of recruitment will influence future population size (Genovart et al., 2018; Penteriani et al., 2011). However, declines in the total population may go undetected for some time if monitoring is based on counts of breeding adults. Immatures may also be exposed to different threats from those faced by adults because of differences in distribution and foraging behaviour (Noren, 2020; Votier et al., 2008).

Seabirds are generally long-lived and philopatric, returning to the same colony each year to breed, and spending the rest of the year foraging at sea. Many species have an immature period extending over several years (Lewison et al., 2012; Schreiber & Burger, 2001), during which individuals live independently. The age at first breeding varies among species and populations, but also among individuals; for example, Weimerskirch (1990) reported a range of 6–13 years for individuals in a single colony of Southern Fulmars *Fulmarus glacialoides*. The reasons for delayed breeding in seabirds are only partially understood, but a long immature period may allow individuals to learn to forage efficiently enough to provide for both themselves and their young (Burger, 1987; Fayet et al., 2015; Lescroël et al., 2019). It may also provide time to find a mate and establish a breeding territory, especially in colonies where nesting space is limited and they must compete with older, established birds (Ainley, 1978; Cachia-Zammit & Borg, 1987; Cadiou et al., 1994). Immature seabirds are difficult to study because much of their time is spent at sea, and their visits to colonies are less frequent and less predictable than those of breeding adults. As a result, the ecology of immatures remains poorly understood in most seabird species.

The age at which immature seabirds first start visiting colonies can be many years before they first breed (Halley et al., 1995; Perrins et al., 1973) and, like age at first breeding, this varies among species, populations, and individuals. The benefits to immatures of visiting colonies in the years before breeding may include opportunities to prospect for a nest or mate (Pickering, 1989; Wails & Major, 2017), learn social skills (e.g. courtship and territoriality; Taylor, 2024), and gain information on local breeding success (Boulinier et al., 2008; Cadiou et al., 1994). The pre-breeding period can be extended if suitable nest sites are limited, and young birds may visit colonies and await an opportunity to nest for several years, acting as "floaters" (Ainley et al., 2024). The question of whether and when immature birds visit a colony before breeding has important implications for their space use and for the threats to which they may be exposed, such as predation at the colony. However, determining immature presence at a breeding colony can be difficult, particularly in species in which immatures resemble adults and are difficult to monitor, such as nocturnal shearwaters.

Shearwaters are seabirds in the family Procellariidae. Most species breed colonially in burrows, often on small islands with no terrestrial predators, and come ashore only at night, when the risk from avian predators is reduced (Keitt et al., 2004; Lockley, 1942; Watanuki, 1986). Some species have also been shown to reduce colony visits on bright moonlit nights, possibly as a predator avoidance strategy (Keitt et al., 2004; Watanuki, 1986). Shearwaters tend to be long-lived (i.e., more than 30 years in some species; Bauch et al., 2020; Bradley et al., 1989; Brooke, 1990) and have a relatively long period of immaturity (e.g., 7–13 y in Cory's Shearwaters *Calonectris borealis*, Mougin et al., 1986, and 4–6 y in Manx Shearwaters *Puffinus puffinus*, Brooke, 1990). Banding studies have identified high numbers of immatures spending time at colonies during the breeding season in multiple shearwater species, including Cory's Shearwater, Scopoli's Shearwater *C. diomedea*, Manx Shearwater, and Short-tailed Shearwater *Ardenna tenuirostris* (Bradley et al., 1999; Brooke, 1990; Cachia-Zammit & Borg, 1987; Mougin et al., 1986). This time is spent most commonly at their natal colony or an adjacent one. Although rates of emigration vary among species, shearwaters generally show strong breeding philopatry, returning to breed at the colony they visited most frequently as immatures (Bradley et al., 1999; Brooke, 1990; Wynn et al., 2020).

