



# Predation of sea turtle eggs by rats and crabs

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## Abstract

Egg predation by invasive and native species may have severe impacts on endangered species and negatively affect species recovery. We assessed the levels of egg predation within green turtle (*Chelonia mydas*) clutches on the island of Diego Garcia (7.42°S, 72.45°E), Chagos Archipelago (Indian Ocean). Native coconut crabs (*Birgus latro*) and ghost crabs (*Ocypode spp.*), as well as introduced black rats (*Rattus rattus*), were predators of eggs, with these species entering nests via tunnels dug obliquely in the sand. Often whole eggs were removed from clutches. For example, the mean clutch size at oviposition (mean 127.8 eggs,  $n=23$ , range = 74–176) was significantly larger than at the end of incubation (mean 110.9 hatched and unhatched eggs,  $n=16$ , range = 9–147). In other cases, egg predation was recorded where the egg had been opened and contents were eaten in the nest. Overall, hatching success (the percentage of eggs laid leading to a hatchling emerging from the egg) was 64.9%, while 3.1% of eggs were predated within nests, 18.1% died during incubation without predation and 13.9% were removed. We reviewed evidence from 34 sites around the world identifying 36 predators that were either native (e.g., crabs, and goannas,  $n=30$ ) or invasive (e.g., rats, and pigs,  $n=8$ ). Depending on location, a predator could be identified as both native and invasive (e.g., dogs). We discuss how either nest protection and/or invasive predator eradication may be used to increase egg survival and when these approaches might be used.

**Keywords** Invasive species · Predator management · Conservation · Rat eradication · Marine protected area (MPA) · Marine turtle

## Introduction

The survival rate of offspring is a key demographic factor that drives the success of populations (Albon et al. 2008) and hence, assessment of factors driving offspring survival has been a central component of ecological studies for many decades (Gibson et al. 2017; Reglero et al. 2018). In the most general terms, there is trade-off between parental investment in individual offspring and their survival. For example, some fish that produce millions of small eggs will tend to have lower rates of survival (Anderson and Gillooly 2021), while some large vertebrates, like whales and elephants, produce a

few large offspring and have extended parental care resulting in higher offspring survival (Lueders et al. 2012). Due to the key role in driving population dynamics, factors that cause long-term changes in offspring survival rates may influence population trajectories (Reichert et al. 2020; Parker et al. 2021). As well as levels of mortality driven by natural predators, other factors that may increase offspring mortality include introduced invasive predators (Spencer 2002), direct human harvesting, including poaching of eggs (Pheasey et al. 2021) and climate warming (Hao et al. 2021).

Sea turtles are a group where several species are endangered, particularly at regional scales, and where many of these disparate factors can play important roles in influencing offspring survival and hence population trajectories (Mazaris et al. 2017). Female sea turtles typically produce several clutches in a single nesting season laying several hundred eggs (e.g., Hays and Speakman 1991). In some parts of the world, there may be high levels of nest predation from natural occurring predators. For example, in Florida, raccoons (*Procyon lotor*) are an important nest predator and have led to efforts of protecting nest sites with metal cages

