



Extreme predation of eggs and hatchlings for loggerhead turtles in eastern Indian Ocean

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Abstract

Understanding predator-prey interactions at the vulnerable egg and hatchling stage of sea turtles is crucial to effectively manage these threatened marine species. Our research quantified ghost crab predation on loggerhead turtles *Caretta caretta* at Gnaraloo Bay and Bungelup Beach, two of the four principal nesting sites for this species in the Southeast Indian Ocean. We counted ghost crab burrows along belt transects as a proxy for crab densities. We used start- and end-of-season nesting inventories to determine egg predation rates, in-situ accelerometers to measure predation activity in nests, and infrared videography to assess predation rates on emerging hatchlings. Ghost crab densities and egg predation rates at Gnaraloo Bay were almost twice those at Bungelup Beach. Egg predation was most prevalent at night and in the first and third trimesters of incubation. We did not observe any hatchlings emerging from nests at Gnaraloo Bay, while we observed predation, mainly by ghost crabs and to a lesser extent by seagulls, on 43% of hatchlings at Bungelup Beach. The alarmingly high rate of mortality due to native predators highlights a need for immediate management actions to mitigate this threat to a globally important loggerhead turtle stock. Our multi-method approach provides a holistic estimation of reproductive success from when eggs were laid to when hatchlings reached the relative safety of the ocean.

Keywords Loggerhead turtle · Ghost crab · Predation · Egg · Hatchling

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Introduction

Predation can impact the abundance, survival, and reproductive success of prey species (Gese and Knowlton 2001; Roos et al. 2018), thereby jeopardising conservation efforts (Sinclair et al. 1998). Much research has focussed on apex predators (e.g. bear, wolf, coyote) and their large ungulate prey (e.g. moose, caribou, mule deer), which broadly adhere to predictable boom-bust dynamics due to feedback mechanisms between predator and prey (Brown and Conover 2011; Keech et al. 2011; Valkenburg et al. 2004; Wakeling et al. 2009). However, such feedback mechanisms may be diminished when a predator has a generalist feeding strategy (Pimm and Lawton 1978). In such cases, the health and size of the predator population may not be intrinsically linked to that of the prey and the predator population may remain stable despite reduced availability of a single prey type (Kratina et al. 2012). This potentially increases the vulnerability of prey species, particularly when population sizes are small (Lingle et al. 2008).

The developing eggs and subsequent emerging hatchlings of sea turtles, whose females migrate and nest on sandy beaches (Ackerman 1997), are vulnerable to predation (Barton and Roth 2007; Caut et al. 2006; Heithaus 2013). Eggs often fall prey to predators or scavengers, including mammals (Engeman et al. 2012; Engeman and Smith 2007), reptiles (Blamires 2004; Lei and Booth 2018; Whiting and Whiting 2011), birds (Burger and Gochfeld 2014) and invertebrates (Baena et al. 2015; Erb and Wyneken 2019). High predation rates, in combination with other pressures, can severely impact recruitment of sea turtle species. Such impacts can result in population declines (Heithaus 2013), which are exacerbated by their life histories being characterised by long-lived, slow maturing individuals, that provide no parental care (Stewart and Wyneken 2004). As a consequence of these multiple pressures, six of the seven species of sea turtles are listed as threatened in the IUCN red list (IUCN 2022).

There have been limited conservation efforts to reduce predation of turtle eggs and hatchlings by forms of predators other than mammals (Department of the Environment and Energy 2017; Engeman and Smith 2007; National Marine Fisheries Service & U.S. Fish and Wildlife Service, 2008). Yet, invertebrates such as ghost crabs (*Ocypode* spp.) can be abundant on sandy beaches in tropical regions (Lucrezi and Schlacher 2014) where sea turtle nesting occurs (Marco et al. 2015). Ghost crabs, which are generalist feeders, (Branco et al. 2010; Marco et al. 2015; Rae et al. 2019), have been implicated in ~5–60% of turtle nests being disturbed and ~1–45% of eggs being destroyed at multiple rookeries around the world (Ali and Ibrahim 2002; Bouchard and Bjørndal 2000; Brown 2009; Butler et al. 2020; Hill and Green 1971; Hitchins et al. 2004; Marco et al. 2015; Zárata et al. 2013). They can predate on ~2–50% of emerging hatchlings (Conant 1991; Erb and Wyneken 2019; Madden et al. 2008; Martins et al. 2021; Peterson et al. 2013; Tomillo et al. 2010).

Most estimates of predation rates on turtle hatchlings have relied on direct observations (e.g. Conant 1991; Erb and Wyneken 2019; Madden et al. 2008; Peterson et al. 2013; Tomillo et al. 2010). Yet, direct observations and human presence are known to influence predator behaviour (Ciuti et al. 2012), and activity of predators and emergence of hatchlings can occur over longer periods than standard observation times (first night of emergence only, first emergent group only) (Conant 1991; Godfrey and Mrosovsky 1997; Tomillo et al. 2010). The use of camera traps (single shot or short bursts, short video clips) adopted in some studies to examine predator-prey interactions (de Faria et al. 2022; Erb and Wyneken

2019) overcomes this issue, but only provide snapshots of those interactions. Additionally, hatchling and predator tracks are likely to be obfuscated by sun, tide, and wind, making *post hoc* examination and analysis of predation activity unreliable. Thus, existing methods to estimate predation rates are limited by methodological shortcomings. Conservation efforts to protect the vulnerable egg development and hatchling phases of sea turtles' life cycles would benefit from accurate estimates of predation rates. Infrared videography (continuous recording) and accelerometry commonly used for other purposes, e.g. monitoring nocturnal activities (Allison and DeStefano 2006), provide field methods to overcome some of these shortcomings and may be used in combination with traditional approaches to assess predation rates of eggs and emerging hatchlings.

The loggerhead turtle *Caretta caretta* is globally listed as vulnerable by the IUCN with a general trend of population decline (IUCN 2022). Of the two distinct loggerhead turtle genetic stocks in Australia, the Southeast Indian Ocean stock on the west coast has been assessed as stable, with climate change and variability, chemical and terrestrial discharge, and fisheries bycatch deemed key threats (Department of Environment and Energy 2017). The focus of sea turtle conservation in the region is currently on these anthropogenic threats (Department of Environment and Energy 2017; National Marine Fisheries Service & U.S. Fish and Wildlife Service, 2008), but a potential threat from native predators has been overlooked. Understanding the levels of predation on nesting populations on the west coast of Australia are important as these are the sole nesting sites for the Southeast Indian Ocean stock (Casale and Tucker 2017).

The aim of this study was to characterise predators and predation rates on loggerhead turtle eggs and hatchlings in the Ningaloo Coast World Heritage Area on the west coast of Australia. A particular focus has been placed on the ghost crabs *Ocypode convexa* and *O. ceratophthalma* as potential predators following many years of anecdotal (Hattingh et al. 2010, 2021) and community concern. These two species have been observed in high numbers on beaches in the region, and the former species is known to display a preference for carnivory despite being a generalist feeder (Rae et al. 2019). To achieve our aim, we combined several wildlife monitoring methods to characterise predation from the time of being oviposited to hatchlings reaching the water. Our approach allowed us to determine: (1) the level of predation on sea turtle eggs and hatchlings and the predators responsible for the predation; (2) the interactions between prey and predator and between predators; and (3) the timing of those interactions during the incubation and emergence periods.

