EGG ADOPTION BY INCUBATING SOOTY TERNS *ONYCHOPRION FUSCATUS*

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SUMMARY

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This study investigated the mechanism by which some Sooty Terns, which lay one egg, are found with two eggs in a nest. Trials in which eggs were placed at different distances from existing nests showed that eggs laid close to nests were sometimes adopted by the nest owner, the probability of adoption depending on the proximity of the new egg to the nest. Eggs placed further from existing nests were unlikely to be adopted and more likely to disappear, probably through predation. The adoption of second eggs appears to lead to prolonged incubation and compromises the success of the host's own breeding attempt. Eggs that have been adopted to form two-egg clutches appear to have been laid accidentally, but why this happens is not known.

Key words: clutch size variation, egg adoption, Seychelles, Sooty Tern, *Onychoprion fuscatus*

INTRODUCTION

Obligate nest parasites, e.g. some cuckoos (Cuculidae) and cowbirds (Icteridae), capitalise on host acceptance of eggs other than their own (Davies 2000). Facultative nest parasites, which parasitise nests of their own or different species, commonly observed in waterfowl (Anatidae) and sometimes observed in other families of birds, also rely on host acceptance of foreign eggs (Lokemoen 1991, Robertson 1998). Adoption can also occur in some species that are subject to intraspecific nest parasitism, in which eggs of conspecific parasites are accepted by hosts, e.g. Common Starling *Sturnus vulgaris* (Feare 1991, Pinxten *et al.* 1991). Apart from instances of intraspecific nest parasitism, however, adoption of eggs of conspecifics appears to be rare.

Sooty Terns *Onychoprion fuscatus* lay only one large egg (egg c. 35 g, adult c. 180 g, c. 20% of adult body mass, Feare 1976a). Occasionally two eggs (very rarely three, pers. obs.) are found in nest scrapes (Feare 1976a, Schreiber *et al.* 2002), but the two eggs almost always differ in colour, pattern, shape, size or a combination of these. By contrast, replacement eggs laid by females are roughly similar in shape and colour to the original (Feare, pers. obs.). Further indication that the second eggs were laid by different females are observations that females that lose an egg take 12 to 14 days to return to the colony to lay a replacement (Feare 1976a); any second egg appearing in a nest earlier than that could not have been laid by the same female.

There appear to be four possible mechanisms for the acquisition of additional eggs: first, the laying of an egg in another bird's nest could be an attempt to parasitise the host nest (Zink 1999). Second, during disturbances within the nesting colony, departing adults sometimes inadvertently roll their egg out of the nest; on their return they roll the egg back into the nest scrape using their bill. In a previous publication, one of us (Feare 1976a) speculated that two-egg clutches were formed when an incubating Sooty Tern adopted an egg that had been laid close to its own scrape, but whether incubating adults do indeed adopt eggs in this way has not been investigated. Third, during intense competition for nest sites during the pre-laying period (Ashmole 1963, Feare 1976a, Feare & Larose pers. obs. 2013), in the absence of territory occupiers, a second pair might select the same nesting territory and scrape; if both pairs return to lay at about the same time, two eggs might be laid in the same nest scrape. Finally, some tern species, in which females outnumber males, form female-female pairs and lay eggs in the same nest, leading to enlarged clutches (Cabot & Nisbet 2013). The sex ratio of adult Sooty Terns is not known.

Some eggs are apparently mislaid in the colony. Ashmole (1963) found that eggs that had been laid at night on Ascension Island failed to hatch and attributed this to accidental laying of eggs outside nest scrapes. On Bird Island, Seychelles, some eggs are laid outside scrapes, but the origin of these is unknown. These may indeed be "accidental" layings, as eggs are occasionally laid even by flying birds (pers. obs.); such eggs break upon hitting the ground.

The incidence of two-egg clutches is low. Feare (1976a) reported five among 422 nests (0.96%) in survey plots on Bird Island in 1973; during a census of the same colony in 2013, we recorded 17 two-egg clutches in 2 254 nests (0.75%) within 50 10 m^2 census plots (unpublished data). One of us (Feare 1976a) found that none of the small sample of two-egg clutches succeeded in fledging two chicks and suggested that, despite possessing two incubation patches (Harrington 1974), Sooty Terns were unable to incubate two eggs satisfactorily. This suggests that there is a cost to adopting a second egg, whatever the mechanism, with a risk that the egg laid by the incubating bird might reduce hatching success.