While the most reliable way to identify immature shearwaters is to recapture birds banded as chicks, they can often also be distinguished by their behaviour. Immatures spend considerable time on the colony surface rather than in burrows or nests (Fayet et al., 2015), and, with no egg or chick to tend, they may instead engage in social or mock-breeding behaviour, as observed in Sooty Shearwaters *A. grisea* and Scopoli's Shearwaters (Cachia-Zammit & Borg, 1987; Richdale, 1944). They often arrive later in the season and leave earlier than breeding adults at the same colony (Campioni et al., 2024; Perrins et al., 1973). They may also be more likely than adults to avoid bright moonlit nights for their visits, presumably because they have less need to attend the colony regularly (Watanuki, 1986) or because of the increased predation risk associated with their tendency to remain on the colony surface rather than enter a burrow (Bourgeois et al., 2008; Mougeot & Bretagnolle, 2000).

Here, we report results of an investigation into the attendance patterns of Streaked Shearwaters at a breeding colony in the Sea of Japan to determine if we could identify the presence of immature individuals. The Streaked Shearwater is a relatively large-bodied shearwater that breeds mainly on islands off the coast of Japan (Oka et al., 2002). Most research on this species has focused on adults, which begin returning to colonies in mid-March and lay a single egg in a burrow in late June to early July (Yamamoto et al., 2010). The chick-rearing period lasts around 90 days, from mid-August to mid-November (Oka et al., 2002). Parents stop provisioning chicks approximately a week before they fledge, after which the colony is deserted for the remainder of the year, when Streaked Shearwaters forage farther south in tropical waters (Yamamoto et al., 2010). Little is known about the presence of immature birds at Streaked Shearwater colonies during the breeding season, but observation of ringed individuals suggests their first return to the colony usually occurs around 4–8 years of age (Sakao et al., 2023).

The main objective of the study was to determine the presence of immature birds at a Streaked Shearwater colony on Awashima Island, Japan, during the chick-rearing period. A time-lapse camera was used to collect data on the number of birds visiting a study plot and the time individual birds spent above ground. These data were supplemented with behavioural observations to estimate the breeding or non-breeding status of individuals. We also investigated how colony attendance changed over the chick-rearing period and with moon phase, as immatures may stop attending the colony before the end of the chick-rearing period and may respond more strongly to high moonlight levels than breeding adults.

METHODS

The study was conducted at a Streaked Shearwater colony on the island of Awashima (38°28′N, 139°14′E, Niigata Prefecture, Japan) between 18 August and 08 November 2017, inclusive (83 nights). The study covered the main part of the chick-rearing period, beginning around the time of chick hatching and finishing at the end of the breeding season. The study colony is located on a steep slope covered by dense, bushy vegetation, and has an estimated breeding population of 84,000 individuals (Shirai et al., 2012).

A Bushnell Trophy Cam HD Aggressor Low-Glow trail camera (low-glow infrared light, 20 MP resolution, 0.2 sec trigger speed, 0.5 sec recovery rate, 30 m detection distance) was deployed at ground level at a site with high nocturnal activity of shearwaters and was set to take one image every five minutes each night between 18h00 and 03h00, corresponding approximately to the period of shearwater colony attendance, from around the time of sunset to a few hours before sunrise (Shiomi et al., 2012). In addition, video footage of the behaviour of Streaked Shearwaters on the surface of the colony was recorded through an infrared night vision scope on seven nights between 13 and 26 August. The observer (ALF) sat in the colony and focussed on filming birds that were sitting above ground for a long time, rather than those landing and going straight to their burrows. This video footage was not used in quantitative analysis but instead served to inform and illustrate interpretations of shearwater behaviour at the colony and to inform our quantitative findings.