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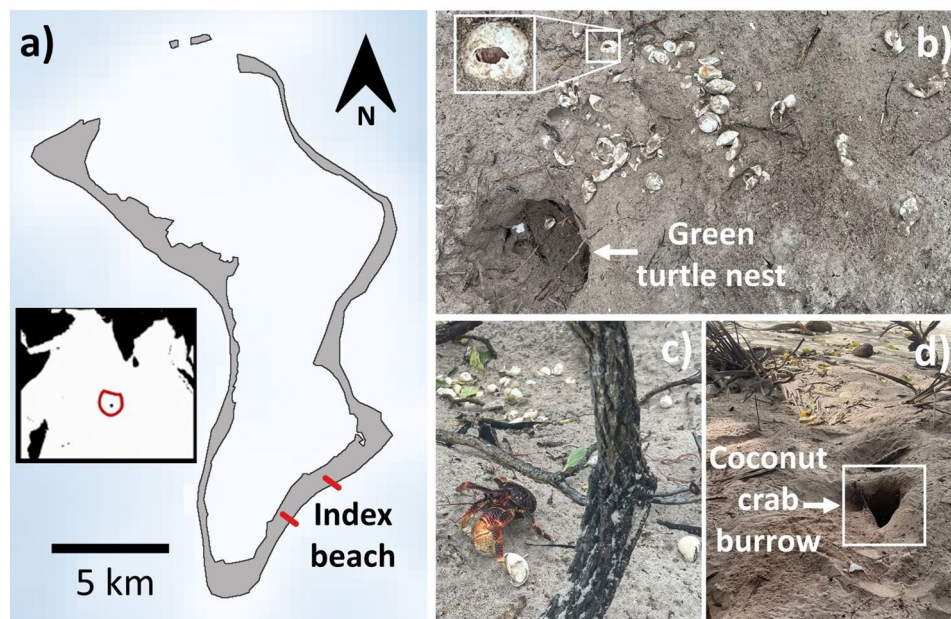
(Engeman et al. 2016) or removal of raccoons from islands as an effective management strategy (Garmestani and Percival 2005), while in Australia, yellow-spotted goannas (*Varanus panoptes*) are important nest predators (Lei and Booth 2017b). Red foxes (*Vulpes vulpes*) are a widely recorded nest predator in the Mediterranean leading to screening of nests with metal grids in Turkey (Kaska 2000; Kaska et al. 2010). In some areas, particularly historically but also more recently, harvesting of eggs has been thought to underpin declines in population abundance (Cáceres-Farias et al. 2022). As embryo mortality increases in sea turtle nests at high nest temperatures, there is also concern that embryo mortality rates will increase associated with climate warming (Laloë et al. 2017; Hays et al. 2017). Conversely, major increases in nesting numbers in some parts of the world have often been attributed to conservation efforts reducing the level of egg poaching (Mazaris et al. 2017).

Given the importance of hatchling survival for sea turtles, we assessed the relative importance of nest predation for green turtles (*Chelonia mydas*) nesting at a major rookery on an isolated island where harvesting or poaching of eggs is zero but where there are a range of potential predators, both natural and introduced. In this way, our work helps identify the importance of managing and / or removing invasive predators that may have several negative ecosystem consequences.

## Materials and methods

The study was undertaken on the island of Diego Garcia (7.42°S, 72.45°E), Chagos Archipelago (Indian Ocean) which lies in the center of one of the world's largest marine protected areas (MPA; Hays et al. (2020)). After two centuries of exploitation, turtles in the Chagos Archipelago have been protected since around 1970 with all life history stages (nests, foraging juveniles, nesting adults) receiving full protection. Diego Garcia is the only inhabited island in the archipelago.

We patrolled the index beach on Diego Garcia (Fig. 1a) at night in search of nesting females and early morning for tracks leading to successful nests or a nesting female. If possible, we counted eggs within clutches as they were laid but if this was not possible (e.g., due to the turtle covering the nest with her rear flippers), then the nest was carefully excavated immediately after the turtle disguised her nest and the eggs were counted and carefully placed back in the same general order as they were laid. Nests were marked via triangulation to tree trunks or branches of nearby vegetation that were marked with different colored tape. The distance from each tree/branch to the nest was recorded along with the tape color and a bearing was taken from each tree to the nest.



**Fig. 1** **a** Diego Garcia (land shaded gray) and the index beach (indicated by the red lines; 2.8 km) with a map showing the location of the Chagos Archipelago in relation to the wider Indian Ocean (red boundary = marine protected area). **b** Remnants of a green turtle nest predated by a coconut crab (*Birgus latro*) with scattered eggshells on the sand surface and pierced eggs with egg remains. **c** A coconut crab

piercing and eating a green turtle egg. Predated scattered eggs can be seen in the background on the sand surface. **d** Coconut crab burrow into a green turtle nest which was used by other predators (e.g., black rats (*Rattus rattus*), ghost crabs (*Ocypode spp.*), strawberry hermit crabs (*Coenobita perlatus*), warrior crab (*Cardisoma carnifex*) to scavenge eggs

