



Competition among males for breeding females as a measure of male abundance in sea turtles

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Received: 1 June 2026 / Accepted: 10 September 2026
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Abstract

Understanding the relative abundance of breeding males and females is particularly important for taxa where skewed sex ratios threaten population viability, including for sea turtles for which climate warming increases risks of population feminisation. We report observations of mating pairs and “attendant” males, i.e. males within a few metres of the focal mating pair, for breeding green turtles (*Chelonia mydas*) around the world. At Isla de Aves (Venezuela, Caribbean), we observed a total of 665 mating pairs across 17 days of intense observations (June–July 2008), and on 50.2% of occasions pairs had attendant males. We mostly observed one or two attendant males per pair, but sometimes observed > 5. These observations suggest that breeding females were not struggling to locate breeding males. In the Chagos Archipelago (Indian Ocean), we made incidental observations from 2015 to 2024, and 6 of 31 observations of mating pairs (19.4%) had attendant males, with a maximum of 5 per pair, again implying there was often an abundance of breeding males, consistent with a previously estimated male-biased hatchling sex ratios at this site. Elsewhere in the world, attendant males have been observed with mating loggerhead turtles (*Caretta caretta*) in Greece and green turtles in the Southern Great Barrier Reef (Australia) and Ascension Island (South Atlantic), all sites where hatchling or juvenile sex ratio estimates again suggest males are not scarce. We suggest that observations of attendant males may be a useful component in the general toolkit for studying male sea turtles and their abundance in breeding areas.

Keywords Attendant male · Operational sex ratios · Climate warming · Feminization · Mating trains · Mating stacks · Sea turtle

Responsible Editor: P. Casale.

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Introduction

Climate change poses a broad threat to Earth's biota, and identifying which taxa will be most heavily impacted, and how those impacts might be mitigated, remain important overarching goals for conservation biology (Ripple et al. 2025). Climate impacts vary across taxa, and include the loss of key habitats and the constriction or spatio-temporal shifting of available thermal niches (e.g. Niederman et al. 2025). For some groups, life-history characteristics increase vulnerability to climate warming. Such groups include reptiles, since many have temperature-dependent sex determination. Consequently, rising incubation temperatures, associated with climate warming, may generate highly skewed hatchling sex ratios, with potential implications for population viability (Boyle et al. 2014; Edmands 2021).

For sea turtles, female hatchlings are produced at warmer incubation temperatures, raising concerns of population feminisation with climate change (Booth et al. 2020; Fuentes et al. 2023; Hays et al. 2025; Laloë et al. 2024; Meylan et al. 2024; Tomillo et al. 2012, 2015). Female-biased hatchling production may ultimately impact the availability of adult breeding males and hence population viability. This makes the assessment of breeding male abundance an important goal for sea turtle populations worldwide, particularly because males remain comparatively understudied (Hays et al. 2010, 2022; García-Cruz et al. 2026). One potentially useful but underexplored source of information comes from observations of turtle mating behaviours in breeding areas (Das et al. 2025). When receptive females and reproductive males overlap spatially, males may compete for access to females and this competition can involve one or more “escort” or “attendant” males associated with a mating pair (Harrison 1954; Booth and Peters 1972). In some cases, a single attendant male may accompany a mating pair, whereas in others several attendant males may be present, apparently attempting to displace the mounted male and gain a mating opportunity. Indeed, Schofield et al. (2006) observed that a mounted male could be successfully dislodged by attendant males, which may bite the mounted male's flippers, neck, tail and carapace. In some cases, attendant males form “stacks” or “trains,” with a mating pair at the front and additional males attached to, or positioned behind, the mounted male (e.g. Booth and Peters 1972).

The occurrence of attendant males with mating pairs may therefore provide useful information on the local availability of breeding males. Although attendant males accompanying mating pairs in sea turtles have been reported anecdotally for many decades, there have been relatively few quantitative descriptions of this behaviour and little consideration of its broader ecological and conservation implications.

Here we explore the utility of observations of attendant male sea turtles accompanying mating pairs and consider how such observations might serve as an indicator of the relative abundance of breeding males. When interpreted with appropriate caution – placing the presence or absence of attendant males in the context of local variations in density, observation conditions, courtship-site structure, female receptivity, and observation timing within the breeding season – we find that attendant male observations can form an important part of the toolkit for assessing breeding male scarcity and monitoring how the relative availability of breeding males and females may change across years under ongoing climate warming.

Materials and methods

We made observations of sea turtles at two sites. The first was Isla de Aves, Venezuela (63.62°W, 15.66°N), a breeding area and the most important nesting site for green turtles (*Chelonia mydas*) in the south-eastern Caribbean with an estimated > 1000 turtles nesting annually (García-Cruz et al. 2015). Isla de Aves is a flat (< 5 m high) sand spit located ~ 670 km north of the Venezuelan mainland and is ~ 540 m long and 30–125 m wide (Fig. 1a) (García-Cruz et al. 2015). Sea turtles close to the island were observed from a height of approximately 18 m from the Base Científico Naval Simón Bolívar (BCNASBO) located on the island. We made observations during the morning and afternoon over 17 days, between 26 June and 12 July 2008, except when weather or sea conditions, such as high turbidity or strong wave action, prevented reliable identification of turtles. Surveys were conducted at 20-minute intervals. The observation area was delimited by an imaginary straight line between the BCNASBO and the north-western end of the island.

