PARENTAL INFANTICIDE BY EGG DESTRUCTION IN RED-BILLED TROPICBIRDS *PHAETHON AETHEREUS* ON THE CARIBBEAN ISLAND OF SINT EUSTATIUS

HAILLEY DANIELSON-OWCZYNSKY[1,2], HANNAH MADDEN[3] & PATRICK G.R. JODICE[4]

[1]*Utrecht University, Heidelberglaan 8, 3584 CS, Utrecht, Netherlands*
[2]*Current address: Royal Netherlands Institute for Sea Research, Department of Coastal Systems, Landsdiep 4, 1790 SZ 't Horntje, Netherlands (hailley.danielson-owczynsky@nioz.nl)*
[3]*Marine Animal Ecology Group, Wageningen University, Droevendaalsesteeg 1, 6708 PB, Wageningen, Netherlands*
[4]*U.S. Geological Survey, South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson, South Carolina 29634, USA*

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ABSTRACT

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Avian reproduction is a process that requires extensive energetic input by parents, particularly in pelagic seabirds. Parental infanticide has rarely been reported in pelagic seabirds, and its frequency among taxa is therefore difficult to determine. Using data from remote cameras, two cases of probable parental infanticide in Red-billed Tropicbirds *Phaethon aethereus* were captured on Sint Eustatius in the 2021–2022 breeding season. Both cases are presented with images collected from remote cameras as evidence. While appearing counterproductive, parental infanticide may provide an alternative reproduction strategy that favors lifetime reproductive success over short term success.

Key words: Caribbean, infanticide, island, Phaethontidae, reproduction, seabird

INTRODUCTION

Incubation and chick rearing are energetically costly and evolutionarily complex processes that require parents to invest resources in offspring, such as providing food resources that they may have otherwise consumed themselves (Hanssen *et al*. 2005, Lobato *et al*. 2006). In long-lived seabirds, rather than maximizing investment in a single reproductive attempt, parents are more likely to employ strategies in their reproductive efforts that maximize lifetime reproductive success (LRS; Stearns 1992). For example, infanticide can be employed as an alternative, emergency reproductive strategy when conditions are unfavorable and infanticide may result in a net gain of reproductive fitness by regulating reproductive effort (e.g., through the cessation of parental energy expenditure), subsequently improving self-survival and ultimately benefitting LRS (Deerenberg *et al*. 1995, Golet *et al*. 1998). Along with a reduction in energetic investment, other benefits of infanticide may include, but are not limited to, exploiting the infant as a food resource through cannibalism, reducing competition for resources, and eliminating foreign offspring (Hrdy 1979, Fujioka 1986, Lobato *et al*. 2006).

Infanticide is likely to be underreported in the literature due to its rapid nature, difficulty in acquiring evidence to prove that it occurred, and the lack of forensic evidence at the nest site, typically due to scavengers consuming remains (Macedo & Melo 1999, Moreno 2012). Avian parental infanticide has been reported primarily in the context of brood reduction, but selective parental infanticide is seemingly very rare (Moreno 2012). Many species of birds, primarily terrestrial species, engage in brood reduction through neglect and ejection of eggs from the nest for self-benefit (Lobato *et al*. 2006). Instances of divorce, competition for nest space, and mate replacement can lead to egg destruction (Fujioka 1986). There is extremely limited evidence, however, of colonially breeding seabirds committing parental infanticide for any reason (Moreno 2012). In Little Egrets *Egretta garzetta*, replacement mates may commit infanticide to ensure that their own brood receives the full investment of their mate (Macedo & Melo 1999, Stephens 1982). Conversely, when a mate's effort is unsatisfactory, Little Egrets may terminate the nest and seek a better mate (Fujioka 1986).

The Red-billed Tropicbird *Phaethon aethereus* (hereafter RBTB) is an understudied pelagic seabird species with a decreasing global population estimate of between 16 000 and 30 000 individuals (BirdLife 2021). RBTB nesting on the Lesser Antillean island of Sint Eustatius in a globally significant colony of 300–500 pairs has been exhibiting high rates of nest failure in the past decade (Madden 2020). The species lays one egg, with the possibility of a second attempt after a failure of a first attempt (Boeken 2016). Adults incubate the egg for ~43 d and raise the chick to fledging at ~80 d (Castillo-Guerrero & Guevara-Medina 2011, Boeken 2016). RBTB nests (n = 338) monitored between 2013 and 2020 at Pilot Hill on Sint Eustatius exhibited a hatching success rate of 0.39 (standard error [SE] = 0.04; Madden *et al*. 2022).