Materials and methods

Study area

The Ningaloo Coast World Heritage Area, on the west coast of Australia, comprises the Ningaloo Marine Park and Cape Range National Park. Field activities focussed on two regions where loggerhead turtle nesting is known to occur, namely Bungelup Beach (-22.282331° S, 113.831570° E) and Gnaraloo Bay (-23.766491° S, 113.553135° E), located at the northern and southern ends of the Ningaloo Coast World Heritage Area, respectively. Bungelup Beach, at the northern edge of the species' range in the region, is recognised as the highest density loggerhead turtle rookery on the west coast of the Australian mainland, (Richards

et al. 2005; Tedeschi et al. 2016). Between ~300 and 500 nests are laid annually at these rookeries, as well as infrequent breeding by green (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*) (Department of Biodiversity Conservation and Attractions 2021, 2020; Hattingh et al. 2018; Markovina 2017). These two mainland rookeries form an important part (~30%) of the Southeast Indian Ocean loggerhead turtle subpopulation, which represents ~1.5% of the global nesting stock (Casale and Tucker 2017; Department of the Environment and Energy 2017). The peak nesting season for loggerhead turtles in the region is early to mid-January, with hatchlings emerging between February and March (Tedeschi et al. 2016; Trocini 2013; Woolgar et al. 2013).

Ghost crab burrow density

Ghost crab burrow counts were determined at each location in the Austral summers of 2019/20 and 2020/21. Within each year, sampling occurred over two periods: December/January and February/March, representing the egg laying and incubation period and the hatchling emergence period, respectively (Department of Biodiversity Conservation and Attractions 2021; Tedeschi et al. 2014; Woolgar et al. 2013).

Active burrow counts are commonly used to determine the relative abundance of ghost crabs (Schlachter et al. 2016). Active burrows are those with unobstructed openings, often with crab tracks and algae fragments around the burrow opening. To estimate active burrow numbers, nine belt transects perpendicular to the waterline were surveyed along a ~1 km long section of beach for each of two sampling days. At each nesting beach, the ~1 km section was located where the highest density of turtle nesting is known to occur, based on nesting density data from past research and monitoring programs for turtles (Hattingh et al. 2011; Trocini 2013). The 5 m wide belt transects started at randomly-allocated positions along the waterline and stretched to the base of the primary dune, to the first line of beach vegetation (see Supplementary Fig. S1). The beach width determined the transect length. Surveys were conducted within three hours of first light (~09h00) to reduce the confounding effect of burrow erosion and collapse linked to rising daytime temperatures.

Within each quadrat, all burrows were counted and the diameter of each burrow was measured to the nearest 5 mm. Since burrows are often very wide at the surface and taper down to a more uniform size a few centimetres below the surface, the measurements were taken at the beginning of this uniform section. As burrow openings of different ghost crab species are indistinguishable, counts are reported at the genus level. As juvenile ghost crabs are unlikely to actively predate on sea turtle hatchlings, only data for mature-sized crabs, with a burrow diameter of >25 mm, were analysed (Peterson et al. 2013). Frequency histograms (C. Avenant, unpublished data) suggested a reasonable separation between juvenile and mature crabs at a burrow diameter of approximately 25 mm.

A crossed design 3-way ANOVA was run to test for differences in burrow densities of mature crabs across factors “Location” (2 levels: Bungelup Beach and Gnaraloo Bay), “Period” (2 levels: egg laying and hatchling emergence) and “Year” (2 levels: Summer 1 and Summer 2). Given that the three-way interaction was not significant, the model was run with only main effects and two-way interactions, so as not to over parametrise. Only the results of main effects and two-way interactions are reported in the results section. $\ln(x+1)$ transformed burrow densities were normally distributed ($p>0.05$), as assessed by Shapiro Wilk’s test for normality. There was homogeneity of variances ($p>0.05$) for all groups, as

assessed by Levene's test for equality of variances. Statistical significance was accepted at the $p < 0.05$ level for main effects and interactions.

In-nest predation

Counts of sea turtle eggs were conducted at the beginning of the egg incubation period and end of the hatchling emergence period at both nesting beaches, Bungelup Beach and Gnaraloo Bay. At each location, sea turtle nests were located, and their positions recorded at the start of the nesting season. Survey teams patrolled beaches between dusk and dawn in search of female loggerhead turtles emerging from the water to nest. Observations were made from a distance to avoid disturbing them during this sensitive stage. Once ovipositing commenced, the turtle could safely be approached from the rear, allowing for a viewing channel to be dug by hand next to the cloaca so that egg laying could be observed without disturbing the turtle. When laying was complete, the female was lifted off the nest by at least two handlers and carried ~2 m away to prevent the female from covering its nest and allowing for a short processing time during egg counts.

Eggs were counted using a handheld 4-digit tally counter. When eggs were handled, care was taken not to rotate eggs vertically or horizontally, to reduce damage to delicate embryonic membranes and blood vessels (Nooren and Claridge 2002). After tallying, eggs were replaced in the nest and the egg chamber filled, taking care to maintain the original shape of the nest and position of eggs and filling sand to the surrounding level (Trocini 2013). Only red light was used when needed, to reduce disturbance to any nesting turtles in the immediate area. Eggs were counted in 5 and 16 nests at Gnaraloo Bay, and 13 and 26 nests at Bungelup Beach during the summers 2019/20 and 2020/21, respectively.

Prior to being filled in, a 3-axis accelerometer (Convergence Instruments Wireless Vibration Meter Data Logger/VSEWmk2–8 g) was placed on top of clutches of eggs in five nests at both locations in both years. Accelerometers recorded vibrations within the nest chamber that could be related to any nest disturbances associated with egg predation. Accelerometry has been used for estimating timing of egg hatching in turtles (Clabough et al. 2022; Rollinson et al. 2019). Clabough et al. (2022) showed that there is very little or no vibrations in incubating nests other than those associated with background noise. Accelerometers were constantly recording, with sampling rate set at 500 Hz and summary intervals at 15 s, with acceleration measured in g (displayed and analysed in dB g logarithmic scale) (Supplementary Fig. S2). Three vibration loggers were lost, while loggers malfunctioned on 10 occasions, and did not record for the full incubation period. Over the two summers, four vibration loggers from Gnaraloo Bay and four from Bungelup Beach provided full data. An additional logger with full data was retrieved from Bungelup Beach in the 2021/22 nesting season.

Vibration data were analysed using the manufacturers Vibration Sentry Manager software. The threshold for background noise, i.e. vibrations associated with tidal movement and wave action, was determined for each individual logger, as the level of background noise could be affected by nest location, e.g. foreshore, backshore or primary dune (see Supplementary Fig. S2 for an example). An additional 5 dB g buffer was added to threshold values to further screen out background noise. For each logger, the time (in seconds) that the vibration data exceeded this threshold, over the period immediately after the nest was filled in, to an estimated one day prior to the hatching of eggs was calculated. Data were

standardised to the number of seconds of vibrations per day. These data were plotted against the corresponding percentage of eggs missing in nests, and the best fitting regression equation was determined. To reveal the lower intensities of vibration more clearly, data were $\log_{10}(x+1)$ transformed and plotted against the corresponding percentage of eggs missing in nests.

The location of each of the surveyed nests was marked with wooden stakes ~60 cm to the landward side of the nest. Nests were left undisturbed for the duration of the ~2-month incubation period. Nests were then monitored for signs of hatchling emergence ~50 days after ovipositing. The first signs of emergence allowed for the estimation of hatching time of other nests, as incubation times varied across seasons and locations depending on summer ambient temperatures. In the days leading up to predicted hatchling emergence, nests were visually inspected for the presence of ghost crab burrows and other signs of predation, e.g. goanna tracks and diggings, egg shell remains.

Fate of eggs was determined from all marked nests after the last observed signs of emergence or ~65 days after ovipositing. Where late-emerging hatchlings were found alive, they were left to complete the beach crawl unaided. Prior to nests being excavated, observations were made on the presence of ghost crab burrows on top of nests. While nests were excavated, further observations were made on burrows entering the egg chamber from the side.