In each survey on Isla de Aves, we counted the number of mating pairs observed, both by eye and through binoculars (I.R. Optics, 10×42) within 500 m of the observation platform. For each pair, we noted the number of attendant turtles and their sex. We defined attendant turtles as those within a few metres of the focal mating pair. In > 100 cases where the sex of attendant turtles could be determined through observations of their extended tail length (Hays et al. 2010), we found they were always males. We therefore assumed that all attendant turtles were males. Our counts were a conservative indicator rather than a quantitative measure of total mating activity around Isla de Aves, as systematic observations were restricted to a limited shallow-water sector and a relatively short period within a longer reproductive season. For example, based on field observations, mating activity begins in early June and continues through

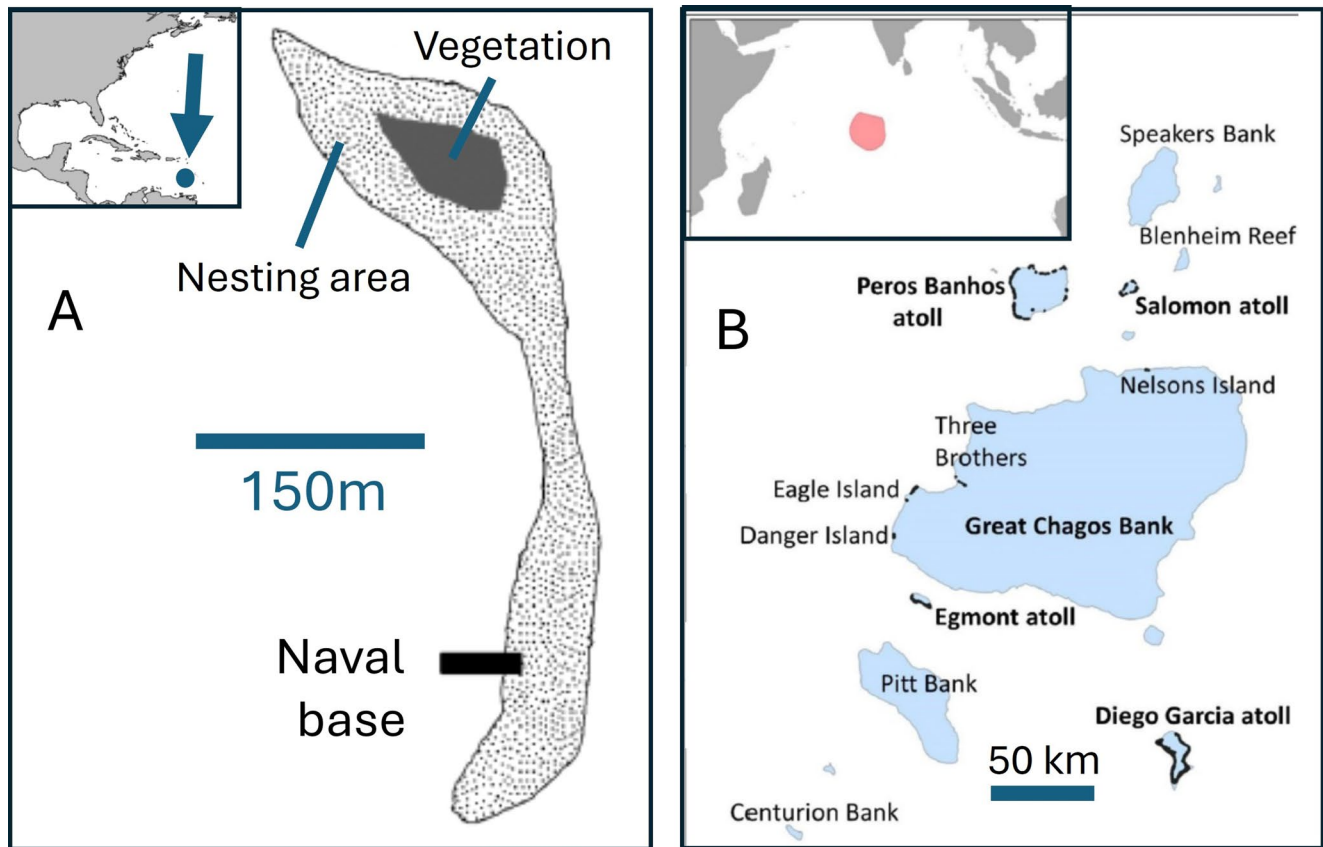


Fig. 1 Location of the study areas (A) Isla de Aves (Caribbean), showing the general location (inset) and the size and shape of the island, including the observation point from the naval base. (B) The Chagos

July, and some males may remain in the area until August, with mating activity also occurring outside the visible surface area, including underwater (M. A. García-Cruz, unpublished data).