In 2013, we investigated further the mechanism by which two-egg clutches are formed in the Bird Island colony through manipulating the presence of additional eggs close to existing nests and recording the fate of these eggs; we also followed a larger sample of two-egg clutches that had been formed naturally to provide a better estimate of the success of such clutches.

STUDY AREA AND METHODS

Study area

These investigations were undertaken in the large (c. 500 000 pairs in 2013) Sooty Tern colony on Bird Island (3°43′S, 55°12′E), a flat coralline cay and the northernmost island of Seychelles. The birds nest here at a density of <7 nests/m^2, mainly on a sandy substrate with herb vegetation <15 cm tall at varying levels of ground cover (Feare *et al.* 1997), but also in areas of sand with plant and coral debris.

Trials involving the addition of eggs close to existing nests

Freshly laid eggs were collected after 16h00 (local time) from a part of the colony where eggs were permitted to be harvested (as a delicacy for Seychellois; Feare 1976b). Each collected egg was marked with a small cross at the pointed end with a marker pen and placed at a measured distance from the egg already present in a nest scrape ("host egg"). The additional eggs were placed at 8, 12, 16 and 20 cm from the host egg in five groups, each of 10 nests. The nests used for these trials, undertaken from 6 to 17 July, were in a part of the colony where laying was progressing and eggs had been laid within 5 days before the start of the trials. The substrate where the trials were undertaken was sand with sparse herb vegetation but abundant debris, including plant, shell and coral remains. These features facilitate nest site recognition (Watson & Lashley 1915), and birds were nesting at high density (4–5 nests/m^2). To investigate whether behaviour towards nearby eggs changed during the course of incubation, a further trial was undertaken on 8–10 July using three groups of 10 eggs, placed 8 cm from the host egg, in the centre of this part of the colony, where host eggs had been incubated for 14 to 20 days.

In each trial the nest contents were recorded after 24 and 48 h. The introduced eggs were recorded as adopted to form a two-egg clutch, not adopted and still in their placed position near the nest, or missing.

Nearest-neighbour distances between nests

Nearest neighbour distances were measured to the nearest centimetre for 50 randomly selected nest pairs in the area where the trials were undertaken.

Hatching success of eggs in "naturally" formed two-egg clutches

On 6 July 2013, 30 nests containing two eggs in a part of the Bird Island colony where birds were estimated to be half-way through incubation, which normally takes 28 days (Feare 1976a), were marked with a numbered wooden stake. The stakes were placed between each nest with two eggs and the nearest neighbour nest containing a single egg. These pairs of nests were monitored daily before 07h00. (Chicks that hatched were guarded more closely by attendant parents in the relatively cool morning than at other times of day, and early after hatching this reduced the risk of chicks running from their scrapes and being attacked by neighbouring adults). Monitoring continued until 23 July, our scheduled day of departure from Bird Island, when clutches in which one egg had already hatched were opened to determine whether these remaining eggs contained viable embryos.

On each visit, the contents of each two-egg clutch and its nearest neighbour were recorded as egg, pipping egg, egg ejected from nest and lying nearby, missing egg, hatched chick, or missing chick.

RESULTS

Trials involving the addition of eggs close to existing nests

Eggs placed near nests already containing an egg were frequently adopted by the incubating adult. In some instances, we watched birds rolling the introduced eggs into the nest, using their bill, as soon as the adults returned to the nest after our disturbance. This sometimes occurred within minutes of our placing the eggs near the nests. In all trials, almost all introduced eggs that were adopted were done so within the first 24 h.

The proportion of eggs that were adopted, and the proportion that went missing (presumed predated, most likely by land crabs *Ocypode cordimana,* which were abundant scavengers and egg predators in the Bird Island colony), varied according the distance that the eggs were placed from the nests (Fig. 1). The probability of an egg being adopted decreased with the distance that the egg was placed from the host egg (regression $y = 10.5 - 0.50\ x$, $r^2 = 0.62$, $P < 0.001$); the probability that an introduced egg would be missing increased with distance from the host egg (regression $y = 2.94 + 0.38\ x$, $r^2 = 0.63$, $P < 0.001$).