METHODS

As part of a broader-scale research project on reproductive success in RBTB on Sint Eustatius, Reconyx camera traps (Reconyx 2017; n = 6) were placed inside active nest cavities (n = 10) during the 2021–2022 breeding season. When an egg was laid, the nest received

a camera within 7 d. Cameras were programmed to continuously take a photograph every five minutes and to additionally capture a burst of three photographs when motion was detected. Here, we present evidence of two cases of apparent parental infanticide through egg destruction by RBTB. There is one published record of possible parental egg destruction by RBTB in the same colony from 2014 (Madden 2014).

RESULTS

The first case of infanticide occurred in nest 80, where an egg was recorded as destroyed on 07 February 2022. The first egg laid in nest 80 was recorded by an observer during a weekly survey on 12 January 2022. On 20 January, a camera was deployed inside the nest cavity. The camera batteries and SD card were replaced on 01 February while the nest was still active; therefore, we retained the camera. During three consecutive weekly nest surveys (26 January, 02 February, and 09 February), bird 146 was identified as being in the nest via a unique identification band on its leg. The bird was thereafter identified in camera photographs by a geolocator fastened to its left leg, as the presence of the geolocator had been coupled to the identity of bird 146 (the mate did not have a geolocator). From 01 February until the destruction of the egg on 07 February, bird 146 was the only parent recorded incubating the egg in images from the cameras. On 04 February, bird 146 began to reduce the time it spent incubating the egg. For periods up to 12 h, the bird would frequently leave the egg unattended but would remain within the nest crevice. During this time, the bird would incubate the egg occasionally, then leave the nest and return to the crevice, but not always to incubate the egg. In the three days leading up to the egg destruction, bird 146 spent only 40.69% of its time incubating the egg, while 28.79% of its time was spent off the egg and 30.52% of its time was spent away from the nest crevice. In contrast, in data procured between 20 January to 04 February, the egg was incubated 100% of the time by bird 146 and its mate. Each time bird 146 departed and returned to the nest, it could be identified in the photographs by the geolocator on its left leg.

On 07 February 2022, at 13h30 local time, bird 146 was recorded by the camera returning to incubation duty after a 6-h period of absence from the nest. At 13h47, the bird's identity was confirmed by the presence of the geolocator on its left leg. At 14h10, bird 146 was photographed in the nest, piercing the egg with its bill (Fig. 1). The bird did not leave the camera frame between being identified and destroying the egg, based on 24 photographs taken over a period of 40 min. This series of photographs documents that bird 146 likely returned to the nest, briefly incubated the egg, then ultimately destroyed the egg, which was between 26 and 41 days old at the time.

Although there were 13 other individuals with geolocators in the colony, the unique identity of bird 146 was checked via its metal band and recorded during each weekly nest survey while the camera was in place, and no other birds with geolocators were observed by researchers within that nest cavity. RBTB show high fidelity to their nest cavities (Madden 2020), and bird 146 occupied the same nest cavity during the 2019–2020 breeding season (Madden 2020). Therefore, our data indicate that it was bird 146 that destroyed the egg.

The second case of infanticide also occurred at Pilot Hill, in nest 823, 101 m southwest of nest 80. The pair occupying this crevice had already invested in two nesting attempts in the breeding season of 2021–2022 that ultimately failed (based on weekly nest survey data). Their first egg was detected in the nest on 19 October 2021 and last recorded on 26 October 2021. The second egg was detected in the nest on 01 December 2022 and last recorded on 28 December 2021. On 18 January 2022, a third attempt was made, and an egg was discovered in the nest during the weekly nest survey. Subsequently, on 20 January, the camera was deployed inside the nest cavity, where the egg was still present. The camera was attended to on 25 January