The second site we observed for the present study was in the Chagos Archipelago (72°E, 6.5°S). From 2015 to 2024, we made incidental observations of mating turtles in the water on 31 occasions while patrolling nesting beaches during three types of daytime surveys. These included track count surveys, to identify nest locations; drone surveys 50–250 m from shore, to count immature turtles; and surveys of ship presence conducted as part of wider habitat surveys or Marine Protected Area (MPA) patrols. For each type, every time we observed a mating pair, we counted the number of attendant turtles. Where tail length could be seen, attendant turtles were always males.

Finally, we searched the literature for quantitative observations of attendant males accompanying mating turtles, starting by using the search terms “escort males”, “attendant males” and “sea turtles” in Google Scholar and Web of Science. From the papers located, we then used forward and backward citations to identify additional publications. For sites where attendant males have been reported, we

compared against estimated hatchling and juvenile sex ratios for that site, using the recent global compilation of sex ratios across all sea turtle species in Tromp et al. (2025).

Results

On Isla de Aves, surveys of mating pairs were conducted on 227 occasions across 17 days (Table S1). A total of 665 mating pairs were observed (Figs. 2 and 3, Table S1) and they had a total of 754 attendant males.

There was no systematic change in the proportion of mating pairs that had attendant males across the 17 survey days ($F_{1,15} = 0.69$, $P = 0.42$) (Fig. 3a) and this proportion was consistently around 50% throughout the day (Fig. 3b). There were attendant males with 50.2% of the mating pairs observed, with the number of attendant males typically being one or two but sometimes >5 (Fig. 3c). Informal reports, outside of our systematic surveys, showed up to 15 attendant males with a mating pair. In the Chagos Archipelago 31 mating pairs of green turtles were observed across all five islanded atolls of which there were attendant males

