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Male scarcity in sea turtles is obscured by optimistic artefacts and misinterpretations of breeding sex ratios and multiple paternity

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ABSTRACT

Temperature-dependent sex determination could make sea turtles vulnerable to climate warming, which is expected to generate increasingly female-biased primary sex ratios, potentially leading to male scarcity and reduced fertility. Optimistic interpretations of breeding sex ratios (BSR) > 1, estimated via genetic analyses, have suggested that male breeding frequency and polygyny may compensate for this female bias. Here, simulations were used to examine how operational sex ratio (OSR), polygyny, and polyandry interact to determine breeding outcomes, and how sampling designs affect inference. Virtual populations were parameterised by the number of reproductive females, OSR, and the maximum number of matings per male. Random mating was simulated under empirically supported patterns in which males do not preferentially mate with unmated females and mated females do not refuse additional copulations. Results show that when male scarcity leads to stochastic exclusion of some females from reproduction, BSR inevitably exceeds OSR—not because males are abundant, but because unfertilised females are excluded from BSR by definition. Furthermore, the partial and asymmetric sampling inherent to genetic studies of clutches produces unavoidable overestimation of BSR and underestimation of polygyny. In contrast, polyandry—and its simplified metric, multiple paternity—can be reliably estimated through sampling. *Re*-evaluation of published studies suggests that low multiple-paternity incidence reflects current male scarcity rather than an early warning, despite apparently favourable BSR estimates. BSR and current egg fertility metrics are insufficient to assess male scarcity in sea turtles and should be abandoned in favour of multiple paternity for conservation assessments under climate change.

1. Introduction

Temperature-dependent sex determination (TSD) could represent a major conservation vulnerability for sea turtles in the context of global climate change, because increasing sand temperatures are expected to lead to more female-biased primary sex ratios (PSR) (Mrosovsky et al., 1984; Mrosovsky and Provancha, 1989). In a context where female-biased PSR appear to be common across sea turtle populations (Hays et al., 2014; Laloë et al., 2024), further warming could result in a depletion of males (Mrosovsky and Provancha, 1992), with potentially serious demographic consequences such as reduced natality due to egg infertility (Hays et al., 2022).

However, it has been speculated that some biological features of sea turtles may, at least in part, compensate for female-biased hatchling production. Two such traits are differential remigration interval, or breeding periodicity, and polygyny, i.e. the capacity of a male to mate with more than one female (Hays et al., 2022). Remigration interval, whereby males typically breed more frequently than females, is thought to promote more balanced operational sex ratios (OSR) (Hays et al., 2010; Stewart and Dutton, 2014), defined as the ratio of sexually active males to fertilizable females in a given breeding season (Emlen and Oring, 1977). Polygyny may further mitigate male scarcity by increasing the reproductive opportunities for individual females and ensuring the fertilization of their clutches (Hays et al., 2022).

Monitoring potential trends that could lead to male depletion is therefore of high conservation interest, yet it remains challenging. OSR is particularly difficult to estimate in wild sea turtle populations due to the cryptic nature of male behaviour and the logistical challenges of observing mating events (Schofield et al., 2017; Staines et al., 2022). On the other hand, breeding sex ratios (BSR) - the ratio of males to females that actually contribute genetically to the next generation (Arnold and Duvall, 1994), i.e. excluding the adults that for any reason do not reproduce successfully - can be theoretically inferred from genetic analyses of offspring, and has been considered as a more accessible proxy

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for studying the reproductive balance between sexes (Wright et al., 2012; Stewart and Dutton, 2014). It is worth noting that some confusion exists in the sea turtle literature regarding OSR and BSR, with the two terms sometimes being used interchangeably (e.g., Hays et al., 2010; Lasala et al., 2013; Shertzer et al., 2018) despite reflecting distinct biological scales.