Nests were excavated by hand and the egg remains removed and inventoried as per protocols and categories derived from Miller (1999). Nest contents were categorised as: (a) hatched eggs (empty shells >50% intact, presumed to have emerged); (b) live hatchling (live hatchling among shells); (c) dead hatchlings (dead hatchling that has left the shell); (d) unhatched eggs – undeveloped (unhatched eggs with no obvious embryo); (e) unhatched eggs – term (unhatched egg with apparently full-term embryo); and (f) eggs missing (start-of-season tally minus post-hatching tally, presumed predated). It should be noted that there is some uncertainty in determining whether an egg had successfully hatched, as fragmentation of shells can be difficult to interpret. Unhatched eggs were opened to determine developmental stage, and eggshells were checked for signs of predation. For nests containing loggers, both vibration and temperature loggers were retrieved. After the inventory, all remains were returned to the nest cavity and covered up with sand. The number of eggs were compared to the number ascertained soon after they were deposited. Hatched eggs are reported as hatching success in the [results](#) section. However, the emergence success, which is often used in conjunction with hatching success was avoided, as nest inventories could not account for hatchlings that were predated inside the nest before they could emerge.

Hatchling predation

During the hatchling emergence period (February/March), nesting beaches at both locations were monitored at dawn and dusk for the signs of imminent or recent hatchling emergence, typically represented by a conical depression in the sand with or without visible hatching tracks. When these signs were observed at a nest, three infrared surveillance cameras (Dahua 2MP Mobile HDCVI IR Eyeball/Cube Cameras), each attached to a 1.5m wooden stake, were placed at intervals covering the fields of view between the nest and the high tide mark (Supplementary Fig. S3). Footage was recorded on digital recorders (Dahua 4MP H.265 Mobile Network Video Recorder with a WD Blue WD10SPZX 2.5” 1 TB Mobile HDD), each powered by a 12 V battery (Motobatt 12 V 130Ah Deep Cycle AGM) and

housed in a 2-person dome tent positioned landward and away from the nest. This setup allowed for high-definition video footage to continuously record during all hours and weather conditions for up to 4 days. At Gnaraloo Bay, the signs of imminent hatching were less clear due to criss-crossing ghost crab tracks potentially obscuring hatchling tracks, and high egg predation rates resulting in low emergence success. Cameras were set up at nests that were marked at the start of the season, and/or set up to record a wider field-of-view to opportunistically capture hatchling emergence from random, unmarked nests. At both locations, these random nests provided a large proportion of the sample size. The remoteness of survey locations allowed for camera setups to record data without fear of disturbance from curious members of the public.

From the video footage, time of emergence, number of hatchlings per emergence event, fate of each hatchling (safe or predated), and identity of predator were recorded. An emergence event was defined as an event when at least one hatchling fully emerged from the nest, but separated from another fully emerged hatchling or group of hatchlings by ≥ 10 min (Santos et al. 2016). At each nest and each day, data were collected from the entire period of hatchling emergence to determine the sequence of predator arrivals and the number of predation events on emerging hatchlings. Data were pooled from the two summers of monitoring. The predation rate per predator was calculated: (1) the number of days on which predation occurred; and (2) the 13 h (crepuscular and night-time hours between 18h00 and 07h00) per day during which hatchlings were observed to emerge. The size of the emerging group of hatchlings and the proportion of mortality was fitted to a power regression for direct comparisons with the findings of Erb and Wyneken (2019).

Results

Ghost crab burrow density

Of the total of 1,755 burrows counted at both locations, 765 were considered to belong to mature-sized ghost crabs. The number of burrows of mature crabs ranged from 0.05 to 0.09 m⁻² (mean 0.07 and 0.01 SE) at Bungelup Beach and 0.14–0.15 m⁻² (mean 0.15 and 0.01 SE) at Gnaraloo Bay. Three-way ANOVA indicated that burrow densities for mature-sized crabs were influenced by Location, but not Period and Year (Table 1). However, there were statistically significant two-way interactions between Location and both Period and Year.

Typically, Gnaraloo Bay had approximately twice as many mature ghost crab burrows as Bungelup Beach across egg laying and hatchling emergence periods (Fig. 1a, b). However, there was no clear trend in burrow densities across periods.

Nest inventories

Start-of-season nest inventories revealed a mean clutch size for loggerhead turtles of 121.7 ± 6.1 SE eggs (range 72 to 190) from 23 nests at Bungelup Beach. Hatching success was estimated at $44.0 \pm 4.9\%$ of eggs (Fig. 1c), including live hatchlings trapped in the neck of the egg chamber and likely suffering from heat exhaustion ($1 \pm 0.5\%$), and dead hatchlings ($1.2 \pm 0.5\%$). Of the eggs that remained unhatched, $7.9 \pm 2.3\%$ were undeveloped

Table 1 Results of a three factor ANOVA testing differences in ghost crab burrow densities of mature-sized (>25 mm diameter) crabs between Location (Bungelup Beach and Gnaraloo Bay), Period (egg laying and hatchling emergence), and Year (summer 1 and summer 2). The 3-way interaction was not significant, and the model was run with only main effects and two-way interactions, so as not to over parametrise. Bolded black numbers signify statistically significant results, and regular numbers non-significant results

	df	SS	F	Sig.
Location	1	4.729	32.968	<0.001
Period	1	0.426	2.971	0.09
Year	1	0.033	0.231	0.633
Location * Period	1	1.117	7.784	0.007
Location * Year	1	1.463	10.201	0.002
Period * Year	1	0.104	0.727	0.397
Error	65	0.143		

$R^2=0.458$ (Adjusted $R^2=0.408$)

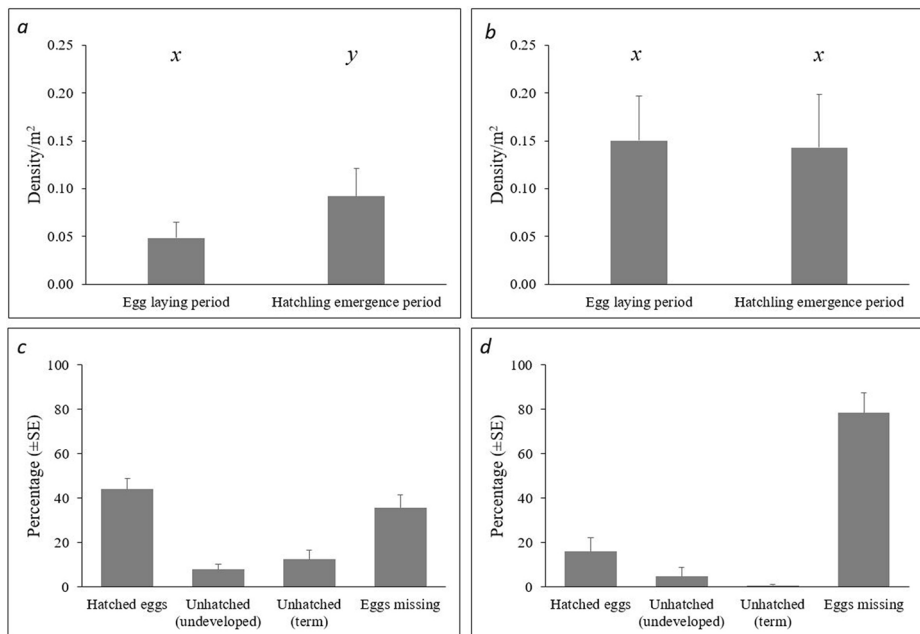


Fig. 1 Mean densities (\pm standard error) of mature-sized ghost crab burrows (>25 mm diameter) during the egg laying and hatchling emergence periods at non-nesting and nesting beaches at (a) Bungelup Beach and (b) Gnaraloo Bay, and the proportional fate (\pm standard error) of eggs based on nest inventories for (c) Bungelup Beach (23 nests & 2,798 eggs) and (d) Gnaraloo Bay (19 nests & 2,325 eggs). Letters above bars indicate significant differences in ghost crab burrow densities between periods based on pair-wise tests

and $12.5 \pm 4.1\%$ contained fully formed term embryos. This left $35.6 \pm 6.0\%$ of eggs unaccounted for and presumed lost to predation. All but one of the surveyed nests at Bungelup Beach had eggs missing, with 30% of these nests having lost more than half of their eggs.