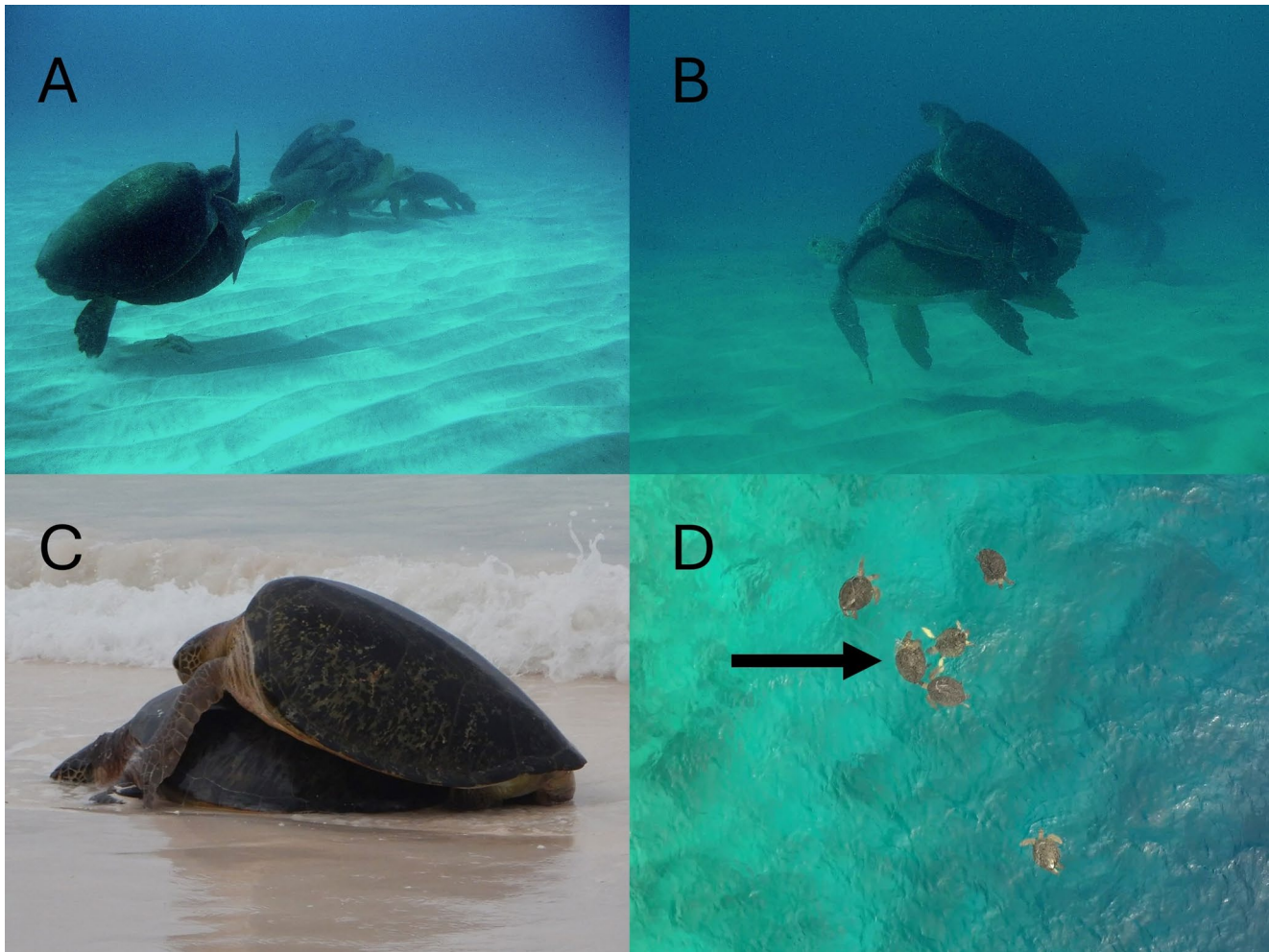


Fig. 2 (A) A mating pair of green turtles at Isla de Aves (foreground) and in the background a mating pair with several attendant males, (B) a stack of 3 turtles at Isla de Aves, comprised of a mating pair plus an additional male, (C) a pair of green turtles at Diego García (Chagos Archipelago) washed ashore while mating and in this case with

an attendant male offshore (not pictured). (D) Drone footage at Nelsons Island (Chagos Archipelago) showing a mating pair (indicated by arrow) and five attendant turtles. Photographs: (A) Marco García-Cruz, (B) Marco García-Cruz, (C) Graeme Hays, (D) Nicole Esteban

on 6 occasions (19.4% of occasions), with a maximum of 5 attendant males (Table S2).

Across the world, we found five additional reports of attendant males with mating pairs (Fig. 4a). For olive ridley turtles (*Lepidochelys olivacea*) at the Rushikulya rookery in Odisha (India), on many occasions mating pairs were observed to have attendant males (Das et al. 2025). For green turtles at Ascension Island (South Atlantic; Lee et al. (2007) 3 out of 3 (100%) mating pairs reported had attendant males. For loggerhead turtles (*Caretta caretta*) at Zakynthos (Greece), 5 of 20 (25%), of observed mating pairs had an attendant male (Schofield et al. 2006). In the southern Great Barrier Reef (sGBR, Australia), this ratio for green turtles was 28 of 83 (34%) of observed mating pairs with attendant males (Limpus 1993), with up to 4 attendant males observed per pair (Jessop et al. 1999). Finally, in the black sea turtle population (*Chelonia mydas agassizii*) at

Colola, Michoacán (Mexico), Delgado-Trejo et al. (2025) reported that for 653 observed mating pairs, 65.7% included one or more attendant males, with up to 17 males associated with a single female. Of the five sites in total with quantitative data on attendant males (our two sites plus three found in the literature), four also had data on hatchling or juvenile sex ratio: Chagos Archipelago, Greece, Ascension Island and sGBR. Of these, none were among the sites where extreme (>90%) female-biased sex ratios have been reported (Fig. 4b).

Discussion

Breeding male sea turtles are notoriously difficult to study because, unlike nesting females, they generally do not come ashore. Hence, the vast majority of work with adult sea