In the trial involving nests with eggs that had been laid earlier and were closer to hatching, 7.0 ± 1.15 (standard error) eggs were adopted, similar to the number adopted at the same distance, 8 cm, in the trials with more recently laid eggs (Fig. 1).

Nearest-neighbour distances between nests

Inter-nest distances in the area of the colony where the trials were undertaken averaged 38.1 ± 0.82 cm, with a range of 27 to 51 cm.

Hatching success of eggs in "naturally" formed two-egg clutches

In two of the nests with single eggs, the incubating adult adopted a second egg during the course of the monitoring, leaving 28 nests with single eggs throughout the study period. Of the nests with two eggs, one was abandoned by the incubating bird; in four cases, one of the eggs was ejected from the nest during incubation (we could not tell whether the ejected egg was that of the incubating bird or the adopted egg), leaving 25 two-egg clutches throughout the study period.

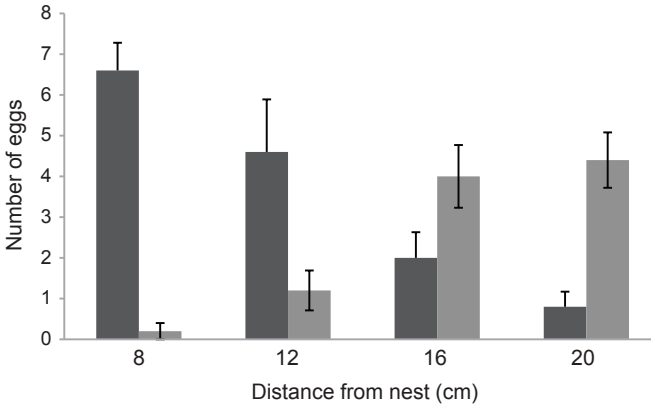

Fig. 1. The number of introduced eggs adopted to form two-egg clutches (dark bars) and the number of eggs that disappeared (pale bars) when fresh eggs were placed at measured distances from nests. Error bars are standard error.

In pairs of clutches in which an egg hatched on or before 23 July, eggs in 21 single-egg nests hatched first, while an egg hatched first in only two two-egg clutches ($\chi^2_1 = 3.83$, $P = 0.05$).

By 23 July, eggs in 22 (78.6%) one-egg clutches had hatched; in only 12 nests (48.0%) had eggs hatched in two-egg clutches ($\chi^2_1 = 3.71$, $P = 0.054$, not significant). Both eggs hatched in only two two-egg clutches: in one the second chick died at two days old; the second hatched on 23 July and the outcome is unknown. On the last day of monitoring, of the five two-egg clutches where one egg had already hatched, examination of the contents of the remaining eggs revealed that three did not have a developing embryo; the remaining two had well-developed living embryos despite being in nests alongside chicks four and ten days old. By 23 July, of the original 30 two-egg clutches, 40 eggs (67%) remained unhatched, and eight (40%) single-egg clutches remained unhatched ($\chi^2_1 = 17.70$, $P < 0.001$).

DISCUSSION

It is clear from the trials that two-egg clutches are formed through the adoption of eggs that appear close to existing nest scrapes by incubating adult Sooty Terns , thus supporting the second mechanism proposed in the Introduction. Two-egg clutches were not formed by other females laying eggs in existing nests, ruling out the third mechanism (selection of same nest scrape by competing pairs) and the fourth mechanism (females of same-sex pairs laying in same nest). These data do not exclude the possibility that eggs laid close to existing nest scrapes might be laid deliberately by second females in the expectation that some will be adopted and reared by the nest owner (intraspecific nest parasitism — the first mechanism).

The trials showed that the likelihood of an egg being adopted was related to its proximity to existing nests, while the likelihood of eggs going missing, presumably through predation, increased with their distance from existing nests. Eggs placed at the maximum distance, 20 cm, were about half the average distance between neighbouring nests in this part of the colony. At this distance, they appeared to largely lie outside the range at which adoption was likely and also outside the range that nest owners were likely to deter egg predators, mainly land crabs. When crabs approached eggs in occupied nests they were repelled by sharp stabs of the bill of the occupier—some persistent crabs were killed.