Several studies have reported BSR values greater than one, interpreting this as equivalent to OSR (Lasala et al., 2013; Lasala et al., 2018; Hatase et al., 2024; Silver-Gorges et al., 2024; Amorim et al., 2025) and therefore as an evidence that sea turtle reproductive traits— specifically higher male breeding frequency relative to females (i.e. shorter male remigration intervals)—may compensate for highly female-biased primary sex ratios and help maintain demographic balance (e.g., Wright et al., 2012; Stewart and Dutton, 2014; Kaska et al., 2025). Such findings have been taken as a source of cautious optimism regarding the resilience of sea turtle populations to climate change.

Nevertheless, no empirical or theoretical validation has yet established that comparisons between BSR and PSR can reliably inform assessments of population vulnerability or adaptive capacity. For instance, by definition, the BSR accounts only for successful breeders and is therefore not really suitable for assessing whether some females remain unfertilised due to an insufficient number of males.

The incidence of multiple paternity, a simplified proxy for polyandry defined as the proportion of clutches that have at least two fathers, has been proposed as an alternative indicator of male scarcity (Hays et al., 2022; Hays et al., 2023). Relatively low values at certain nesting sites, compared with others of the same species, have been interpreted as a potential early warning of future fertility constraints, and a value of zero has been proposed as a signal of imminent infertility risk (Hays et al., 2023). However, so far no empirical or theoretical support of this prediction has been provided.

Finally, the most direct approach would be to detect and monitor the most concerning consequence of male depletion, namely infertility, quantified through egg infertility (the proportion of eggs within a clutch that are unfertilised) and hatching success (the proportion of eggs within a clutch that hatch) (Maurer et al., 2021; Hays et al., 2022). However, to date no such evidence has been reported, even at nesting sites where extremely female-biased sex ratios are suspected (Hays et al., 2022).

Moreover, the potential effects of sampling design on estimation of BSR and other potential indicators of male scarcity have not been considered to date. In such studies, sampling is inherently asymmetric, as the effective sampling unit is the female—through her clutch—rather than the male. This asymmetry, particularly in the context of behavioural traits such as polyandry and polygyny, might affect BSR estimates when only a subset of the actual breeding population is represented in the sample. Although Quennessen et al. (2025) investigated the level of sampling, within and among clutches, needed for identifying most of the breeding males, that exercise provided no information on the effect of sampling for estimating BSR or assessing possible cases of infertility due to male scarcity.

Accordingly, this study addresses four main objectives. First, the interdependencies among sea turtle reproductive behavioural traits—specifically polyandry (including multiple paternity) and polygyny—and sex ratios (OSR and BSR) are examined to clarify expected patterns under different scenarios. Second, the influence of sampling design on the estimation of these sex ratios and associated behavioural variables is evaluated. Third, currently available data are interpreted within this conceptual framework, with emphasis on the conservation implications of accurately understanding reproductive dynamics in sea turtles. Finally, guidance is provided on the most appropriate approaches for assessing potential cases of male scarcity in sea turtle populations.

2. Materials and methods

2.1. Assumptions on mating behaviour and implications for infertility risk under male scarcity

On the basis of the available knowledge, sea turtle males and females are here assumed to exhibit different mating behaviours. Males are assumed to actively search for females and multiple matings, even visiting multiple breeding grounds (Wright et al., 2012; Casale et al., 2013). Females are generally less active than males, would not actively search for males, apart frequenting breeding areas. These assumptions are supported by direct observations of behaviour at breeding areas (Schofield et al., 2006; Papafitsoros et al., 2022) and by the fact that males are not selective and are even attracted by turtle-shaped decoys, that were used by turtle fishers to capture large numbers of males (Rebel, 1974). It is further assumed that the number of matings a male can perform is not unlimited but constrained by intrinsic male characteristics (e.g. energetic reserves). Assuming random mating, under conditions of a low male-to-female operational sex ratio (OSR), the probability that a male mates repeatedly with the same female is expected to be low, and the number of multiple matings of a male (MM) therefore tends to correspond to polygyny. Based on available evidence (Sakaoka et al., 2013), females are assumed to be unable to store sperm from previous breeding seasons; therefore their clutches can be fertilised only through matings occurring within the current breeding season. Females are also assumed to mate with multiple males and not to refuse additional copulations after the first mating, as indicated by documented cases of high polyandry (Table 1). The number of matings is expected to depend primarily on the frequency of male–female encounters, as demonstrated by Lee et al. (2018).