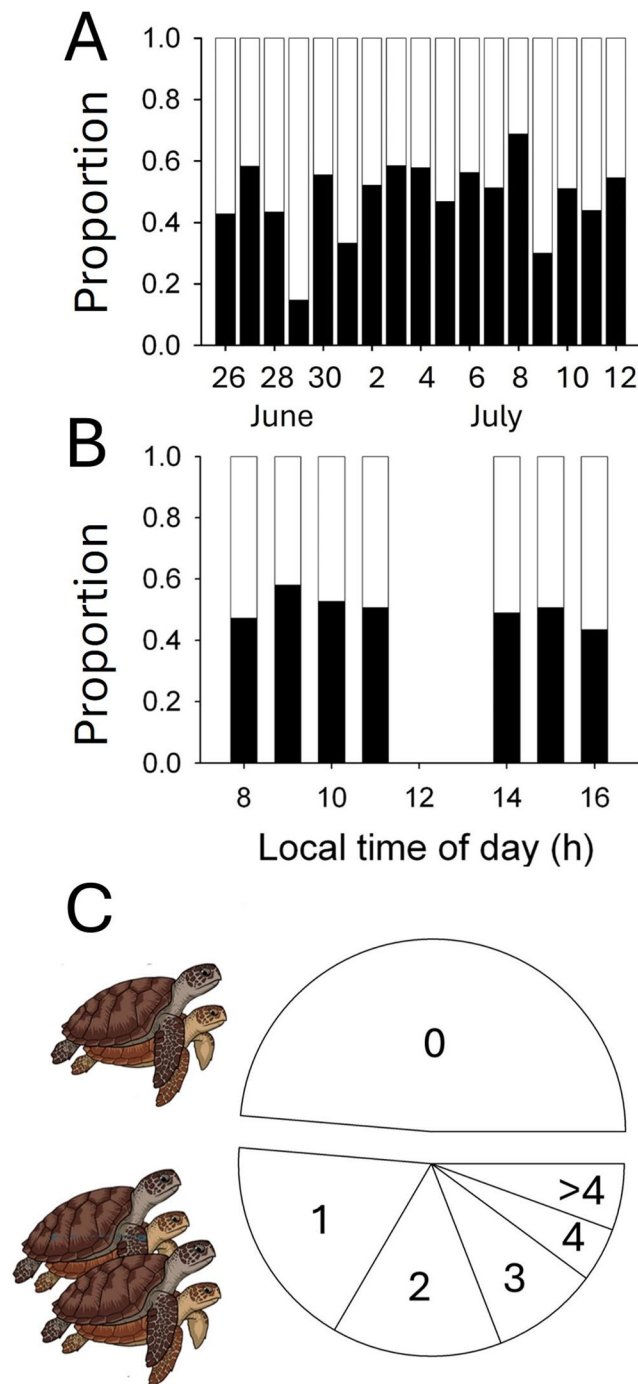


Fig. 3 At Isla de Aves in 2008, the proportion of mating pairs with (solid bars) and without (open bars) at least one attendant male across (A) different days and (B) different hours of the day. (C) The number of attendant males for 665 observations of mating pairs at Isla de Aves. For 50.2% of observed mating pairs there was at least one attendant male (lower half of pie diagram)

turtles has focussed on nesting females and the number of nests or nesting females is commonly used as a proxy for population abundance (Hays et al. 2025). However, such beach-based indices provide little direct information on the

male component of breeding populations. Our fieldwork and literature review revealed reports of mating pairs across species and across the globe with attendant males always being observed in areas where there were not strongly female-biased hatchling sex ratios. These results highlight how observations of mating activity may provide a useful indicator of the relative ratio of breeding males to females, and thereby shed light on whether female-biased hatchling sex ratios translate into low breeding male availability.

Value of direct marine observations

In our search, we found relatively few previous studies using direct observations to study breeding sea turtles. However, the value of observing turtles in the marine breeding environment rather than relying only on nesting beaches is clear, even from just these few studies. Our observations at Isla de Aves and in the Chagos Archipelago add to this growing evidence for the value of observing mating pairs and recording the presence of attendant males (e.g. Staines et al. 2022). With sea turtles, direct observations from boats or snorkellers have been used to quantify the operational sex ratio (OSR, the ratio of males and females available to breed each year), as well as the seasonal transition from the initial arrival of breeding males to the arrival of breeding females and mating, followed by the departure of males before the nesting season (Hays et al. 2010). More recently, OSR has been estimated from drone imagery, in which males and females are distinguished using tail length and behaviour (Schofield et al. 2017). Drone imagery has also been used to distinguish among behaviours such as active mating, courting and searching by males, and resting by females (Staines et al. 2022).

Importantly, systematic observations of mating groups can generate quantitative indices of male participation and male-biased reproductive interactions. For example, direct observations of mating and nesting have been blended with long-term satellite tracking to show the chronology of male arrival at the breeding area, female arrival, mating, nesting and male and female departure (Schofield et al. 2013) and shore-based observations have revealed the relative timing of mating and nesting seasons (Godley et al. 2002). In addition, long-term observations at Colola (Mexico), provide a particularly useful comparison: Delgado-Trejo et al. (2025) reported 336 h of observations, 653 mating groups, 1986 male and 669 female Pacific green turtles, with an estimated ratio of 2.96 males per female and mating groups including up to 17 males per female. Similarly, Limpus (1993) showed that male green turtles in the southern Great Barrier Reef could be studied at courtship areas, where males were identified as breeding if they mounted, were attendant to a mounted pair, or were associated with an adult-sized