Nests were monitored for signs of hatching after 60 days of incubation. Nests were excavated at least 65 days after clutch deposition. For each excavation, hatch success was recorded through counts of empty eggshells and unhatched eggs. Unhatched eggs were opened to determine the stage at which development had stopped, using descriptions and diagrams from Smith et al. (2021). The number of predated eggs (eggs with small, snipped hole / slit;  $\sim 1.5$  cm) indicative of being opened by crabs (Maros et al. 2003) were recorded (Fig. 1b–d). Nests were also excavated after observing hatching events from nests where the clutch size was not counted at oviposition. Nest depth was measured to the top and bottom of the egg chamber. Nests (marked and un-marked) were checked for signs of predation, to note the predator and incident (e.g., type and number of predators around the nest, location of burrow or access point, and the number of opened eggs if seen on the surface).

## Global review

We compiled studies that identified predators of sea turtle nests around the world. To do this, we searched WoK using the search terms under TOPIC (“sea turtle\*” AND “nest predat\*”), (“sea turtle\*” AND “egg predat\*”), (“marine turtle\*” AND “nest predat\*”) and (“marine turtle\*” AND “egg predat\*”) and then completed a backward citation search from the most recent paper (Espinoza-Rodríguez et al. 2023). Only dominant primary and secondary predators were included in the global review. Other predators reported in studies that were found to cause little impact are listed in the results section but are not included in the global predator map.

## Results

### Field observations

Although not observed in nests where oviposition and excavation counts were conducted, there were observations of predators in nests that we had come across during other data collection along the index beach. We observed ghost crabs (*Ocypode spp.*), coconut crabs or robber crabs (*Birgus latro*) and black rats (*Rattus rattus*) consuming turtle eggs at the sand surface (Fig. 1b–d). In all these cases where we observed eggs being predated, the adjacent nest had at least one tunnel running obliquely down toward the nest chamber. On many separate occasions of opportunistic observations of unmonitored nests, we observed recently laid clutches (in the last week or so) with eggs removed from the nest and eaten on the sand surface. Between 05/02/2021 and 31/03/2021 counts of eggs on the sand surface close to fresh burrows ranged from 2 to 69 eggs (mean  $\pm$  SD:  $14.8 \pm 16.1$  eggs,

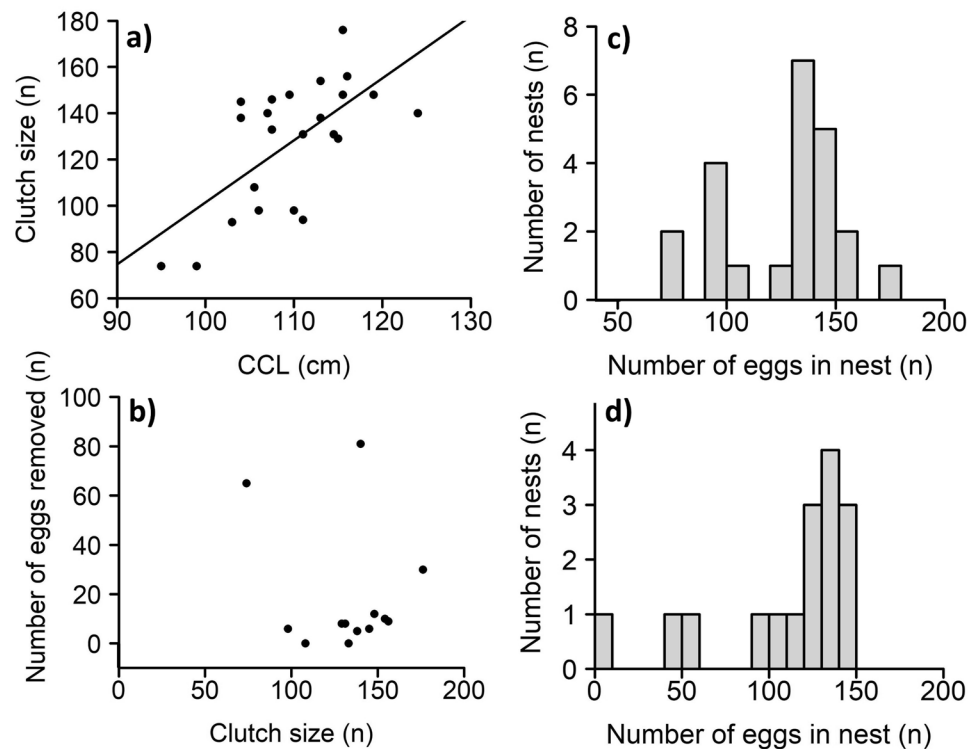
$n = 25$ ; Fig. 1b; c, Table S2). Coconut crabs dig large burrows (Fig. 1d) into the nests and the eggs are usually brought to the surface where evidence lies in scattered eggshells on the sand. These large burrows present an opportunity for rats, ghost crabs, strawberry hermit crabs (*Coenobita perlatus*), that were observed utilizing the burrow and scavenging eggs. Hermit crabs, smaller ghost crabs, warrior crabs (e.g., *Cardisoma carnifex*), and fiddler crabs (*Uca spp.*) were observed to loiter around predated nests and feed on dried eggshells presumably left by coconut crabs. Rats were also observed digging down into the sand. From observations on Diego Garcia, it seems coconut crabs cause the most impact to nest success, with one individual able to decimate a nest by removing a large proportion of eggs, along with creating an opportunity for other predators to enter the nest easily.