Fig. 1. Red-billed Tropicbird *Phaethon aethereus* 146 on Sint Eustatius destroying its egg at 14h10, 07 February 2022. (Photo credit: Hailley Danielson-Owczynsky)

and remained inside the nest cavity. On 25 January 2022, at 14h25 local time, bird 098 switched incubation duties with its mate within nest 823. Bird 098 was identified at 07h37 on 26 January during a weekly nest survey. The bird was removed from the crevice, identified by the band on its right leg, and returned to the nest. After being identified during the nest survey on 26 January, bird 098 did not leave the camera frame before destruction of the egg on 30 January (i.e., 4 d later). There were no predators visible at the time of egg destruction, indicating possible infanticide by bird 098 (Fig. 2). Bird 098 was resting and incubating until 06h21 on 30 January, at which point the bird began to stand and interact with the egg. At this time, the egg was between 12 and 18 days old. In the photographs, the bird had its back toward the camera until 06h25 when it lifted its head and presented a wet bill (Fig. 2). The egg was not visible in the camera frame at this time. However, the presentation of the wet bill led us to the initial suspicion that infanticide had occurred, as the bill had previously been dry (Fig. 2). At 06h31, bird 098 left the nest, and in subsequent images the broken egg was visible in photographs, with no predators present in any images.

DISCUSSION

We suggest that the events reported here are cases of parental infanticide and that they can be explained by life history theory. Long-lived species may choose to allocate energy preferentially towards self-survival over reproduction if the probability of successful reproduction is low or if the egg may represent that of a non-mate (Deerenberg *et al*. 1995, Schultner *et al*. 2013). For example, in a study that compared Pacific and Atlantic Black-legged Kittiwakes *Rissa tridactyla* subjected to the same stress, parents from the Pacific population, which tend to be longer-lived than the Atlantic population, were more likely to abandon their nests (Schultner *et al*. 2013). In contrast, parents from the Atlantic and control populations did not exhibit nest abandonment behaviour. Although the conditions influencing reproductive success on Pilot Hill at the time of the infanticides reported here have not been characterized, it is possible that conditions unfavorable for reproduction may have led the long-lived RBTB to employ parental infanticide as a strategy to prioritize survival and LRS over short-term reproduction. Infanticide instead of abandonment may be a method to clear the nest space quickly and deliberately; following the destruction of the egg in 2021–2022, the pair made another attempt in March 2022 (fate unknown).

Although we suggest that our observations are consistent with life history theory, other more proximate or environmental mechanisms may also have lead to the destruction of the eggs. However, the two focal nests did not appear to differ from most nests in the study area. At Pilot Hill, the average orientation of the primary nest cavity opening was 235° (SE = 5.95, n = 108 nests), the nests had an average of 1.6 (SE = 0.06) openings and an exposure level of 2.8 (SE = 0.126; scored on a scale of 1–5, where 1 = most sheltered and 5 = completely exposed). Our two focal nests appeared similar, having orientations within 77° and 21° of the average, two openings each, and exposure scores of 2 and 3. Both focal nests also supported one or both members of the same pairs and successfully fledged chicks in previous seasons, further indicating that nest quality was not poor enough to consistently lead to nest failure.

The parents also may have broken the eggs accidentally. Although the nests at Pilot Hill typically have a layer of sand, the eggs ultimately rest in a rudimentary scrape. Eggs may be broken accidentally during turning, or even during defense from a predator. In these two cases, however, no predator was observed during or immediately after the breakage of the egg, indicating that an accidental breakage during defense was unlikely. In contrast, when camera data (n = 4) showed that predation was the cause of nest failure, predators were clearly seen interacting with or breaking the egg in the photographs. It is also possible that parents poorly executed egg-turning, although these parents were not inexperienced and successfully fledged chicks in previous years. Eggs could also break during regular incubation activities if shell thickness was compromised from contaminants. We