These assumptions have important implications for estimating the number of males required to fertilise all females within a population. In a hypothetical scenario in which males preferentially mate with unmated females before mating with females that have already mated (i.e. if previously mated females refuse subsequent copulations or if males are less attracted by females that have already mated), all females could mate and be fertilised when the number of males equals Females/MM. However, this scenario is not supported by current knowledge. Instead, under the assumptions outlined above — random mating and the absence of mate selectivity in both males and females — some females are expected to mate with more males than others. Consequently more males than Females/MM are required to fertilise all females. Even more males would be required in case the distribution of males and females do not perfectly overlaps, because males would mainly focus on a subgroup of females.

2.2. Relationships between reproductive behaviour (polyandry, polygyny) and sex ratios (OSR, BSR)

Virtual sea turtle populations were simulated in R (R Development Core Team, 2025) with the aim of providing insights into the general influence of individual variables on one another. The simulations were not intended to derive exact quantitative relationships applicable as conversion factors for real populations.

Each virtual population of adult turtles potentially reproducing in a given year was constructed based on three independent variables: the number of potentially reproductive females in a year (F); the operational sex ratio (OSR, defined as the proportion of adult males relative to adult females potentially reproducing in a given year); and the number of matings performed by each male (MM). A range of values for these three variables was explored to assess their effects on the derived variables described below. MM was capped at a maximum value of six, consistent with the maximum number of females reported to mate with a single male in the literature (Hays et al., 2022; Heppell et al., 2022).

The number of breeding males in a given year was then calculated as $M = F \times OSR$, assuming that none of these males fails to mate. For each

Table 1
Incidence of multiple paternity (MP; proportion of clutches with more than one father), polygyny (PG; number of females mating with the same male), polyandry (PA; number of males mating with the same female) and breeding sex ratio (ratio of breeding males: females) obtained through genetic data for different sea turtle species and nesting sites. <20: all or part of the clutches with less than 20 samples. MP obtained from a minimum of 20 sample per clutch are highlighted in bold. In some cases where it was possible, values were here re-calculated from a subsample with more than 20 samples per clutch.