### Clutch size

Nests were excavated between 66 and 76 days after eggs were laid (mean  $\pm$  SD =  $73 \pm 3$  days,  $n = 19$ ). The clutch size, measured at oviposition, ranged from 74 to 179 eggs (mean  $\pm$  SD =  $127.8 \pm 27.4$  eggs,  $n = 23$ ). Clutch size increased in larger turtles, with the CCL explaining 42% of the variance in the number of eggs per clutch (Fig. 2a,  $F_{1,21} = 15.1$ ,  $r^2 = 0.42$ ,  $P < 0.001$ ). The number of hatched and unhatched eggs remaining in the nest at the end of incubation ranged from 9 to 147 eggs (mean  $\pm$  SD =  $110.9 \pm 40.3$  eggs,  $n = 16$ ), i.e., 13.2% lower than the mean number at oviposition. Where both the number of eggs at oviposition and at excavation was measured for the same clutch, the number at excavation was similarly 13.9% lower, a difference that was significant (means 133.1 and 114.6 eggs, respectively, paired  $t$  test,  $t_{12} = 2.61$ ,  $P = 0.023$ ). In some cases, the difference in number of eggs at oviposition and at excavation was extreme. For example, one clutch had 74 eggs at oviposition but only 9 at excavation, while for another the numbers were 140 and 81, respectively (Fig. 2b; c; Table S1). In no cases were entire clutches dug up.

The number of hatchlings emerging from nests was mean  $\pm$  SD =  $85.4 \pm 46.4$  ( $n = 16$  clutches). For clutches where both the number of eggs at oviposition and the number of hatchling emerging were assessed, the mean  $\pm$  SD hatching success (% of eggs laid that led to hatchling emerging from the egg) was  $64.9 \pm 38.5\%$  ( $n = 13$  clutches). The mean number of eggs per clutch with holes indicative of crab predation within the nest was 4.1 eggs, i.e., 3.1% of the mean number of eggs at oviposition, and the mean number of eggs that failed to complete development but were not predated was mean  $\pm$  SD =  $24.2 \pm 34.2$  eggs per clutch ( $n = 13$ ), i.e., 18.2% of the mean number of eggs at oviposition. Nest depth to the top of chamber was mean  $\pm$  SD =  $52 \pm 12$  cm ( $n = 13$ ) and to the bottom of the chamber was mean  $\pm$  SD =  $66 \pm 14$

**Fig. 2** For green turtles on Diego Garcia, Chagos Archipelago, we show the **a** relationship between the curved carapace length (CCL) and clutch size ( $F_{1,21}=15.1$ ,  $r^2=0.42$ ,  $P<0.001$ ). **b** relationship between clutch size and the number of eggs removed from the nest between oviposition and excavation ( $F_{1,11}=0.41$ ,  $r^2=0.04$ ,  $P=0.5$ ) and the distribution of the number of eggs at **c** oviposition and **d** excavation (Table S1)



cm ( $n=13$ ). Crabs excavated between 1 and 3 burrows angled at around  $45^\circ$  to reach the top of the egg chamber.