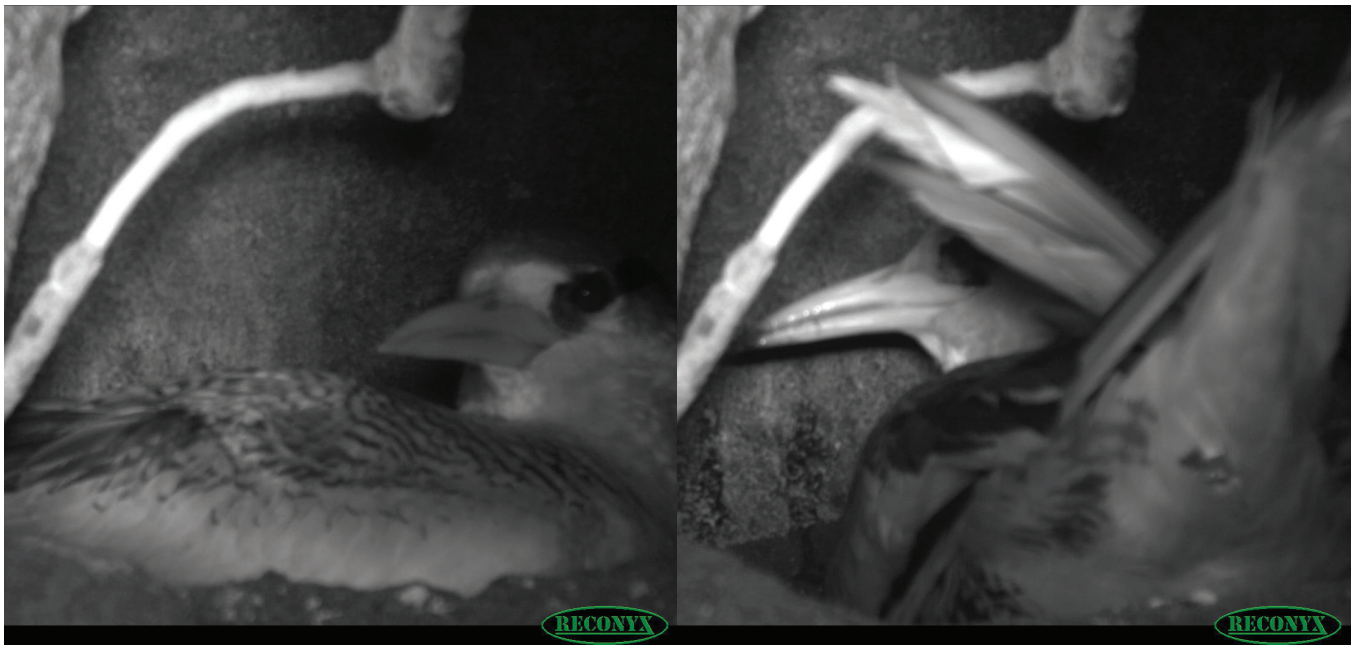

Fig. 2. Red-billed Tropicbird *Phaethon aethereus* 098 on Sint Eustatius, showing dry bill 5 min prior to suspected infanticide at 06h20 (left), and wet bill after suspected infanticide at 06h25 (right), 30 January 2022. (Photo credit: Hailley Danielson-Owczynsky)

had not, however, observed this type of egg breakage regularly in this colony throughout the past five years of monitoring, suggesting that if shell thickness was the cause of egg breakage, it was not a common occurrence. Lastly, eggs could fail from abandonment (n = 6 cases during this study), but it seems unlikely that this would lead to eggs breaking in the manner observed in this study.

Given the rapid nature of the destruction of the eggs in our study, and the subsequent consumption of the egg contents and shell by nest scavengers, opportunities to witness and record occurrences of infanticide are limited. In the two days between the egg destruction and the subsequent nest survey, cameras in both nests captured activity by crabs *Gecarcinus ruricola*, lizards *Pholidoscelis erythrocephalus*, rats *Rattus rattus*, and insects. It is therefore possible that this type of parental infanticide occurs more often than assumed. In the future, more widespread use of camera traps in nest cavities might improve our understanding of nest failure during the incubation stage, especially between nest monitoring visits. Such data may allow us to assess whether parental infanticide by RBTB (and other seabirds where nest surveys are occasional or infrequent) is a more common occurrence than previously noted. Determining the frequency of infanticide and understanding the drivers of this behavior may help researchers clarify some of the factors surrounding reproductive success and reproductive strategies in long-lived seabirds, many of which are of conservation concern.

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