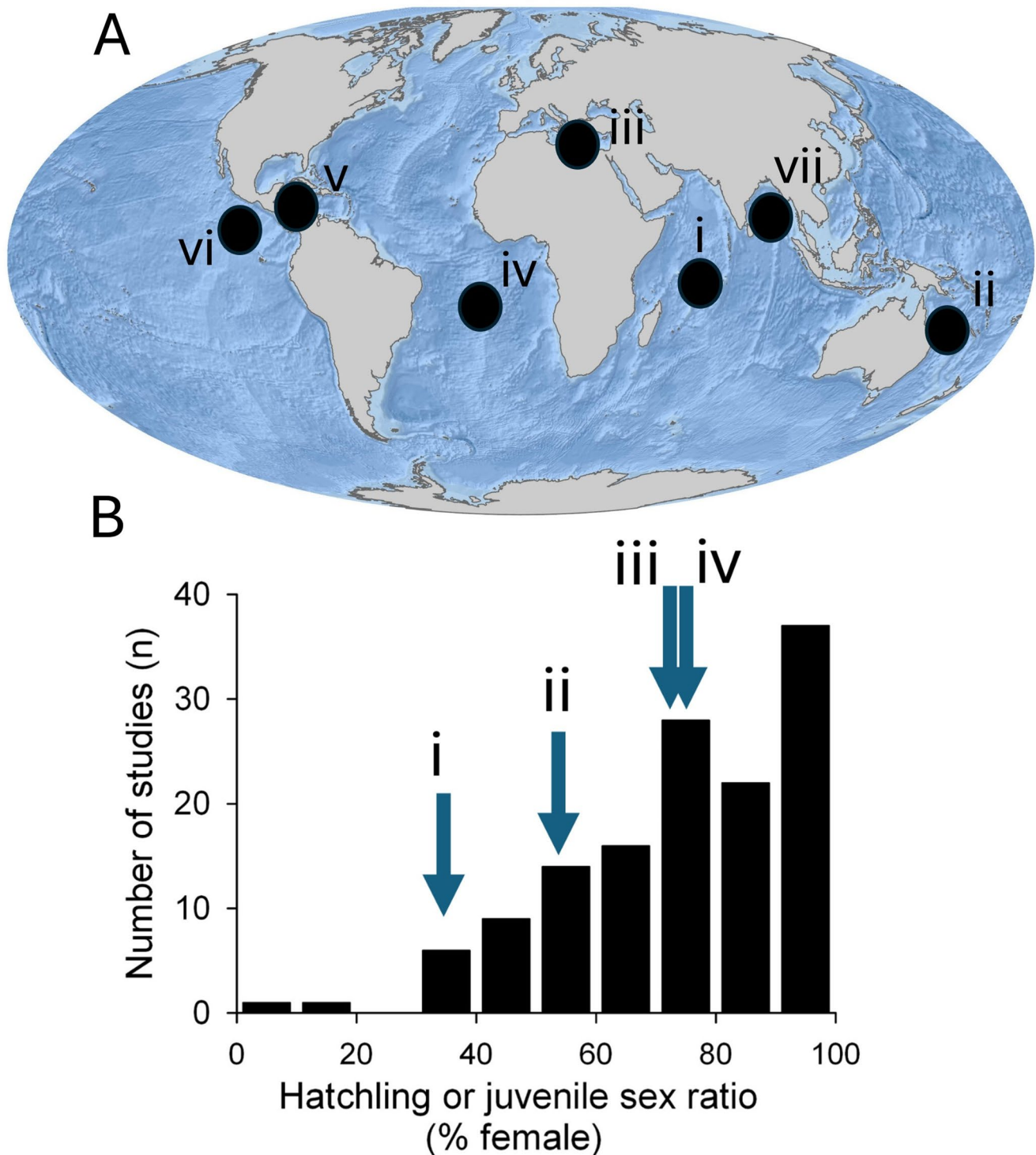


Fig. 4 (A) Sites around the world where mating pairs have been observed with at least one attendant male. i=Chagos Archipelago (Indian Ocean) (green turtle, this study), ii=southern Great Barrier Reef (Australia) (sGBR) (green turtle, Limpus 1993; Jessop et al. 1999), iii=Zakynthos (Greece) (loggerhead turtle, Schofield et al. 2006), iv=Ascension Island (south Atlantic Ocean) (green turtle, Lee et al. 2007), v=Isla de Aves (Venezuela) (green turtle this study), vi=Colola (Mexico) (black turtle, Delgado-Trejo et al. 2025),

vii=Odisha (India) (olive ridley turtle, Das et al. 2025). (B) Frequency distribution of 138 records of hatchling or juvenile sex ratios reported around the world (from Tromp et al. 2025). Arrows indicate sites of reported observations of attendant males with mating pairs. i=Chagos Archipelago (19.4% of pairs observed with attendant); ii=sGBR (34%), iii=Greece (25%); iv=Ascension Island (100%). See text for details

female, while Booth and Peters (1972) provided an early example of direct observations of courtship behaviour.

Evidence from Isla de Aves

Set against the backdrop of these previous studies, at Isla de Aves we showed that over a 17-day observation window, mating pairs had attendant males just over half the time. At this site, the nesting season is thought to peak in August and September (García-Cruz et al. 2015), so our observations preceded the nesting season which is a time when mating activity has been shown to be maximal at other green turtle nesting sites (Godley et al. 2002) and in other sea turtle species (Schofield et al. 2013). Our observations did not extend across sufficient weeks to assess the potential seasonal changes in the relative abundance of breeding males and females that have been observed elsewhere (Hays et al. 2010). Because observations were restricted both temporally and spatially, the intensity of reproductive activity we observed likely underestimates the total mating activity occurring around Isla de Aves.

Nevertheless, our consistent observations of attendant males accompanying mating pairs at Isla de Aves suggest that males were locally abundant during the observation period, and that the observed breeding females were unlikely to be experiencing mate limitation. These observations suggest that there was likely not a strongly female-biased OSR within the observed breeding aggregation, which is an encouraging finding in the context of climate warming and the threat of feminisation in sea turtles (Fuentes et al. 2023). To date, however, no estimates based on nest temperatures, incubation conditions, or other hatchling sex-ratio studies have been conducted; these would be valuable in the future to assess whether the Isla de Aves population is showing signs of feminisation.