The mean clutch size was 122.4 ± 5.0 SE eggs (range 66 to 158), from 19 nests at Gnaraloo Bay, with hatching success for only $16.0 \pm 6.3\%$ of eggs (Fig. 1d), including 0.3% and

1.2% live and dead hatchlings, respectively. Just over $5.5 \pm 5.0\%$ of each clutch comprised unhatched eggs, which included $4.7 \pm 4.0\%$ undeveloped eggs and $0.8 \pm 0.5\%$ with term embryos. This left $78.5 \pm 9.0\%$ of eggs which were unaccounted for, again presumed lost to predation. Only a single nest at Gnaraloo Bay had no missing eggs, while 68% of nests had $>90\%$ missing eggs. Ghost crab burrows (≥ 1) were present on top of 84.2% of nests at Gnaraloo Bay, compared to 13.0% of nests at Bungelup Beach, just prior to the end-of-season inventories. Numerous burrows were present in the walls of egg chambers in those nests at Gnaraloo Bay.

Accelerometers showed that nests at Gnaraloo Bay experienced a mean of 58.0 ± 51.7 SE seconds of vibrations above threshold per day, compared to 16.8 ± 10.9 s per day for Bungelup Beach, over the incubation period. There was a strong positive relationship between vibration time and the percentage of missing eggs from the nests across both beaches, (Fig. 2a). The duration of vibrations tended to be greater during the night than day (Fig. 2b, c), with only a single nest at Gnaraloo Bay experiencing an exceptionally high duration of vibrations during daytime.

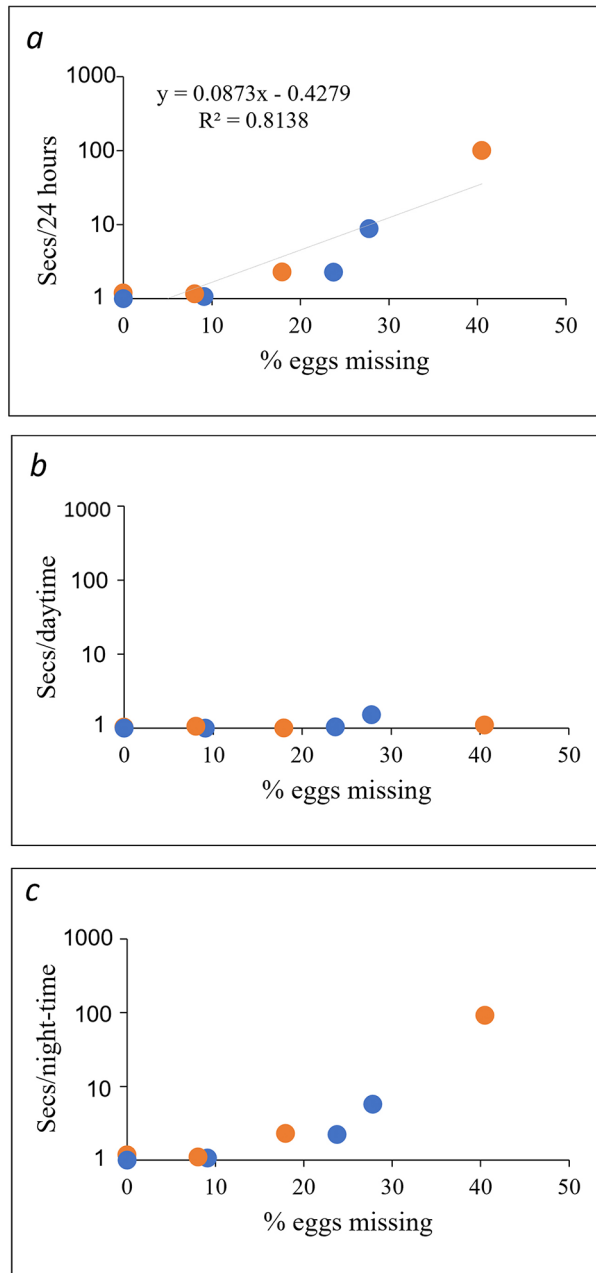
A mean of 37.4 ± 24.2 SE seconds of vibration above the threshold per nest per day of incubation was recorded over a total of 436 days of incubation from nine nests. Using combined data across locations, the vast majority of these vibrations occurred in the 1st (77.6%) and 3rd (19%) trimesters, while only 3.3% occurred during the 2nd trimester. All 1st trimester vibrations occurred within the first 15 days of incubation, with the majority occurring in the first two days of incubation (Fig. 3a). All 3rd trimester vibrations occurred within the final 17 days of incubation, with the majority (94.4%) occurring within the final 13 days of incubation (Fig. 3b).

Hatchling predation

From 2,643 h of video footage recorded at Gnaraloo Bay over the two sampling summers, no hatchling was seen to emerge from 13 broad fields-of-view along which cameras were deployed. In comparison, from 5,023 h of video footage at Bungelup Beach, 283 and 579 loggerhead turtle hatchlings from 11 and 25 nests were observed emerging during 2019/2020 and 2021/2022 nesting seasons, respectively. Combined, these hatchlings emerged during 198 discrete emergence events, ranging from one to 92 hatchlings emerging per event, with a mean of 4.4 ± 0.7 SE hatchlings per event. Predation occurred at 33 of 36 nests and during 181 (91.4%) of these emergent events, at which time a mean of 1.9 ± 0.2 SE hatchlings were predated per event. Overall, a mean of $42.6 \pm 8.8\%$ of hatchlings were predated and $53.1 \pm 14.9\%$ made it safely to the water, while the fate of $4.3 \pm 2.0\%$ was unknown (Fig. 4a).

The main predators of hatchlings were ghost crabs (Fig. 5a-c), which predated 277 from a total of 862 emerging hatchlings, with 0 to 30 being predated per nest. On average, $31.8 \pm 5.8\%$ of hatchlings were predated by ghost crabs (Fig. 4a), with the vast majority predated by the golden ghost crab (*O. convexa*). The horned ghost crab (*O. ceratophthalma*) was only observed to predate three hatchlings. Silver gulls (*Croicocephalus novaehollandiae*) directly predated on a mean of $7.4 \pm 3.5\%$ of hatchlings, while $3.1 \pm 1.8\%$ of hatchlings were indirectly predated via klepto-parasitism (Figs. 5a, c and d and 4a) from crabs. A black rat (*Rattus rattus*) directly predated 0.1% of hatchlings and klepto-parasitised another 0.1% from a crab (Figs. 5e and 4a), and while not quantified, the sand goanna (*V. gouldii*) was also recorded digging up eggs and hatchlings from within a nest (Fig. 5f).