In summary, when assessing the fate of eggs within a clutch about 13.9% of eggs were removed, 3.1% were predated and left inside the nest, 18.1% failed to complete development (not predated) and 64.9% emerged as hatchlings.

### Predators of sea turtle nests around the world

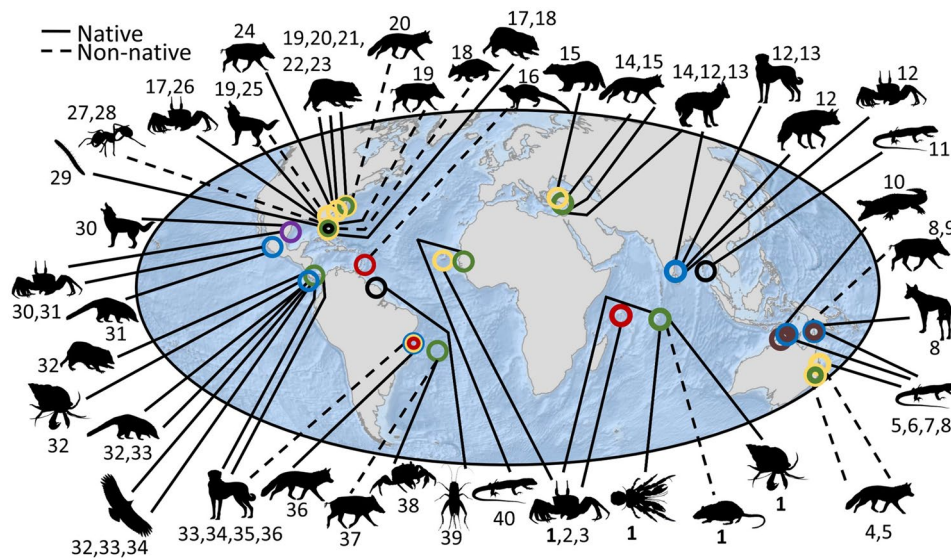
From 40 studies (including our current study), we found a range of both vertebrate and invertebrate predators of sea turtle nests around the world as well as native and invasive species (Fig. 3; Table S3). We found predation studies at 34 sites for all sea turtle species, including green, loggerhead (*Caretta caretta*); olive ridley (*Lepidochelys olivacea*), hawksbill (*Eretmochelys imbricata*), flatback (*Natator depressus*), leatherback (*Dermochelys coriacea*), and Kemp's ridley (*Lepidochelys kempii*) turtles. Thirty-six predator species were identified, eight of which were identified as invasive, including feral pigs, *Sus scrofa* (Pereira et al. 2023); red foxes (Lei and Booth 2017b); armadillo, *Dasypus novemcinctus* (Engeman et al. 2006); Asian mongoose *Herpestes javanicus* (Leighton et al. 2011), and rats (present study). Depending on the site location, a predator could be classed as invasive or native (e.g., dogs and coyotes). From our global review, we found the most important predators are medium sized mammals (e.g., pigs, red foxes), crabs (e.g., yellow crab, *Johnnagarthia lagostoma*) and *Varanus* spp. Some of the species we have included (in Fig. 3)

are classed as secondary or opportunistic predators but are still known to cause damage to nests (e.g., rats, and vultures). Other predators were found in our search but were recorded as having little impact on nests at the study site (and excluded from Fig. 3) include, striped skunk (*Mephitis mephitis*), Tayra (*Eira barbara*), opossum (*Didelphis* spp.), caracara (*Caracara cheriway*) and maggots (Espinoza-Rodríguez et al. 2023), spotted skunk (*Spilogale putorius*), and bobcats (*Felis rufus*; Engeman et al. 2006), Northern river otter (*Lontra canadensis*), American mink (*Mustela vison*), crow (*Corvus* spp.), and snakes (Butler et al. 2020).