The estimates of the relative abundance of males associated with mating pairs that we made and found in the literature may not directly reflect operational sex ratios (OSR) in the areas where observations were made. In captive green turtles, Ye et al. (2020) describe how breeding females are actively pursued, with several males flocking to breeding females simultaneously while ignoring non-receptive females. If this pattern of males targeting only receptive females holds in wild populations, then some females breeding in any given year may no longer be receptive since they have already mated, and males may not pursue them, leaving males to aggregate around the smaller remaining number of receptive females. Nevertheless, attendant male occurrence still provides evidence that receptive females are not having difficulty finding mates. It should be noted that at nesting beaches around the world where egg fertility has been reported accurately, generally very high fertility is

recorded, indicating that enough males are usually present to fertilize females (e.g. Booth et al. 2021; Lavigne et al. 2025; Phillott and Godfrey 2020). In captive green turtles, Wood and Wood (1980) describe the period of female receptivity to males as lasting only 2–4 days. This observation was made in a small pond with high male-female encounter rates. It might be expected that in wild sea turtles, this period of female receptivity will vary with male encounter rates, and females might remain receptive until mating occurs. Given the high number of males we observed at Isla de Aves, it might be expected that this is a site where the period of female receptivity is relatively short. However, this should be treated as a hypothesis rather than a conclusion, because female receptivity in the wild may vary with mating history, local density, arrival timing, and the probability of encountering males.

Another possibility is that most breeding females had not yet arrived during our study on Isla de Aves, transitorily inflating the % of pairs observed with attendant males. Earlier male arrival at the start of the breeding season has been noted in loggerhead turtles in Greece, where early in the season there may be nearly 100% males before the arrival of breeding females, producing strong seasonal shifts in the observed sex ratio at a breeding area (Hays et al. 2010; Schofield et al. 2013). However, our observations were conducted over a 17-day period, during which the proportion of attendant males remained consistently high, suggesting that receptive females and multiple reproductive males were already present in the study area throughout the observation period. In contrast, if a large number of breeding females had been arriving within our 17-day observation window, we might have expected the proportion of mating pairs with attendant males to decline over time, which was not the case. However, seasonal patterns may differ among populations. For example, at Colola, Delgado-Trejo et al. (2025) reported monthly variation in the OSR, with values increasing from September to December, indicating that male and female availability may change in different ways depending on local breeding phenology. Therefore, we appreciate that observations across many weeks or months are ideal to assess changes in the relative numbers of breeding males and females, reflecting their different arrival and departure times from the breeding area (Hays et al. 2010; Schofield et al. 2013, 2017; Delgado-Trejo et al. 2025).

Observations at Isla de Aves showed that attendant males were present throughout the day. Captive studies with green turtles have also shown that mating may occur during both the day and night (Ye et al. 2020), so it is perhaps not surprising that attendant males were present throughout the daytime observation period at Isla de Aves. These observations raise the question of when breeding male turtles might be resting. Outside of the breeding season, data from depth

loggers suggests that green and other sea turtle species engage in regular benthic resting at night, with very consistent U-shaped dives, both in terms of depth and duration (e.g. Houghton et al. 2002; Hays et al. 2004). Comparable studies on males during the mating season could reveal whether males rest at night, alternate between short resting bouts and active searching, or show diel shifts in courtship and competitive behaviour. For both males and female sea turtles, a useful avenue to explore diel activity patterns in the breeding season would be the deployment of depth loggers or accelerometers, ideally combined with drones, shore-based observations, photo-identification or acoustic/satellite tracking, mirroring approaches used with success elsewhere (e.g. Schofield et al. 2017; Staines et al. 2022).

Attendant males as indicators of breeding male availability

We suggest that observations of mating pairs with attendant males can form a useful part of the general toolkit of methods available to study breeding male sea turtles. It may be possible to develop single metrics for the abundance of attendant males, for example combining the % pairs with attendant males with how many males are attending. For example, on Isla de Aves we observed 665 mating-pairs and they had a total of 754 attendant males, so the mean number of attendant males per mating pair was $754/665 = 1.13$. This mean number of attendant males per mating pair might be a useful quantitative index for future comparisons, for example within the same site across seasons and years. We appreciate that not all approaches for studying breeding males will be feasible to implement at all breeding sites. One caveat of the approach of recording the presence of attendant males is that observations are generally restricted to shallow water, close to shore, even though mating can also occur far from land (e.g. Lee et al. 2007). For example, counts of mating pairs of green turtles at Ascension Island are relatively easy to make from the shore due to an abundance of turtles in relatively calm water close to land (Godley et al. 2002). At other sites turtles may be at a lower density, further from shore and in rougher water, making direct observations far more difficult, such as in the Chagos Archipelago. Likewise, drones may be highly effective in clear, shallow, nearshore breeding areas, as shown by Schofield et al. (2017) and Staines et al. (2022), but may be less useful where water turbidity, depth, weather, distance from shore or local regulations limit visibility and survey effort. Another caveat of observing mating pairs is that receptive females might remain unmated and therefore undetected. Observations of attendant males may complement other approaches that may reveal the relative abundance of males. For example, multiple paternity

within clutches indicates that females encounter and mate with more than one male (Lee et al. 2018; Hays et al. 2023).