Fig. 2 Relationship between the duration of vibration (seconds) per day and percentage of missing eggs of loggerhead turtle nests for the $\text{Log}_{10}(x+1)$ transformed data for (a) day and night combined, along with the line of best fit and linear equation and R^2 , (b) daytime only, and (c) night-time only, at Bungelup Beach (blue dots) and Gnaraloo Bay (orange dots), from 8 nests from which accelerometers were retrieved. Transformed data are shown to clearly show the lower durations of predation that occurred



At those nests where predation occurred, golden ghost crabs were typically first on the scene and involved either directly or via klepto-parasitism in predation of hatchlings on 28 (84.8%) occasions. Ghost crabs were seen gathering near nests prior to hatchling emergence at 25 nests and were the first predators to arrive after first hatchling emergence at a further 7 nests. In contrast, a silver gull was the first predator to arrive at only one nest. However, the

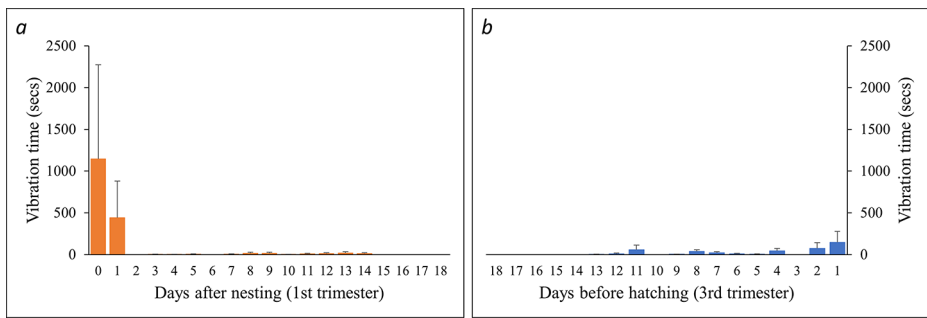


Fig. 3 Mean vibration time (\pm standard error) per day over the 18 days after nesting and the 18 days before hatching that represent the mean duration of 1st and 3rd trimesters of egg incubation, respectively, from nine loggerhead turtle nests on the Ningaloo coast. Negligible amounts of vibrations were recorded during the 2nd trimester

appearance of silver gulls after the arrival of ghost crabs occurred at 7 of the 9 nests where gulls were involved in predation. This resulted in both predators aggregating around several nests prior to hatchlings emerging.

Based on pooled data across all videoed nests, hatchlings emerged between 18h00 and 07h00, with peak emergence occurring between 20h00 and 23h00 (Fig. 4b). Predation by both ghost crabs and silver gulls generally occurred during all these hours, as did safe journeys to the water by hatchlings.

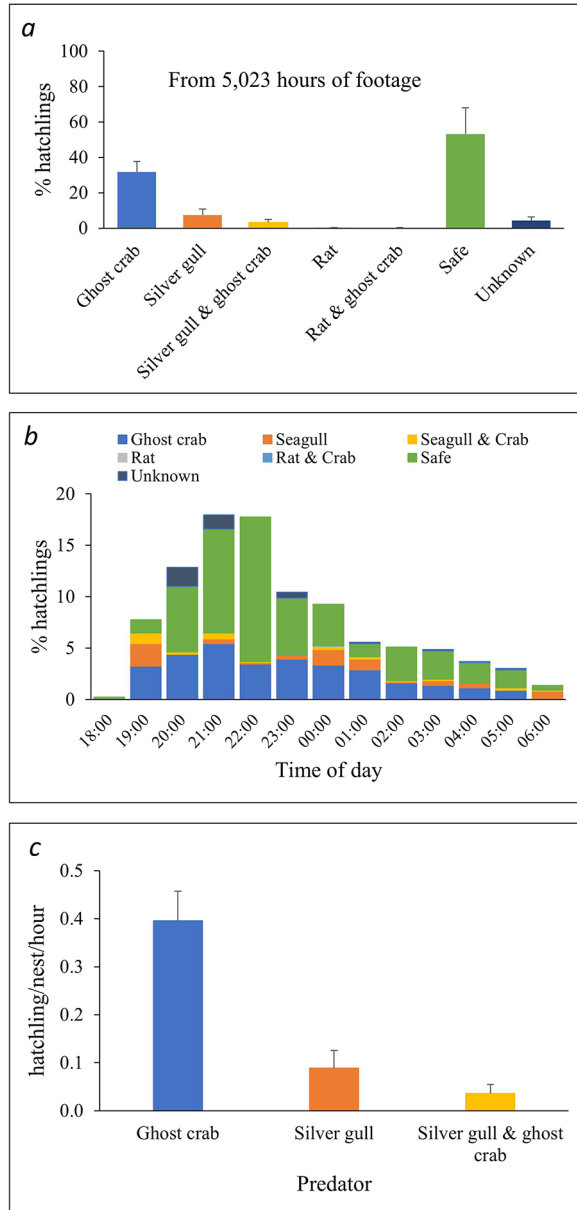
Considering that the sun and wind likely destroyed olfactory and visual cues from the previous night's emergences, the first emergence event of each day and at each nest was considered as a unique first emergence event for a nest, allowing for the order of predator arrival to be assessed. Thus, 47 first emergence events were recorded across both years, from which ghost crabs were the first to reach the nest on 30 occasions and silver gulls on three occasions, while hatchlings emerged unopposed on 14 occasions. Ghost crabs predated emerging hatchlings at a mean rate of 0.4 ± 0.1 SE hatchlings per hour of emergence (hr^{-1} emergence), compared to 0.1 and $<0.1 \text{ h}^{-1}$ emergence for silver gulls and kleptoparasitism, respectively (Fig. 4c).

The level of predation was greatest when hatchlings emerged alone (92.2% of 115 single emergence events, Fig. 6a). As the size of emergent groups increased, so did their chance of surviving the beach crawl and reaching the relative safety of the water. Of the 15 emerging groups with >10 hatchlings, 18.5% of 454 emerging hatchling were predated, 75.8% made it to the water, and the fate of 5.7% was uncertain. An exponential decline in mortality was demonstrated between the size of emergent groups and the proportion of predation by all predators (Fig. 6b) and by ghost crabs (Fig. 6c).

Discussion

Our multi-method approach has allowed the first comprehensive assessment of predation by a range of native predators on the early life stages of the loggerhead turtle (*C. caretta*) from ovipositing of eggs to emerging hatchlings reaching the water. We show that $<20\%$ of those eggs laid in nests at loggerhead turtle rookeries along Australia's Ningaloo coast developed

Fig. 4 The fate of hatchlings to different predators based on 5,023 h of video footage, including (a) proportional fate (\pm standard error), (b) fate per time of emergence, and (c) predation rates (\pm SE) per predator of loggerhead turtle hatchlings at Bungelup Beach (36 nests & 862 hatchlings). There is no figure for Gnaraloo Bay as no hatchlings were observed to emerge from nests



into hatchlings and survived the beach crawl to the water. Nest inventories indicated that 13 and 84% of nests were disturbed and \sim 40 and 80% of eggs were predated at two of the four significant rookeries of the species' distinct Southeast Indian Ocean stock. Predation was predominantly by the endemic golden ghost crab *Ocyropode convexa*. These levels of disturbance on nests and predation on eggs have been observed for sea turtles elsewhere, but mainly by mammals. For example, foxes and jackals predated 68% of *C. mydas* and