Species/Nesting site	Country	MP	PG	PA	BSR (M:F)	N females (clutches)	N samples/ clutch	Source
Caretta caretta								
Zakynthos	Greece	0.93		3.60		15	<20	Zbinden et al. (2007)
		1.00		3.77		13	≥20	
Dalyan	Turkey	0.56	1.00	1.98	2.00	41	<20	Kaska et al. (2025)
St. George Island	Florida	0.18	1.00	1.24	1.30	33	<20	Silver-Gorges et al. (2024)
		0.17	1.00	1.17		12	≥20	
Melbourne beach	Florida	0.31		1.40		70	<20	Moore and Ball (2002)
Sanibel Island	Florida	0.25	1.00	1.56	1.46	16	<20	Lasala et al. (2020)
Sanibel Island	Florida	0.70	1.00	2.51	2.47	51	<20	Lasala et al. (2018)
Wassaw Island	Georgia, USA	0.75	1.00	2.65	2.71	72	<20	Lasala et al. (2013)
Povoação Beach	Brazil	0.72	1.09	2.04	2.09	42	<20	Amorim et al. (2025)
Mon Repos Beach	Queensland	**0.33**				24	≥20	Harry and Briscoe (1988)
Mon Repos Beach	Queensland	0.66		2.03	2.03	29	<20	Howe et al. (2018)
		0.80		2.00		20	≥20	
Dirk Hartog Island	Western Australia	**0.36**			1.14	14	≥20	Tedeschi et al. (2014)
Yakushima Island	Japan	0.19	1.00	1.30	1.31	26	<20	Hatase et al. (2024)
Chelonia mydas								
Alagadi	Cyprus	**0.30**	1.00	1.55	1.40	20	≥20	Wright et al. (2012)
Ascension Island		**0.61**				18	≥20	Lee and Hays (2004)
Tortuguero	Costa Rica	0.92	1.00	2.92	2.92	12	20	Alfaro-Núïez et al. (2015)
Great Barrier Reef	Australia	**0.09**				22	≥20	Fitzsimmons (1998)
Sabah Turtle Islands Park	Malaysia	0.71				14	<20	Joseph et al. (2017)
		0.64				11	≥20	
Redang Island, Terengganu	Malaysia	0.36				22	<20	Joseph et al. (2017)
		0.30				20	≥20	
Lepidochelys olivacea								
Playa Hermosa	Costa Rica	**0.31**		1.46		13	≥20	Jensen et al. (2006)
Ostional	Costa Rica	0.92		2.85		13	<20	Jensen et al. (2006)
		0.91		2.82		11	≥20	
Galibi	Suriname	0.20				10	<20	Hoekert et al. (2002)
		0.22				9	≥20	
Playa de Escobilla Sanctuary	Oaxaca, Mexico	0.60	1.00	3.07	3.07	15	<20	González-Cortés et al. (2021)
		0.62				13	≥20	
Lepidochelys kempii								
Rancho Nuevo, Tamaulipas	Mexico	0.58				26	<20	Kichler et al. (1999)
Eretmochelys imbricata								
Gulisaan	Sabah, Malaysia	0.20	1.00	1.20	1.20	10	<20	Joseph and Shaw (2011)
		0.22				9	≥20	
Cousine Island	Seychelles	0.09	1.00	1.09	1.09	43	<20	Phillips et al. (2013)
Dermochelys coriacea								
St Croix	US Virgin Islands	0.24		1.31		55	<20	Stewart and Dutton (2014)
			1.17		1.02	46	<20	
Playa Grande	Costa Rica	**0.1–0.3**				20	≥20	Crim et al. (2002)

male, a random group of MM females was sampled from the pool of F females, allowing the same female to be selected more than once. This approach assumes that the number of males a female mates with depends on male–female encounter rates and that females do not refuse copulations during the mating period (see above). It is further assumed that males and females are fully spatially overlapping, such that each male has an equal probability of encountering any female in the population.

Based on these pairings, a matrix of individual males × females was constructed, and the number of females that actually mated (Fm) was calculated by counting how many females of the matrix mated with at least one male. Then, the proportion of breeding females relative to the total number of females available for reproduction (Fm/F) was also calculated. The sex ratio of actual breeders (BSR, breeding sex ratio) was then calculated as M/Fm. For each individual turtle, polygyny (defined as the number of individual females mating with each male) and polyandry (defined as the number of individual males mating with each female) were calculated, together with their respective population-level averages.

2.3. Effects of sampling on sex-ratio and behavioural estimates

Sex-ratio and behavioural estimates may be affected by sampling at two different levels: the clutch (i.e. the proportion of eggs sampled from a clutch) and the population nesting site (i.e. the proportion of clutches sampled from the total laid).

Regarding sampling at the clutch level, the proportion of eggs sampled from a clutch may affect the capacity of detection of multiple paternity (defined as >1 father). To detect multiple paternity sampling design should be able to detect at least the second father in order of number of eggs fathered. This represents a simplified problem compared with ascertaining the total number of fathers (Quennessen et al., 2025).