The trail camera images (n = 8,562) were checked manually for the presence of shearwaters. "Individual visits" were defined from the images as follows: arrival and departure times were recorded for each individual shearwater, with arrival time defined as the time of the first image in which the bird was present and departure time defined as the time of the first subsequent image in which it was absent. If a bird was visible in the same location in two consecutive images, it was assumed to be the same individual unless there was strong reason to believe otherwise (for example, if more than one bird was active or interacting in the same area and it was impossible to distinguish between individuals in consecutive images). Cases in which a bird was already present at 18h00 when the camera started (n = 59) were assigned an arrival time of 18h00, and cases where a bird was still present at 03h00 when the camera stopped recording (n = 4) were given a departure time of 03h00. Because of the reduced accuracy in these cases, all analyses were performed both with and without them; however, this did not significantly alter results, so they were retained (details in Appendix 1, Section S1, available on the website). Six nights were removed from the dataset because visibility was severely obscured by rain or moving vegetation during storms.

All analyses were performed with R 4.2.2 (R Core Team, 2022). The duration of each visit, in minutes, was calculated by subtracting arrival time from departure time. The time a bird spent on-screen was therefore used as a proxy for time spent at the colony outside of burrows. Hereafter, we use the term "duration of colony visit" to refer to the time spent above ground (thus, what we describe as a "short visit" may still be preceded or followed by a long period inside the burrow). This duration is accurate to the nearest five minutes, as images were captured at five-minute intervals (thus, a bird observed in only one image was assigned a colony visit duration of 5 min). The resulting dataset comprised 682 individual visits across 72 nights. The number of individual visits was also calculated on a per-night basis. Moon phase values for each night were obtained from the "suncalc" package (Thieurmel & Elmarhraoui, 2022) and sine-transformed to convert the circular variable into a linear one for use in linear models.

Response variables (number of visits per night and duration of visits) were checked for normality and homoscedasticity. Because both variables were non-normally distributed, appropriate alternative distributions were used (see below). The distribution of durations was examined to assess its range and variability. Visual inspection indicated a bimodal distribution, and the threshold between the two peaks was determined by minimising the sum of variances (as in Fayet et al., 2021). Generalised linear models (GLM) with a Poisson distribution were used to test the predictive power of date and moon phase on the number of birds visiting the colony. GLMs with a negative binomial distribution (package "MASS"; Venables & Ripley, 2002) were used to test the predictive power of date and moon phase on the duration of colony visits.

RESULTS

Changes in Colony Attendance Over the Study Period

The number of individual visits recorded within the colony per night decreased significantly over the study period (GLM; parameter estimate: -0.03 ± 0.002; n = 72, z = 13.96; P < .001; Fig. 1A).

Variability in Duration of Visits at the Colony

The estimated duration of colony visits varied between 5 and 530 min. Over the study period, colony visit duration decreased (negative binomial GLM; parameter estimate: -0.01 ± 0.003; n = 671; z = -3.79; P < .001; Fig. 1B). Closer inspection of this pattern indicated that this decrease was largely caused by a sharp decline in longer visits from the end of September (Fig.1B). However, the trend before this point differed from the overall pattern, with a significant increase in visit duration up to 29 September (negative binomial GLM; parameter estimate: 0.01 ± 0.006; n = 511; z = 2.03; P = .043). Before this date, visits of > 400 min occurred consistently, whereas after this date only a single visit exceeded 200 min, on 12 October. This abrupt decline in long visits was not accompanied by a similar decrease in the number of birds recorded at the colony, which instead showed a more gradual reduction over the study period (Fig. 1A).

Distribution of Colony Visit Duration

The distribution of visit durations across the whole season was strongly right-skewed, with a long tail (Fig. 2A). The largest peak occurred at approximately five minutes, with 62.3% of observations lasting 10 min or less, although some visits lasted up to 530 min.