### Discussion

Predators impact sea turtle clutches in a number of ways. In some parts of the world, entire clutches can be dug up and predated. For example, in Australia, dingoes (*Canis lupus dingo*), goannas, and feral pigs can cause complete loss of flatback and olive ridley nests through nest excavation and consumption or damage to every egg in a clutch (Nordberg et al. 2019). However, this type of nest excavation and entire nest destruction was not observed on Diego Garcia, but instead it appeared as if eggs were being removed individually by crabs and rats entering the nests via tunnels. We report both coconut crabs and ghost crabs predated eggs and to the best of our knowledge we report the first observations of coconut crabs actively burrowing into sea turtle nests to





**Fig. 3** Examples of common sea turtle nest predators identified across the world (Table S3) shown by icons including mammals (e.g., canids, procyonids, pigs, mongoose, armadillo), reptiles (goannas, salt-water crocodiles), invertebrates (e.g., ghost crabs, coconut crabs, ants, mole crickets). Secondary and opportunistic predators of accessible nests are also included, such as rats, birds (e.g., vultures), and hermit crabs. 1=coconut crab, ghost crab, rat, hermit crab (present study); 2=ghost crab (Marco et al. 2015); 3=ghost crab (Hitchins et al. 2004); 4=red fox (O'Connor et al. 2017); 5=red fox, goanna (Lei and Booth 2017b); 6=goanna (Lei et al. 2017); 7=goanna (Lei and Booth 2017a); 8=goanna, feral pig, dingo (Nordberg et al. 2019); 9=feral pig (Whytlaw et al. 2013); 10=saltwater crocodile (Whiting and Whiting 2011); 11=Asian water monitor (Sivasundar and Devi Prasad 1996); 12=ghost crab, hyena, feral dog, jackal (Tripathy and Rajasekhar 2009); 13=domestic dog, golden jackal (Bhupathy 2003); 14=red fox, golden jackal (Brown and Macdonald 1995); 15=red fox, badger (Baškale and Kaska 2005); 16=Asian mongoose (Leighton et al. 2011); 17=raccoon, ghost crab (Brost et al. 2015); 18=raccoon, armadillo (Engeman et al. 2006); 19=feral pig, coyote (Butler et al. 2020); 20=red fox, raccoon (Halls et al. 2018); 21=rac-

coon (Welicky et al. 2012); 22=raccoon (Engeman et al. 2010); 23=raccoon (Ratnaswamy et al. 1997); 24=feral pig (Engeman et al. 2019); 25=coyote (Lamarre-DeJesus and Griffin 2015); 26=ghost crab (Bouchard and Bjorndal 2000); 27=red fire ant (Parris et al. 2002); 28=red fire ant, tropical fire ant, little fire ant (Wetterer et al. 2014); 29=click beetle larvae (Donlan et al. 2004); 30=coyote, ghost crab (Shaver 2020); 31=raccoon (García et al. 2003); 32=raccoon, hermit crab, coati, vulture (Espinoza-Rodríguez et al. 2023); 33=coati, vulture, dog (Fowler 1979); 34=vulture, dog (Burger and Gochfeld 2014); 35=dog (Siqueira-Silva et al. 2020); 36=domestic dog, fox (Nayelli Rangel Aguilar et al. 2022); 37=pig (Pereira et al. 2023); 38=yellow crab (de Faria et al. 2022); 39=mole cricket (Maros et al. 2003); 40=Nile monitor (Sampaio et al. 2022). Symbol color: green=green turtle (*Chelonia mydas*); yellow=loggerhead (*Caretta caretta*); blue=olive ridley (*Lepidochelys olivacea*); red=hawksbill (*Eretmochelys imbricata*); brown=flatback (*Natator depressus*); black=leatherback (*Dermochelys coriacea*); purple=Kemp's ridley (*Lepidochelys kempii*). Non-native=imported, invasive or introduced. Icon source: R package Rphylopic (Gearty et al. 2023)