The minimum number of eggs that must be sampled from a clutch to detect the presence of a second father was estimated, given that this father contributed a known proportion of offspring. The calculation was based on the hypergeometric distribution, which describes sampling without replacement from a finite population. For a clutch of fixed size ($N = 100$) eggs, we assumed that a proportion (p) of eggs was sired by the least-contributing father, corresponding to K = pN eggs (rounded to the nearest integer). The probability of detecting at least one egg from this father was then evaluated when n eggs were randomly sampled from the clutch without replacement. The probability P of detecting at least one egg from the second father is:

$$P = 1 - \frac{\binom{N-K}{n}}{\binom{N}{n}}$$

For a specified confidence level $\alpha = 0.95$, the minimum sample size n was defined as the smallest integer for which $P \geq \alpha$. This value was obtained by iteratively increasing n from 1 to N and identifying the first value meeting the confidence criterion. The procedure was repeated across a range of values for the proportional contribution of the least father (p = 0.01–0.50), generating a relationship between paternal contribution and the minimum number of eggs required to reliably detect multiple paternity. Results were plotted by the function ggplot2 in R.

Regarding sampling at the population level, the effect of the proportion of females sampled from a population nesting site was investigated through the virtual populations simulated as above. Twelve sampling levels were simulated: 0.01, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0. Observed BSR, polygyny and polyandry were calculated from the sample of observed females (clutches).

3. Results

3.1. Relationships between reproductive behaviour (polyandry, polygyny) and sex ratios (OSR, BSR)

In several scenarios with different OSR and polygyny given values, a subset of females in the virtual populations resulted not to mate (Fig. S1), and relatively balanced OSR values together with relatively high polygyny were required for nearly all females to mate (Fig. S2). For a given OSR, as the proportion of unmated females increased as a consequence of decreasing polygyny, BSR increased, because the number of breeding males remained constant while the number of breeding females declined (Fig. S3). As OSR decreased, BSR did not decline at the same rate and progressively exceeded OSR (BSR > OSR) as a consequence of non-breeding (unmated) females not being accounted for in BSR. This effect was exacerbated under lower polygyny values (Fig. 1). Polyandry approximated polygyny when OSR = 1 and was lower or higher than polygyny when OSR was lower or higher than 1, respectively (Fig. S4). High proportions of mated females were associated with relatively high levels of polyandry (Fig. S5) and its simplified outcome, multiple paternity (Fig. 2).

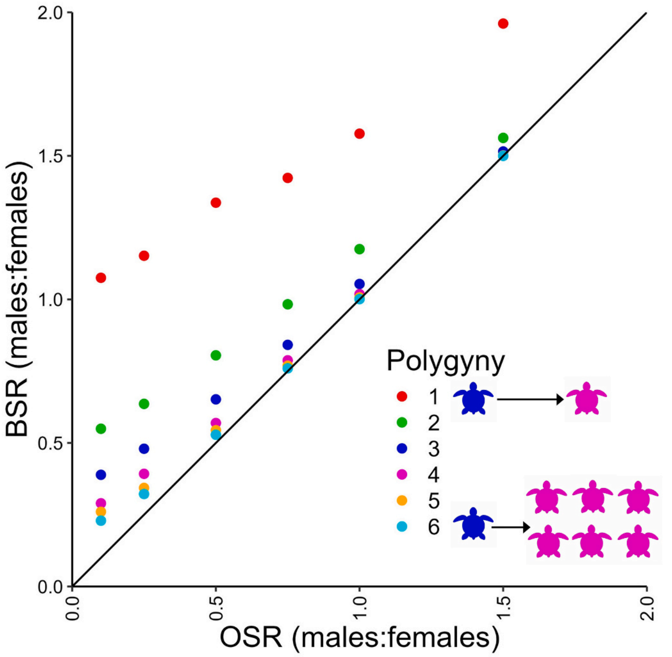

Fig. 1. Breeding sea ratio (BSR, males: females ratio) as a function of operational sex ratio (OSR, males: females) and polygyny (number of females mating with each male), simulated in a virtual population of 1000 sea turtle females. If all females reproduced, BSR should equal OSR (diagonal line). Color of points represent different levels of polygyny.