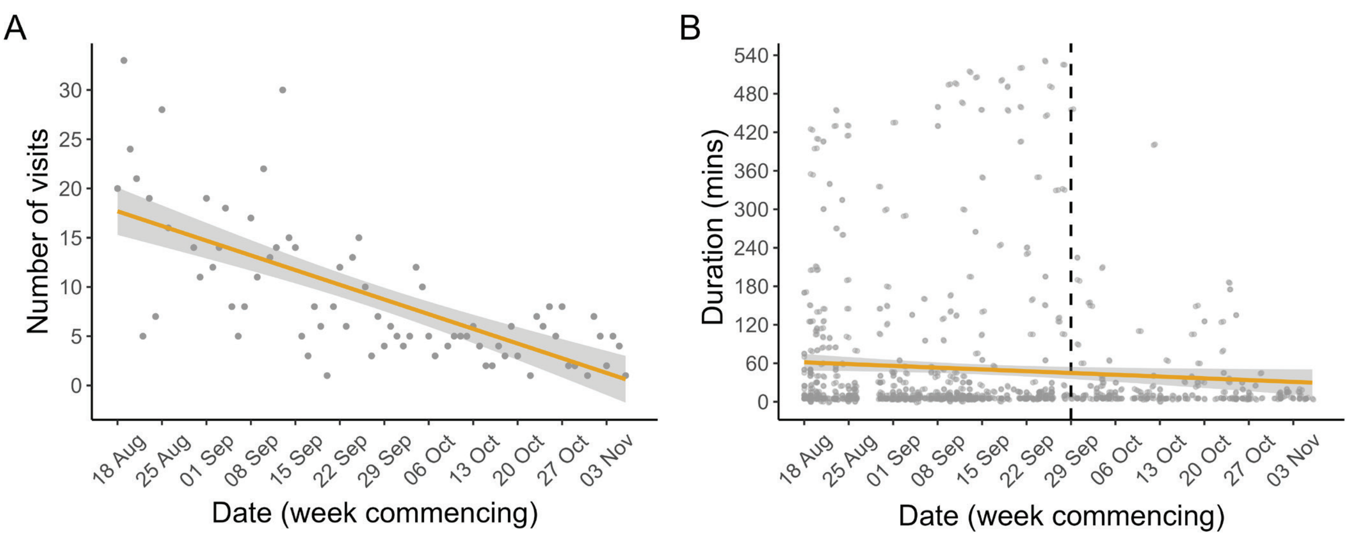

Fig. 1. Changes during the study period in (A) the total number of individual visits recorded per night and (B) the estimated duration of visits. The dashed vertical line in (B) indicates a sharp decline in longer visits after 29 September. The orange line represents the regression fit, with grey shading representing 95% confidence intervals.

There was a substantial difference between the mean (50.5 min) and the median (10 min), reflecting the skewed distribution of the data. A second, smaller peak of longer visits was also visible; minimising the sum of variances identified the threshold between the two peaks at 355 min (Fig. 2B).

Influence of Moon Phase on Colony Attendance

Moon phase had no significant effect on numbers of birds visiting, when controlling for date (GLM; parameter estimate: 0.10 ± 0.12; $n = 72$; $z = 0.79$; $P = .428$; Fig. 3A). However, moon phase did have a significant negative effect on visit duration when controlling for date (negative binomial GLM; parameter estimate: -0.99 ± 0.18; $n = 671$; $z = -5.49$; $P < .001$; Fig. 3B).

At-Colony Behaviour

The video footage recorded through the infrared scope revealed examples of Streaked Shearwater behaviour above ground at the colony, with a focus on the birds that spent extended periods of time on the colony surface (Fig. 4 and Supplementary Video, Appendix 1, available on the website). Shearwaters were filmed sitting on the ground or on low branches in shrub vegetation, often in groups of three individuals, and sometimes in gatherings of five or more. These groups sat close together and were frequently very active and vocal, and exhibited social interactions such as allopreening. There were also instances of individuals or groups sitting on the surface for long periods, often for over an hour, apparently only resting or sleeping, with no obvious intention to visit a nest. Finally, there were examples of behaviour normally associated with breeding, such as digging and clearing burrows, gathering nest material, and a potential mating attempt.