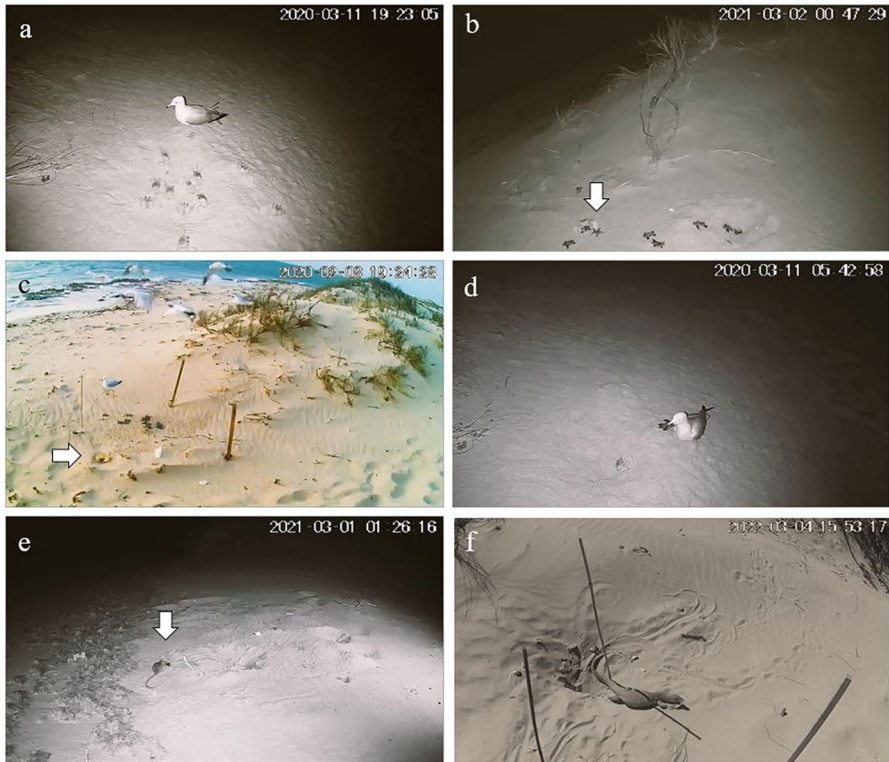
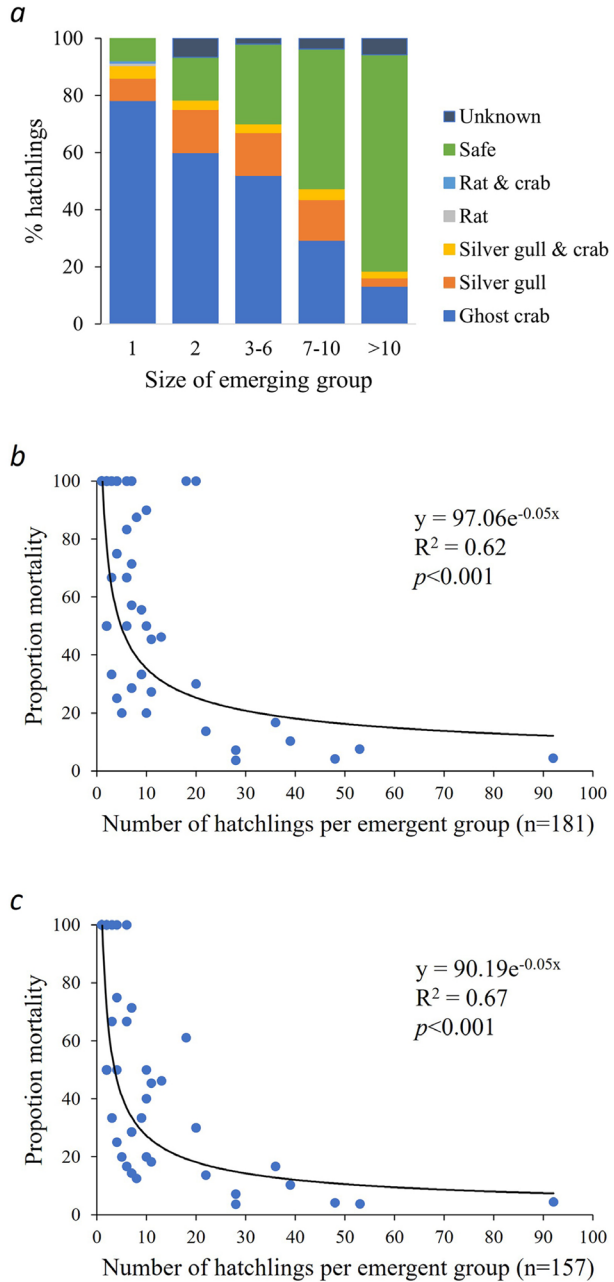


Fig. 5 Predators of loggerhead turtle hatchlings emerging from nests, which were recorded by infra-red video camera over consecutive days in the summers (2019/20 and 2020/21) at Bungelup Beach in the Cape Range National Park, Western Australia. Representative images captured from the videos for: (a) capturing predators aggregating where hatchlings are about to emerge; direct predation of emerging hatchlings by (b & c) ghost crabs and (c) silver gulls; klepto-parasitism by (c & d) silver gulls; and (e) a rat; and (f) a goanna digging eggs from a nest (filmed in the summer of 2021/22)

loggerhead turtle eggs in Turkey, while raccoons, feral hogs and coyotes combined predated 45% of loggerhead turtle eggs in Georgia, USA (Brown and Macdonald 1995; Butler et al. 2020). Furthermore, invasive rats predated ~23% of *E. imbricata* eggs and hatchlings combined in the U.S. Virgin Islands (Witmer et al. 1998) and hatchlings comprised up to 45% of rat stomach contents in New Caledonia (Caut et al. 2008). Invasive predators are widely thought to be more harmful to prey populations than native predators (Salo et al. 2007), however, the invasive black rat *Rattus rattus* at the Ningaloo coast accounted for only 0.2% loss of hatchlings. In contrast, the endemic golden ghost crab, and to a lesser extent, the native silver gull *Croicocephalus novaehollandiae*, was responsible for most of the 43% of predation on emerging hatchlings. As has been shown for other prey species (Brown and Conover 2011; Keech et al. 2011; Valkenburg et al. 2004; Wakeling et al. 2009), these high levels of predation are likely to have an impact on the abundance, survival, and reproductive success of this vulnerable sea turtle species. However, high predation rates by native species that are generalist feeders (Rae et al. 2019; Smith and Carlile 1993) may not be directly linked to the fluctuations in reproductive success of sea turtles (Pimm and Lawton

Fig. 6 (a) Proportional contribution of predation by different predators on different sizes of emerging hatchling groups, and the relationship between size of emerging hatchling group and proportion mortality by (b) all observed predators and (c) ghost crabs only, with a power regression line. Only emergence events that had hatchling mortality are included in b and c



1978). Furthermore, recruitment of invertebrates, such as ghost crabs, is not directly linked to population size (Underwood and Fairweather 1989). These combined characteristics of predators provide an additional challenge for conservation programs to protect turtles' early life history stages, since the weak link between predator and prey population size makes it

difficult to apply and/or assess the success of mitigation strategies, and any lethal control of native species could be controversial.

Predation on turtle eggs

Based on the assumption that predation is the cause of missing eggs (Marco et al. 2015), we conclude that the golden ghost crab is responsible for the majority of the predation on loggerhead turtle eggs on the Ningaloo coast. We did not directly observe predation of eggs inside nests or observe any ‘slits’ in egg shells as described by Maros et al. (2005) as a sign of predation by crabs. However, we observed multiple burrows and active burrowing by crabs, bringing sand and egg shell fragments to the surface at nests, and on one occasion, a ghost crab carrying a whole egg across the beach. Furthermore, ghost crab burrow densities at this location were twice as high as those at Bungelup Beach, where egg loss was half of that found at Gnaraloo Bay (40 vs 80% loss). One caveat is the potential for bias when using egg shell fragment counts for estimating egg fate, resulting from either biological traits of the sea turtle species or from human error (Ceriani et al. 2021). However, Ceriani et al. (2021) found that nest inventories of loggerhead turtles had the lowest error among the four sea turtle species studied. The sand goanna *Varanus gouldii* was the only other predator observed digging in the nests, but this was observed very infrequently and could not be quantified. Goannas are a major predator of turtle eggs on beaches in Australia’s tropical north (Blamires 2004; Lei and Booth 2017). Dingo (*Canis dingo*) tracks were occasionally observed, but none leading to or away from known nests. Whilst circumstantial, and limited by a small sample size, vibration data further supports predation being responsible for the missing eggs, with a strong positive relationship between the duration of vibrations and proportions of eggs missing. Furthermore, far greater levels of vibrations detected at night when ghost crabs were typically observed scavenging on the beach (Pers. obs.), suggests that these crabs are mainly responsible for the vibrations. It is therefore likely that the golden ghost crab, and to a lesser extent, the sand goanna, produced the vibrations recorded by accelerometers in the nests.