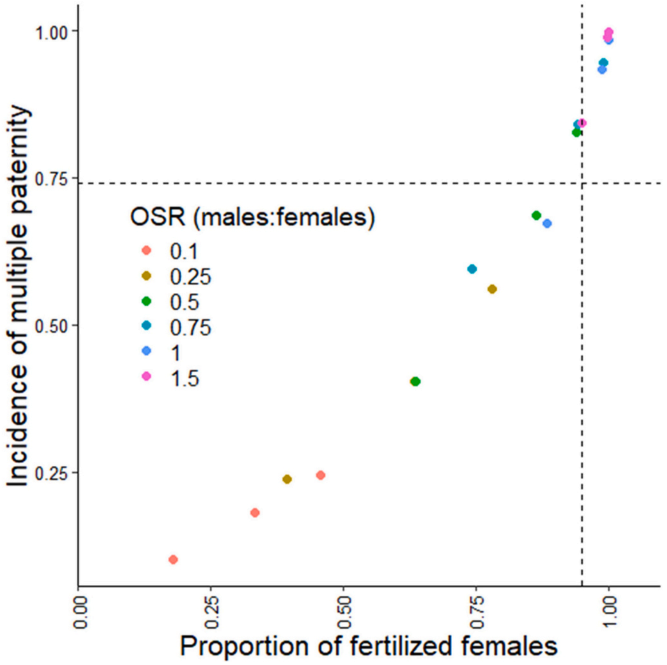

Fig. 2. Relationship between the incidence of multiple paternity (proportion of females that mated with more than one male) and proportion of fertilised females, resulting from different operational sex ratios (OSR, males: females ratio) and polygyny values (number of females mating with each male), simulated in a virtual population of 1000 sea turtle females. For each OSR value (color) three cases of different polygyny values (2,4,6) are shown. The vertical dashed line indicates where 95% of females are fertilised. Horizontal dashed line: incidence of normal multiple paternity (MP = 0.74) estimated by Hays et al. (2023) based on PSR values.

3.2. Effects of sampling on sex-ratio and behavioural estimates

Regarding clutch-level sampling, based on a hypergeometric probability framework, a sample of 20 eggs/hatchlings would be sufficient to detect a second father when the first father has an occurrence of 0.87 (see Fig. S6 for the relationship between the number of hatchlings sampled from a clutch of 100 eggs and the percentage of eggs sired by the father to be detected).

Regarding population-level sampling (defined as the proportion of sampled clutches relative to the total number laid), any degree of sampling resulted in an overestimation of BSR (observed BSR > BSR; Fig. 3)

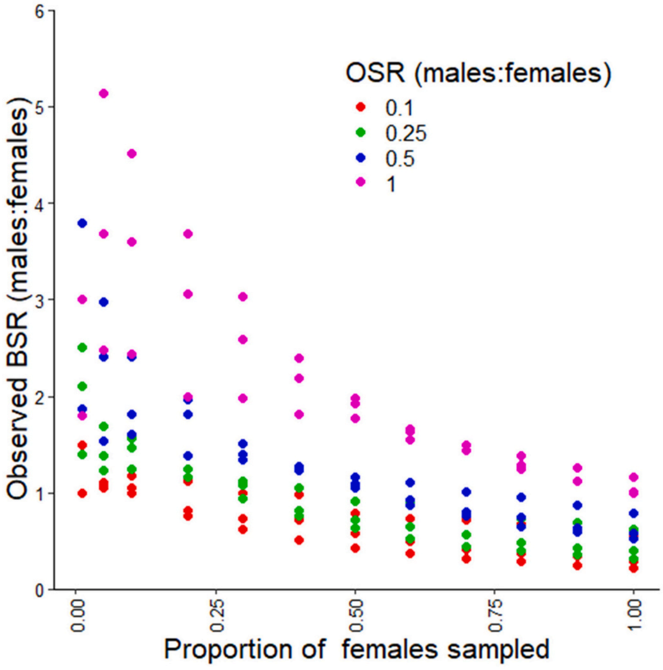

Fig. 3. Observed breeding sea ratio (BSR, males: females) as a function of sampling effort (proportion of sea turtle female sampled) and of operational sex ratios (OSR, males: females) and polygyny (number of females mating with each male), simulated in a virtual population of 1000 sea turtle females. Four OSR values (color) and three polygyny values (2,4,6) for each OSR value (shown as points of the same OSR color) were simulated.