DISCUSSION

This study documents aspects of the attendance patterns of Streaked Shearwaters at a colony from the late incubation to the late chick-rearing period. Both the number of birds visiting and the duration

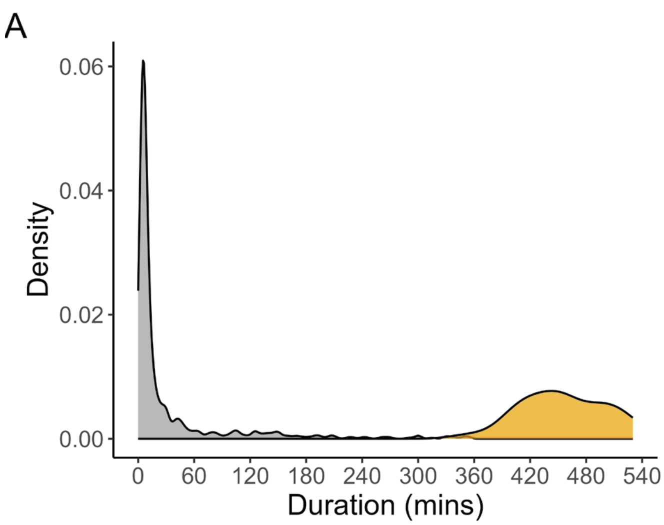

Fig. 2. Distribution of visit duration, showing two peaks (grey and yellow). (A) All data; (B) for visual clarity, only durations ≥ 15 mins are shown.

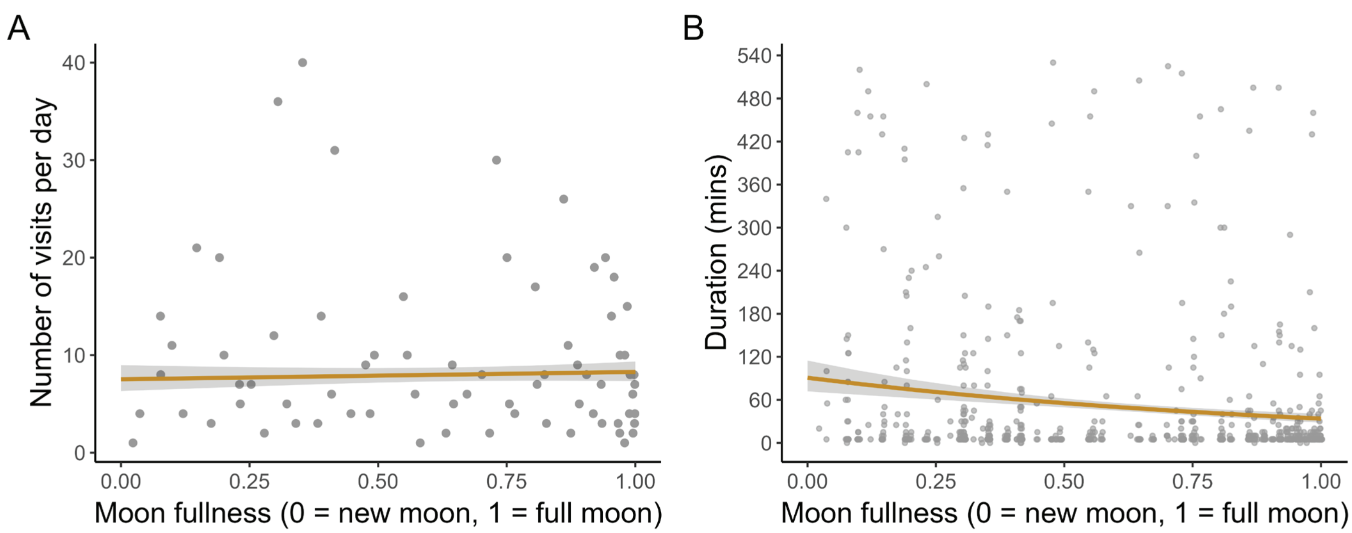

Fig. 3. Effect of moon phase (sine-transformed) on (A) the number of visits per day and (B) visit duration. The orange line shows the regression fit; grey shading represents 95% confidence intervals.