predate eggs. Coconut crabs play a critical ecological role in Indo-Pacific island ecosystems. As omnivores, they feed on an array of plants and animals and their scavenging activity aids decomposition of rotting material (Stensmyr et al. 2005). Through active hunting, coconut crabs act as a top predator on island ecosystems and have been referred to as the 'ruler of the atoll', even sometimes killing birds (Laidre 2017). Our observations suggest that the impact of direct egg predation by coconut crabs is magnified by their tunneling into nests, thereby creating a pathway for other predators. Similarly, in Australia, Lei and Booth (2018) found that the opening of a nest by a goanna caused a significant increase in visitation rates to the nest by other goannas and crabs. On high-density sea turtle nesting beaches, clutches are dug up by subsequent nesting turtles and causes a significant loss of eggs directly and provides an opportunity for other predators to find eggs (Ocana et al. 2012).

Our findings add to the growing evidence that crabs can be important predators of sea turtle nests. For example, Marco et al. (2015) reported that in unprotected loggerhead turtle nests on Cape Verde (Atlantic Ocean), on average ghost crabs (*Ocypode cursor*) predated 50% of the eggs. Furthermore, Marco et al. (2015) suggested that dominant crabs might defend the nest they prey upon, sequentially removing eggs over a period of time. On Trinidad Island in Brazil, de Faria et al. (2022) observed yellow crabs predated eggs as they were laid by green turtles and report an average loss of 3 eggs per nest during the nesting stage. Similarly, ghost crabs have been reported predated high numbers of turtle eggs in other parts of the world (e.g., > 15% of eggs in the Seychelles (Hitchins et al. 2004)). In other areas, crab predation is lower. For example, for green turtles in Malaysia, just 1.3% of eggs were lost due to ghost crab predation (Ali and Ibrahim

2002). The drivers of this variable impact of ghost crabs are unknown but may be linked to crab density or the ability of crabs to access clutches is linked to nest depth. Certainly, on Diego Garcia it appears that tunnels dug by coconut crabs is a route of access to eggs for ghost crabs, allowing them to access deeply buried eggs that might otherwise be unavailable. On some nesting beaches, crab predation is frequent on hatchlings crawling from the nest to the sea which can cause a significant decrease in hatchling recruitment (Martins et al. 2021).

Across the world, rats introduced to islands have had huge negative ecosystem impacts such as declines in seabird numbers (Lock 2006; Caut et al. 2008; Carr et al. 2013). These seabird declines in turn can impact ecosystem functioning such as loss of nutrients, from bird guano, decreasing coral reef ecosystem productivity and diversity (Graham et al. 2018) even resulting in a change in coral reef fish behavior (Gunn et al. 2023). Rats also impact sea turtles. For example, in New Caledonia, invasive rats heavily predate on seabird eggs and chicks; however, in the absence of birds outside of their nesting season, rats shift their diet and prey on green turtle hatchlings (Caut et al. 2008). Although, rat predation of hatchlings has been reported, to our knowledge, our study is the first to report observations of rat predation on sea turtle eggs, likely facilitated by nest access through the burrows created by coconut crabs.

While our study was not able to resolve the relative importance of crab versus rat predation, we were able to show that together these predators were having a major impact, predating almost 15% of eggs. Addressing the relative importance of these different predators might potentially be addressed using modern camera technology. For example, Lei and Booth (2017b) elegantly used cameras to identify predators of turtle nests in Australia.