Our estimates of 80 and 40% predation rates on eggs at Gnaraloo Bay and Bungelup Beach, respectively, were higher than those attributed to ghost crab predation rates of 12% on loggerhead turtles in Surinam and 20% on *E. imbricata* eggs in the Seychelles (Hill and Green 1971; Hitchins et al. 2004) (Table 2). Predation rates on eggs appear to be positively related to ghost crab densities, though confirmation of such a relationship would need estimations from other sites with varying densities. While densities of *O. quadrata* at loggerhead turtle rookeries in Florida did not appear to influence predation rates on turtle eggs, only 12% of egg losses were attributed to ghost crabs whereas raccoons were the most important egg predator (Table 2). Burrow densities in the current study were similar to those found elsewhere in locations with turtle nests and several locations in the absence of turtle nests, e.g. 0.05–2.8 m⁻²*O. quadrata* burrows in Brazil (Turra et al. 2005), <0.00–0.23 m⁻²*O. ceratophthalma*, *O. madagascariensis* and *O. ryderi* burrows in South Africa (Lucrezi 2015), 0.45–2.11 m⁻²*O. cordimana* burrows in northeast Australia, and 0.0–1.15 m⁻²*O. convexa* burrows on the temperate west coast of Australia (Supplementary Online Material in Rae et al. 2019). Thus, ghost crabs are numerous at beaches around the world and need to be considered as potential predators on beaches where they co-occur with nesting sea turtles.

Table 2 A comparison of the predation levels of sea turtle nests and eggs in peer reviewed articles across sea turtle species at different locations across the globe

Location	Turtle species	Main predators	# Nests	% Nests predated	% Eggs predated	Source
Gnaraloo Bay, Western Australia	<i>C. caretta</i>	Ghost crab	19	95	78.5	current study
Georgia, USA	<i>C. caretta</i>	Raccoon, feral hog, coyote, ghost crab, etc.	19,158	12–31	44.9	Butler et al. 2020
Bungelup Beach, Western Australia	<i>C. caretta</i>	Ghost crab	23	96	38.8	current study
Florida USA	<i>C. caretta</i>	Raccoon, ghost crab	97	35–48	33.6	Bouchard and Bjorndal 2000
Florida, USA	<i>C. caretta</i>	Raccoon, ghost crab	10	~71	31	Barton & Roth, 2008
Maio Island, Cape Verde	<i>C. caretta</i>	Ghost crab	59	68	29	Martins et al., 2022
Cousine Island, Seychelles	<i>E. imbricata</i>	Ghost crab	141		19.3	Hitchins et al. 2004
Bigisanti Beach, Surinam	<i>C. mydas</i>	Ghost crab	100	60	12	Hill and Green 1971
Florida, USA	<i>C. caretta</i>	Ghost crab	24		6.3	Brown 2009
Peninsular Malaysia, Malaysia	<i>C. mydas</i>	Ghost crab	643	30	1.3	Ali and Ibrahim 2002
Galapagos Islands, Ecuador	<i>C. mydas</i>	Ghost crab	1,039	5.4	0.8	Zarate et al., 2013
Everglades NP, USA	<i>C. caretta</i>	Raccoon	2,712	75–85		Davis and Whiting (1977)
Akyatan Beach, Turkey	<i>C. mydas</i> , <i>C. caretta</i>	Fox	93	68		Brown & MacDonald 1995
Wreck Rock, Australia	<i>N. depressus</i>	Goanna	42	17–58		Lei and Booth 2017
Mundabullangana & Wreck Rock, Australia	<i>N. depressus</i>	Goanna	254	38–52		Blamires et al., 2003
Sunshine Coast, Australia	<i>C. caretta</i>	Fox	206	19–52		O'Connor et al., 2017
Cape York Peninsula, Australia	<i>N. depressus</i> , <i>L. olivacea</i> , <i>E. imbricata</i>	Feral pig	179	40		Whytlaw et al. 2013
US Virgin Islands	<i>E. imbricata</i>	Rat		10–20		Witmer et al., 2007

Based on the earlier assumption that vibration data reflects predation, egg predation appears to be most prevalent during the 1st and 3rd trimesters of egg incubation, following a similar pattern of predation by mammals (predominantly raccoons) on freshwater turtle nests (Geller and Parker 2022). Furthermore, this activity appears to be far higher within two days of nesting and again within ~13 days of hatching and emergence. Soil disturbance from nest construction and the mucus-like fluid discharged by ovipositing females likely provides strong olfactory cues for scavenging predators soon after nesting (Oddie et al. 2015). In comparison, increased heat, olfactory signals and movement of late-stage

embryonic turtles may alert predators to nest locations. This is likely to be the case for ghost crabs, which have well-developed sensory capabilities that can detect prey by sight, sound, smell and vibration (Lucrezi and Schlacher 2014). Metabolic heat produced by developing hatchlings is highest during the 3rd trimester, and can exceed adjacent sand temperature by as much as 2.5 °C (Gammon et al. 2020). In addition, embryonic fluid of hatched eggs, disturbed soils from movements of hatchlings, and hatchling vocalisations may also attract predators, as suggested by Geller and Parker (2022) for freshwater turtles. In contrast, Lei and Booth (2017) found no trend in the timing of predation on loggerhead turtle nests by goannas.

Predation on turtle hatchlings

Thousands of hours of videography with infrared capacity showed no hatchlings emerging from nests at Gnaraloo Bay, where egg predation was exceptionally high. This suggests that relatively few hatchlings emerge from this location due to the high egg predation discussed above. Indeed, not a single hatchling track was observed anywhere on the beach at first and last light when cameras were inspected. In comparison, large numbers of hatchlings were observed to emerge from nests at Bungelup Beach where predation on eggs was half that seen at Gnaraloo Bay. Videography showed that the golden ghost crab is the main predator of hatchlings at Bungelup Beach (~32%), while the silver gull *Croicocephalus novaehollandiae* accounted for ~8% loss of hatchlings through direct predation and a further ~3% loss through klepto-parasitising hatchlings from ghost crabs. While these predation rates are comparable to the findings of other studies (Table 3), the constant observations over a full 24-hour cycle or multiple days using infrared videography in our study provides an accurate assessment of the predation rates on sea turtle hatchlings. Ghost crabs predated at similarly high levels (51 and 24%) on loggerhead turtle hatchlings in Cape Verde and North Carolina, respectively (Martins et al. 2021; Peterson et al. 2013), but higher than ghost crabs in other regions (Table 3). Furthermore, predation rates on loggerhead turtle hatchlings were positively correlated to ghost crab burrow densities in Cape Verde (Martins et al. 2021) and North Carolina (Peterson et al. 2013). However, the inherent biases in methods used in these and other studies could under- or over-estimate predation rates on hatchlings (e.g. extrapolating trends from limited observation times). The high level of predation recorded for ghost crabs is perhaps not surprising given that they are highly opportunistic foragers (Lucrezi and Schlacher 2014), and in the case of *O. convexa*, displays a preference for carrion or animal flesh over other forms of food that are available on beaches (Rae et al. 2019).