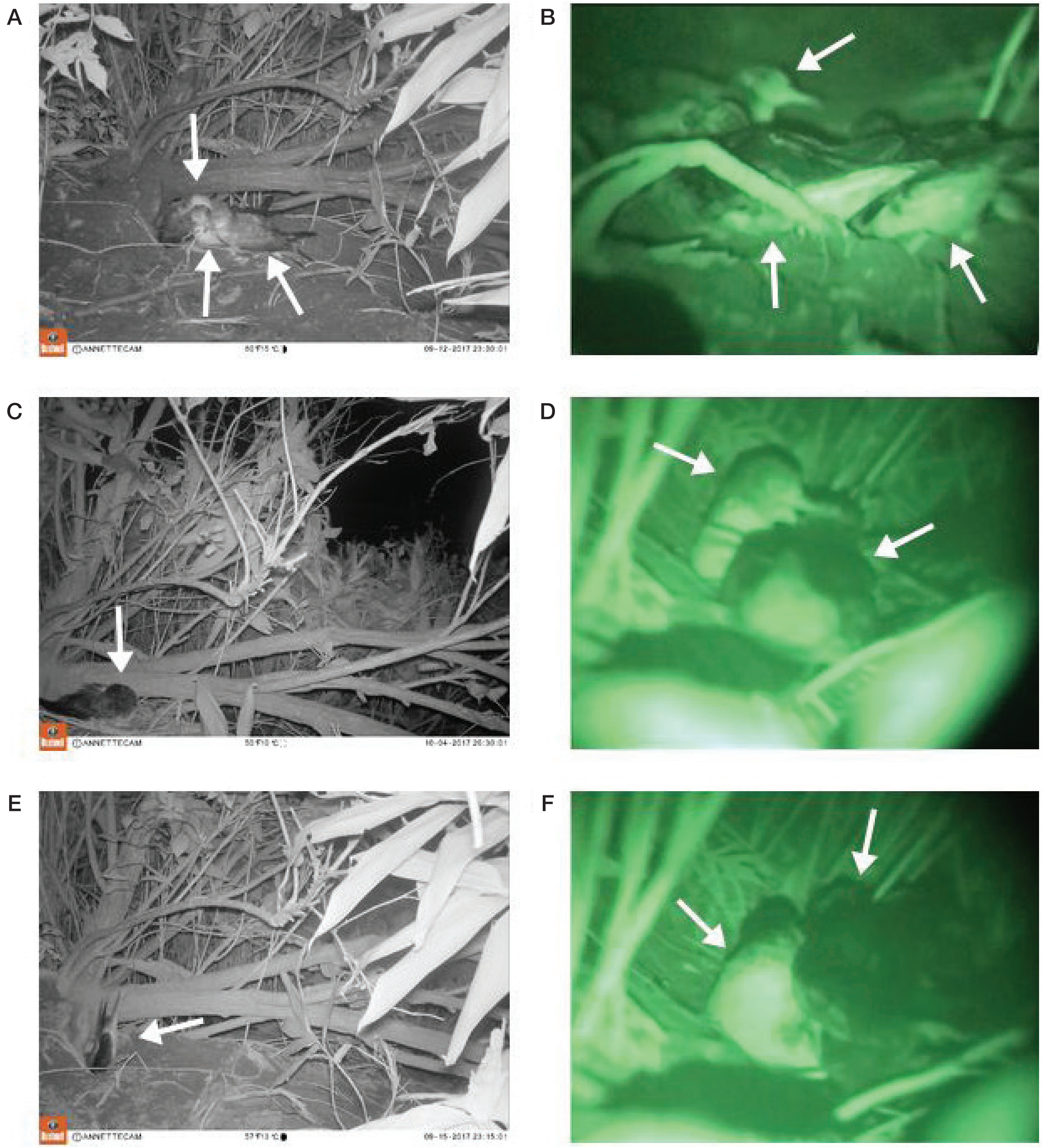

Fig. 4. Examples of Streaked Shearwater behaviour recorded using a Bushnell trail camera (A, C, E) and an infrared night vision scope (B, D, F): (A) three birds roosting on the ground in close proximity; (B) three birds roosting together; (C) a bird sleeping on the ground for several hours; (D) two birds allopreening; (E) a bird digging a burrow; (F) attempted mating. White arrows indicate individual birds.