To date, when attendant males are observed close to mating pairs, these observations have often gone unreported or considered anecdotal or unimportant. We highlight how reporting these observations in a systematic manner, such as through the proportion of mating pairs with and without attendant males, may provide a useful index of the relative abundance of breeding males across different study sites and hence may help triage where breeding males are scarce. Long-term studies are particularly important as sex ratios are expected to change (e.g. Laloë et al. 2024). For example, male attendance observed presently reflects hatchling sex ratios produced in the past when conditions may have been cooler. Although our sampling period of 17 days provided useful information, longer-term studies of attendant males at individual sites across many years, might have utility to identify long-term trends in the relative abundance of males in the face of climate warming. It should be noted that the relationship between female reproduction and adult sex ratio may be highly nonlinear. For example, it may only be when a threshold for low male abundance is reached, that there is a sudden drop in female mating success (e.g. see Hays et al. 2023).

Observing attendant males may supplement other approaches for assessing male abundance. When attendant males are frequently observed, there may also be a high incidence of multiple paternity within clutches, since the incidence of multiple paternity seems related to male-female encounter rates (Lee et al. 2018), and hatchling sex ratios may not be massively female biased (Hays et al. 2023). Indeed, our preliminary consideration of this second prediction suggested that reports of attendant males are at sites that do not have extremely high (e.g. > 90%) female-biased hatchling sex ratios. Given the low number of observations to date, this pattern should be treated as a testable hypothesis, also because attendant male prevalence may depend on local turtle density, female receptivity, mating-site structure, male arrival timing, observer detectability, and the spatial scale over which mating activity is recorded. Clearly, expanding studies of the incidence of attendant males to other sites would help test these predictions in more detail.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-026-04959-7>.

Acknowledgements We thank the Ministerio del Poder Popular para el Ambiente (MINPPA) for issuing the required research permits (#41–0495, #2325, and #2012) and for its long-term collaboration in sea turtle conservation at Isla de Aves. We are also grateful to the Instituto Venezolano de Investigaciones Científicas (IVIC) and its Centro de Estudios Avanzados (CEA) for their institutional support. We acknowledge the Armada Nacional Bolivariana (ANB) for providing logistical support during the field activities, and the personnel of the BCNASBO

for their kindness and continued support. We also extend our sincere thanks to Javier Medina for his valuable support and collaboration. We thank the many observers for reporting incidental sightings of mating green turtles in the Chagos Archipelago, especially Yolanda Barnes, Marcus Barrett, Tom Franklin, Antenor Guzman, Jeanne Mortimer, Malcolm Nicoll, Carina Rees and Holly Stokes.

Author contributions M. (A) G-C led all fieldwork in Isla de Aves, along with data curation validation and visualization. M.A.G-C and K.R-C conducted funding acquisition, experimental design, project administration & supervision, and editing. V. F-R. contributed to experimental design, data validation, data curation, and fieldwork in Isla de Aves. J.B contributed to experimental design and fieldwork in Isla de Aves. R.S.B. contributed to data curation and editing. N.E and G. C.H. completed all fieldwork in the Chagos Archipelago. M.A.G-C compiled the Isla de Aves data and N.E. the Chagos Archipelago data. G.C.H. conceived the manuscript and led data analysis and writing with contributions from all authors.

Funding This research was supported by the Venezuelan Institute of Scientific Research (IVIC), Precomprimido CA, Helmerich Payne of Venezuela, and The Boyd Lyon Sea Turtle Fund, which provided research funds and equipment. The contributions from Precomprimido CA and Helmerich Payne of Venezuela were made as part of the LOCTI (Ley Orgánica de Ciencia, Tecnología e Innovación) program. G.C.H. and N.E. were supported by the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science (Grant numbers BPMS-2017-4 and BPMS-820633).

Data availability The dataset supporting this study is stored in the electronic supplementary material and the main text.

Declarations

Competing interests No conflicts of interest or competing interests to declare.

Ethical approval The animal study on Isla de Aves was approved by the Ministerio del Poder Popular para el Ambiente (permits #41–0495), which was the competent authority in Venezuela at the time. All research activities were carried out in compliance with the national regulations in force in Venezuela and in accordance with international standards of animal welfare. The study was conducted in accordance with the local legislation and institutional requirements. The research in the Chagos Archipelago was approved by the Swansea University (SU-Ethics-Student-250618/917; SU-Ethics-Staff-100619/152; IP-2021-01) and Deakin University Ethics Committees and the British Indian Ocean Territory (BIOT) Administration of the UK Foreign, Commonwealth and Development Office (permits 0002SE14, 0007SE15, 0001SE16, 0002SE17, 0009SE18, 0004SE19, 0006SE19, 0001SE22, 0007SE23, 0007SE24) and complied with all relevant local and national legislation.

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