Soon after some eggs were placed close to existing nests, we saw incubating adults roll the additional eggs into their scrapes using their bills, confirming that egg adoption was a consequence of their behaviour when their own eggs had been moved by departing incubating birds when disturbed. The incorporation of eggs placed 8 cm from host eggs half-way through incubations indicated that the propensity to adopt eggs did not diminish as incubation advanced.

In the pairs of two-egg/single-egg clutches, we did not know the dates of laying of any of the eggs. However, given the high synchrony of laying in Sooty Terns on Bird Island (Feare 1976a), we can reasonably assume that the temporal distribution of laying of the original eggs in the two sets of nests selected for observation would have been similar. On this basis, hatching would also be synchronised to the same extent, and we would expect that eggs in the pairs of marked nests should hatch at about the same time. The significantly greater number of single eggs that hatched first compared with eggs in two-egg clutches, and the greater number of unhatched eggs in the two-egg clutches at the end of the study, support a previous finding by one of us (Feare 1976a) that incubation in nests with adopted eggs is prolonged.

While Sooty Terns have two incubation patches (Harrington 1974), parental care of the egg involves three processes: incubation at night and during cooler parts of the day, shading the egg during periods of hot sun, and periodic wetting of the egg using sea water (Feare 1976a). The efficiency of one or more of these behaviours could be compromised by the presence of more than one egg in a nest, delaying hatching.

The time difference between laying of the host egg and the adoption of the second was unknown in our observed nests, but in the trials most adoptions occurred within 24 h of placing an egg close to a nest. However, in addition to the trial at nests with eggs at a more advanced stage of incubation, showing that adults adopted nearby eggs half-way through incubation, in "natural" two-egg clutches, eggs were adopted late in incubation in two of the nests originally containing a single egg. The time interval between laying of the host egg and the adoption of a second can thus be variable, depending on when an egg appears close to a nest, rather than on any particular stage during incubation. The longer this time interval, the more likely that the adopted egg would not hatch; after the hatching of the host egg, adults spend progressively less time at the nest site (Feare 1976a), and incubation of the second egg would be expected to cease. However, in one of the two-egg clutches, one of the unhatched eggs at the end of the study still had a living embryo 10 days after the first egg hatched. If the time interval between laying of the host egg and adoption of a second is short, however, both eggs may hatch at approximately the same time, as we found in one of our nests. In this nest one chick failed to survive, but whether this chick was from the host egg or the adopted one is unknown. In cases like this, the host chick may be at risk. In both this study and the earlier one (Feare 1976a), some eggs in two-egg clutches were ejected during incubation; again, we do not know whether these were host or adopted eggs. Ejection of the former would compromise the owner's reproductive success, whereas ejection of the latter raises the issue of whether adults can recognise eggs that are going to fail and eject them to reduce the risk of extending the incubation time of their own egg. The continuing presence of second eggs lacking embryos in three nests indicates that some non-viable second eggs are not recognised.

As the nearest-neighbour nest distances showed, nests are spaced at distances at which eggs are unlikely to be adopted by their nearest neighbour. The eggs that are adopted are most likely eggs that have apparently been laid accidentally, not in a scrape, and therefore not defended by an incubating adult. To understand the adoption process more fully, we need to know the causation of such accidental layings. Possibilities include competition for nest sites, confusion over the geographic location of nest sites (Watson 1908), laying by birds that do not have nest sites, or disturbance during laying. The hatching success of accidentally laid eggs seems to be very low, so it is unlikely to be a parasitic strategy adopted by some females (first mechanism in the Introduction). More observations are needed to understand the 'accidental laying' phenomenon.

There appear to be no published accounts of the frequency of two-egg clutches in other Sooty Tern colonies. On Ascension Island, John Hughes (pers. comm.) has recorded 0.23% of such clutches in 66 424 nests examined between 1996 and 2009. In colonies in the

Hautman Abrolhos islands off Western Australia, Nic Dunlop (pers. comm.) has not observed any two-egg clutches in many years of observation. In both places, nesting is at much lower densities than on Bird Island (Feare pers. obs.). On Ascension, nesting takes place on bare lava rock; on the Abrolhos, on the ground beneath dense low bushes, mainly of *Nitraria* and *Atriplex*. If indeed the frequency of egg adoption varies with habitat and neighbour nest proximity, this will cast further doubt on a role for intraspecific nest parasitism in egg adoption.

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