There are essentially two methods to reduce predation of sea turtle eggs: protection of nests or eradication of the predator. Predator eradication is certainly an option where predators are an introduced species. For example, introduced feral pigs historically decimated green turtle nests on Trindade Island, Brazil and pig removal has led to recovery of nesting numbers (Pereira et al. 2023). Similarly, on Keewaydin Island, Florida, pig eradication resulted in a decrease from 87% to just 1% of nests destroyed by this invasive predator (Engeman et al. 2019). In some cases, eradication of invasive species may have very broad ecosystem benefits. For example, ongoing efforts to remove rats from oceanic islands, including within the Chagos Archipelago (Russell and Holmes 2015; Benkwitt et al. 2021) is designed primarily to benefit sea birds and also improve the quality of neighboring reefs, but may have the additional benefit of reducing predation on turtle eggs (our study).

Our global analysis revealed that predation of sea turtle eggs is more often than not by native animals, such a

raccoons and crabs. In cases of high predation by native animals, then protection of nests, for example with cages, may help reduce predation both with clutches relocated to hatcheries as well as those protected in situ (Marco et al. 2015). For example, in Georgia, large mesh screens are designed to protect nests from raccoons and secondary smaller mesh screens to protect against ghost crabs (Butler et al. 2020). In Guinea-Bissau, Sampaio et al. (2022) used a variety of techniques to protect green turtle nests from Nile monitors (*Varanus niloticus*), including scent covering, by sprinkling clove essence aqueous solution on the surface sand to mask the scent of turtle eggs, track covering to remove visual cues and square metal nets (over and buried into the sand). In some cases, however, protection via fences has not been sufficient, for example, in Java, Indonesia, all fenced and unfenced natural nests were predated by monitor lizards (Maulany 2013). Such approaches to protect sea turtle nests from native predators may be costly and difficult to implement and so it may be important to assess if such predation is having an important negative impact on a population's trajectory, before deciding if intervention is warranted. For example, both at Diego Garcia and in the Cape Verde Islands, with 17% and 50% predation by crabs, respectively, nesting numbers are increasing (Mortimer et al. 2020; Hays et al. 2022), suggesting that crab predation is not sufficient to prevent population increases.

Often in sea turtle research, clutch size is estimated by excavating nests once hatchlings have emerged and then by counting shell fragments and unhatched eggs. We echo the concerns of Marco et al. (2015) that such clutch size estimates may be compromised at sites where eggs are being removed from clutches by crabs. In those cases, obviously the clutch size will be underestimated, sometimes vastly, at nest excavation. In an extreme case we found that only nine eggs remained in the nest chamber at the end of incubation while Marco et al. (2015) reported that 100% of eggs could sometimes be removed from clutches by crabs. In common with many studies, we found that larger females (with a resulting larger body cavity) had a higher reproductive effort and tended to lay more eggs per clutch (van Buskirk and Crowder 1994). The most parsimonious explanation for why clutch size increases with female size is that females are minimizing the energetic cost of nesting per egg laid (Hays and Speakman 1991). In other words, laying many more and smaller clutches would be much more energetically expensive compared to a few large clutches. It might be argued that larger clutches might be more susceptible to being located and, hence, predated, if they have a larger odor signature. However, we found no relationship between clutch size and the number of eggs removed, suggesting that clutches were located by predators regardless of their size.

In summary, we identified predation of sea turtle nests by crabs and rats but, while levels of predation could sometimes be very high for individual nests, nest predation does

not seem to be preventing an increase in nesting numbers. Presumably, the impacts of nest predation on Diego Garcia are offset by the complete protection nests receive from any human harvesting.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-023-04327-9>.

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**Data availability** All data generated or analyzed during this study are included in this published article and its supplementary information files.

**Code availability** Not applicable.

## Declarations

**Conflict of interest** No conflicts of interest or competing interests to declare.

**Ethical approval** All work was approved by Swansea University and Deakin University Ethics Committees and the British Indian Ocean Territory Administration (BIOTA) of the UK Foreign, Commonwealth and Development Office. Protocols were approved by research ethics committee of Swansea University (Ethics Reference Number: STU\_BIOL\_157334\_011020182616\_1; AWERB IP Reference Number: IP-2021-01). The study was endorsed through research permits (0001SE21, 000XSE22) from the Commissioner's Representative for BIOTA and research complied with all relevant local and national legislation.

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