of visits decreased over the study period. While the decrease in the number of visits was gradual, the decrease in visit duration became markedly steeper during the final four weeks of the study. There was also evidence of a moon phase effect on visit duration, although not on the number of birds visiting. The duration of visits showed a bimodal distribution, with a main peak of short visits and a smaller peak of longer visits lasting six or more hours. These likely represent visits by breeding adults and immature individuals, respectively, which is consistent with behaviour documented in other shearwater species and is supported by the behaviour we recorded from birds spending time on the surface.

The existence of long-duration visits, extending more than six hours, is notable. During the chick-rearing period, breeding adults visit the colony in order to feed their chick. Because Streaked Shearwaters attend the colony only at night and must forage for themselves and their chick between visits, they would be expected to avoid spending extended periods sitting on the colony surface. This behaviour, likely accounting for the high number of birds visible for 10 min or less, is typical of breeding shearwaters and has been observed in Streaked Shearwaters on Awashima Island (A. Fayet, personal observations, Müller et al., 2018) and at other colonies (Lee & Yoo, 2004), as well as in other shearwater species (e.g. Bourgeois et al., 2008; Brooke, 1990; Tyson et al., 2017). It therefore seems unlikely that the long visits, during which birds spent several hours on the colony surface without visiting a nest, were made by breeding adults.

Breeding Streaked Shearwaters do commonly spend multiple hours at the colony, even when their chick is several weeks old (Shirai, 2016), although evidence in other shearwater species suggests that if breeding adults spend several hours at the colony, it is typically within their burrows (Bourgeois et al., 2008; Ogawa et al., 2015; Warham, 1996). Therefore, we cannot rule out the possibility that some of the long-duration visits were made by breeding adults, or by failed breeders or adults taking a sabbatical year from breeding. However, we argue that because these birds would already have a mate and a burrow, they would be less likely to spend extended periods of time on the surface or to engage in the social behaviour we recorded (discussed below). Our interpretation is also consistent with empirical evidence from other burrow-nesting seabirds that adults spend less time on the colony surface than immatures (Wails & Major, 2017; Warham, 1996).

Therefore, based on the duration of these visits and the behaviour we observed and recorded on camera, these birds are more likely to be immature individuals spending time at the colony socialising and gathering information in preparation for breeding in future seasons. This interpretation would align with evidence of similar behaviour in other shearwater species (Mougin et al., 1986; Perrins et al., 1973; Serventy, 1957), as well as with a recent analysis of recoveries of banded nestlings of Streaked Shearwaters, which showed colony visits by birds as young as one year old, well before the age of first breeding in this species (Sakao et al., 2023).

Moreover, the longer visits and associated behaviours observed in the Streaked Shearwaters are consistent with immature behaviours previously reported in procellariiforms related to nest site competition and mate selection. In the Manx Shearwater, for example, Brooke (1990) reported that fights often occur over burrows and that burrows are dug at least a year before they are used (although additional maintenance is usually required at the start of the breeding season), while Harris (1966) found immatures occupying burrows, often in pairs. Our video footage captured burrow digging, which has no obvious practical purpose for a breeding adult during chick-rearing but could be undertaken by an immature securing and preparing a burrow for future breeding or practising their burrowing skills. We also recorded numerous social interactions, frequently involving groups of more than two birds that allopreened or sat together on the ground for extended periods. This resembles courtship behaviour and group social interactions observed in non-breeding individuals in Scopoli's Shearwaters (Cachia-Zammit & Borg, 1987), Sooty Shearwaters (Richdale, 1944), and Manx Shearwaters (A. Fayet, personal observations), as well as socialisation behaviours observed in other seabird families (e.g., Taylor, 2024; Wails & Major, 2017).