The relatively high levels of predation on hatchlings by silver gulls was unexpected since quantified data on hatchling predation by birds are rare. Only two studies have quantified bird predation on hatchlings. Great frigatebirds took 100% of emerging *C. mydas* hatchlings during the day on Europa Island (Lagarde et al. 2001), and herons and caracaras predated on 4.5% of *D. coriacea* hatchlings at night in Costa Rica (Tomillo et al. 2010). Silver gulls, eagles, kestrels and crows were observed taking *C. mydas* and *N. depressus* hatchlings by day in eastern Australia (Limpus 1973), while vultures, grackles, storks, caracaras and chickens were seen to take eggs from exposed *L. olivacea* nests in Costa Rica (Burger and Gochfeld 2014). Based on our study, birds clearly have the potential to contribute to hatchling mortality. When present at turtle nests, silver gulls were seen to consume multiple

Table 3 A comparison of sea turtle hatchling predation during the beach crawl, in peer reviewed articles using different methods across sea turtle species at different locations across the globe

Location	Turtle species	Main predators	# Nests	# Total hatchlings	% Mortality	Method	Source
Europa Island, Indian Ocean	<i>C. mydas</i>	Frigatebird	35	1,828	100%	Direct observations using binoculars, daytime only	Lagarde et al. 2001
Boa Vista, Cape Verde	<i>C. caretta</i>	Ghost crab	56	2,354	50.3	Direct observation, controlled release of hatchlings, hatchery	Martins et al. 2021
Bungelup Beach, Western Australia	<i>C. caretta</i>	Ghost crab, silver gull	36	862	42.9	Infrared videography, continuous over multiple days	current study
North Carolina, USA	<i>C. caretta</i>	Ghost crab	10	42	23.8	Direct observation	Peterson et al. 2013
Playa Grande, Costa Rica	<i>D. coriacea</i>	Ghost crab, heron, caracara	47	779	16.7	Direct observation, 1st emergent group only	Tomillo et al. 2010
North Carolina, USA	<i>C. caretta</i>	Ghost crab	14	586	11.3	Direct observation, 1st emergent group only	Conant 1991
Florida, USA	<i>C. caretta</i>	Ghost crab	66	1,089	7.6	Motion-activated trail camera, direct observation, track analysis	Erb and Wyncken 2019
Playa Ostional, Costa Rica	<i>L. olivacea</i>	Ghost crab, hermit crab	2,913		<4	Direct observation, not described	Madden et al. 2008
Trinidad Island, Brazil	<i>C. mydas</i>	Yellow crab	33	2,494	2.7	Post-event observations, controlled release of hatchlings	Santos et al. 2016

hatchlings in quick succession, as opposed to ghost crabs that can feed on a single hatchling over many hours or days. This feeding behaviour likely reflects their opportunistic foraging strategy (Smith and Carlile 1993) and size.

Ghost crabs were usually the first predator to assemble on top of nests and predating on the emerging hatchlings, which potentially attracted other predators like silver gulls. As discussed above, the early detection of turtle nests by ghost crabs is likely due to their sensory capabilities, but nests could also be discovered by chance when crabs construct burrows for purposes other than predation, particularly on beaches where ghost crab numbers are high. Once hatchlings have emerged, the speed and agility of ghost crabs (Burrows and Hoyle 1973; Hafemann and Hubbard 1969) make them highly efficient at capturing slow-moving loggerhead turtle hatchlings, as observed in the current study. However, predation success was affected by the size of the emerging hatchling group. Even when multiple predator species were present, survival rates of hatchlings were greater when larger hatchling groups emerged. Our findings concurred with other studies on predation by ghost crabs on loggerhead turtle hatchlings in Florida and Cape Verde (Erb and Wyncken 2019; Martins et al. 2021), as well as *C. mydas* hatchlings preyed upon by the brachyuran land crabs in Brazil (Santos et al. 2016), thereby supporting the predator swamping hypothesis (Ims 1990).

Management and conservation considerations

Contrasting our findings, mammals are considered responsible for predation of early life phases of sea turtles elsewhere in Australia and globally (e.g. Butler et al. 2020; O'Connor et al. 2017; Whytlaw et al. 2013). Conservation policy and mitigation efforts have thus focussed on removing feral mammals from high conservation areas. In Australia, the Environmental Protection and Biodiversity Conservation Act (1999) makes provision for threat abatement measures against predation by the European red fox, feral cats, feral pigs (*Sus scrofa*), and for reduction of impacts of exotic rodents on offshore islands (Department of the Environment and Energy 2017). Invasive predator control has been successful at several mainland and island locations in the study region where sea turtles are known to nest (Algar et al. 2020; Greenslade et al. 2013; Marlow et al. 2015). For example, a long running trapping and 1080 (sodium fluoroacetate) baiting program has eradicated foxes and feral cats, reducing nest predation by introduced predators to negligible levels. However, the high predation rates by native ghost crabs and silver gulls provide a challenge for conservation policy and mitigation efforts.

The most recent Australian sea turtle recovery plan does not have recommendations for the control of predation on eggs and hatchlings by native predators like ghost crabs or silver gulls (Department of the Environment and Energy 2017), which along with other native predators like goannas (Lei and Booth 2017), have been shown to be the most important predators at many sea turtle rookeries. The 40 and 80% egg losses seen on the Ningaloo coast exceeds the 30% loss intervention threshold for sea turtle egg mortality in Australia for most sea turtle species (Department of the Environment and Energy 2017). Furthermore, this threshold does not consider the additional predation of emerging hatchlings, which was shown to be high in this study when hatchlings emerged. Indeed, our study suggests that 80% of the loggerhead turtle eggs and/or hatchlings suffer predation. Based on this level of mortality, conservation intervention is likely to be needed. Conservation strategies in relation to silver gull predation could focus on minimising interactions between humans and gulls, particularly in terms of food sources to keep gull populations low. However, since the abundances of ghost crabs are most likely influenced by natural processes such as recruitment success related to oceanographic processes, the strategies to control their populations will be more challenging.

Gnaraloo Bay and Bungleup Beach form two of the four important rookeries (offshore Dirk Hartog Island and Muiron Islands group form the remaining two) of the Southeast Indian Ocean loggerhead genetic stock (Casale and Tucker 2017). There is little to no genetic mixing among loggerhead stock, with mating generally occurring between turtles from the same location (Shamblin et al. 2014), and both males and females homing back to natal sites where mating occurs close to nesting beaches (Clusa et al. 2018). This highlights the vulnerability and importance of protecting the Southeast Indian Ocean stock. Since loggerhead turtles have a late maturation age (Casale et al. 2011), high levels of predation on eggs and hatchlings, even sustained over 20–30 years, are unlikely to be detected in the adult population until decades later. Thus, research is needed to determine if the high predation rates seen by ghost crabs in our study are characteristic of sea turtle egg and hatchling predation at other sea turtle rookeries for the Southeast Indian Ocean stock, and stocks elsewhere. Additionally, predation control measures need to be considered and tested, and where possible, implemented at rookeries where predation levels are above the established thresholds.

However, any manipulated control measures should be mindful of the role predators play across the broader food web, like the role sea turtles play in the transport of nutrients and energy to beach ecosystems (Vander Zanden et al. 2012).

This study has adopted multiple approaches to provide a holistic estimation of reproductive success from when eggs were laid to when hatchlings reached the relative safety of the ocean. When combined with traditional methods, the technologies used in this study are relatively non-invasive and minimise observational biases. In addition, in combination, they effectively capture all types of predation over many days. Accelerometry has provided a complementary approach to traditional start- and end-of-season inventories (e.g. Marco et al. 2015; Whitmore and Dutton 1985), allowing interpretation of what might occur inside nests over the entire incubation period, when direct observations are complicated and not feasible. Furthermore, infrared videography provides the capacity for an assessment of all types of predation over the full diurnal cycle and over several days of emerging hatchlings, as well as interactions between predator and prey and between various predators. Differing predation monitoring methods each come with their own inherent biases (Erb and Wyneken 2019; Isaac and Pocock 2015), which can affect the veracity of results. We believe that we have come up with an approach that is both cost effective and time efficient, while producing data on sea turtle egg and hatchling predation at a higher resolution than has previously been achieved, which will benefit conservation programs for all sea turtles.

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Data Availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethical approval All research protocols included in this paper have been approved by the Western Australia Department of Biodiversity, Conservation and Attractions (licence number TFA 2019-0164-3, FO 25000181-3), the Western Australia Department of Primary Industries and Regional Development (exemption number 3474, 250917621), and the Edith Cowan University Animal Ethics Committee (23080). The procedures comply with the Animal Welfare Act 2002 (Western Australia) and the requirements of the *Australian code for the care and use of animals for scientific purposes*.

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