The gradual decrease in the number of Streaked Shearwaters observed attending the colony over the study period is to be expected among breeding individuals, as increasing numbers of birds either successfully complete or fail in their breeding attempt and no longer have a critical need to attend the colony regularly. In contrast to this gradual decline, however, we detected a sudden decrease in longer visits from the end of September, with virtually no long visits after this date. This pattern suggests either a sudden behavioural change or a change in the purpose of colony visits (or in the types of birds visiting the colony). This decrease occurred well before the end of chick-rearing, which continues until late October to early November on Awashima Island (K. Yoda, personal observation; Shirai et al., 2012) and is therefore unlikely to represent a final exodus of breeding birds at the end of the season. Instead, it might reflect a sudden decrease in the number of immatures visiting the colony, long before the end of the chick-rearing period. This interpretation is again consistent with patterns of colony attendance in other shearwater species, in which immatures stop attending the colony well before the end of the breeding season (Perrins et al., 1973; Richdale, 1944; Serventy, 1957).

The relationship between duration of colony visits and moon phase suggests only a small effect of moonlight on Streaked Shearwater colony attendance in this study, possibly differing between adult and immature individuals. In other shearwater species, colony avoidance corresponding to lunar cycles is usually interpreted as a predator avoidance strategy in higher light levels, prompted by shearwaters' lack of agility on land, which makes them vulnerable to predation (Keitt et al., 2004; Watanuki, 1986). Alternatively, it has been suggested that shearwaters can forage more efficiently on moonlit nights and therefore spend more time foraging and less time at the colony (Ravache et al., 2020; Yamamoto et al., 2008). Some procellarid studies have also found stronger moonlight avoidance among non-breeding compared to breeding individuals, explained by the less urgent need for non-breeders to attend the colony, combined with the higher predation risk they face by sitting on the surface rather than in burrows (Bourgeois et al., 2008; Mougeot & Bretagnolle, 2000; Watanuki, 1986).

In this study, we found no effect of moon phase on the number of birds attending the colony. We did, however, find a negative effect of moon phase on visit duration, with a lower average time spent on the colony surface when the moon was fuller. This result is noteworthy because, although it is consistent with findings in other shearwater species, it contrasts with previous research in Streaked Shearwaters. At the same colony on Awashima, van Tatenhove et al. (2018) found no effect of ambient light levels on colony arrivals and departures. However, their study used direct moon illumination measurements in the field, which would have accounted for cloud cover more accurately than the moon phase values used in our study.

The relatively large body size of Streaked Shearwaters compared with other procellarids may reduce the threat they face from nocturnal predators and, consequently, their behavioural response to moonlight levels. Predation on Streaked Shearwaters on Awashima Island has mainly been by feral cats *Felis catus* and Japanese rat snakes *Elaphe climacophora* (van Tatenhove et al., 2018), which are less affected by light levels than avian predators. The evidence in the present study of a greater moonlight effect on long-duration visits provides further support for the presence of immature birds, which have more flexibility to avoid the colony. However, the discrepancy between these findings and previous evidence highlights the value of further investigation into the effect of moonlight on the behaviour of Streaked Shearwaters.

CONCLUSION

This study provides new information on aspects of the colony attendance patterns of Streaked Shearwaters. Our results suggest that immature individuals attend the colony during the chick-rearing period, based on estimated visit durations and observed behaviour similar to that of immatures in other shearwater species. This finding has implications for the demographic structure of the Streaked Shearwater population at Awashima Island and highlights that the threats faced by shearwaters at the colony, including predation by feral cats, extend beyond the breeding cohort and are likely also to affect future breeders. In the future, large-scale banding of chicks could provide further insights by enabling the identification of individuals of known age. This would allow more detailed investigation of the ecology of immature Streaked Shearwaters both at and away from the colony, including the potential threats they face and their demographic impacts on the population.

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