and an underestimation of PG (observed PG < PG; Fig. 4), with the magnitude of these effects increasing as sampling intensity decreased. At very low sampling levels the observed polygyny tended towards 1. The effect of sampling on the observed BSR was similar across female populations of different sizes (Fig. S7). Sampling did not affect the observed polyandry, which approximated the real polyandry across all sampling scenarios except at very low absolute sample size, and varied only as a function of polygyny and OSR (Fig. 5).

4. Discussion

4.1. *Relationships between reproductive behaviour (polyandry, polygyny) and sex ratios (OSR, BSR)*

This study simulated virtual sea turtle populations, representing a simplification of real populations in which additional biological and environmental factors may influence reproductive dynamics. Notwithstanding these limitations, these simplified models are informative with respect to fundamental patterns that are also expected to apply to natural populations.

Within a single breeding season, OSR and polygyny can be considered as the fundamental biological variables determining the remaining reproductive metrics (BSR and PA). OSR derives from the adult sex ratio and sex-specific remigration intervals (Hays et al., 2010; Stewart and Dutton, 2014), whereas polygyny depends on the capacity of males to perform a given number of matings. In practice, polygyny (PG) may be lower than the maximum number of matings per male if repeated matings occur with the same female. However, under low OSR conditions, this is unlikely.

In the unrealistic scenario in which males mate with all unmated females before mating with females that have already mated (i.e. if previously mated females refuse subsequent copulations), all females would mate when OSR × PG = 1. However, this scenario is not supported by current knowledge (see Assumptions in the Methods and references therein).

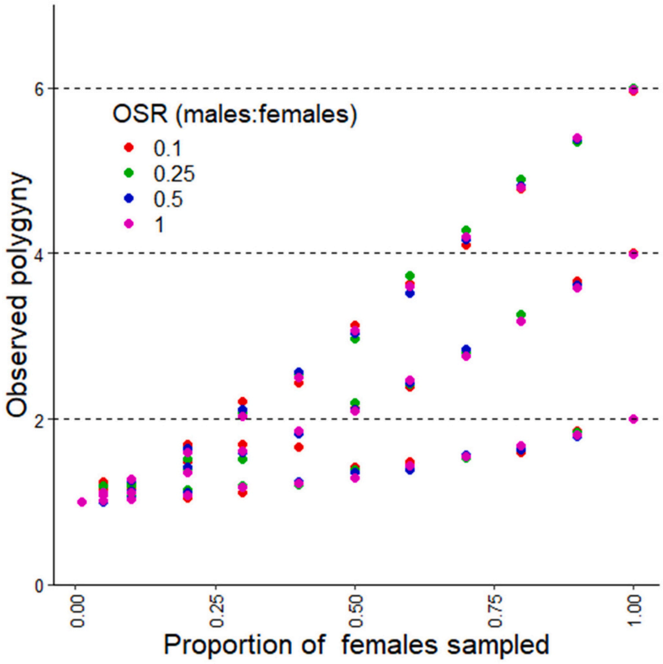

Fig. 4. Observed polygyny (number of females mating with each male) as a function of sampling effort (proportion of sea turtle female sampled) and of operational sex ratios (OSR, males: females) and real polygyny, simulated in a virtual population of 1000 sea turtle females. Four OSR values (color) and three real polygyny values (2,4,6) for each OSR value (shown as points of the same OSR color) were simulated. Horizontal dashed lines indicate the three real polygyny values.

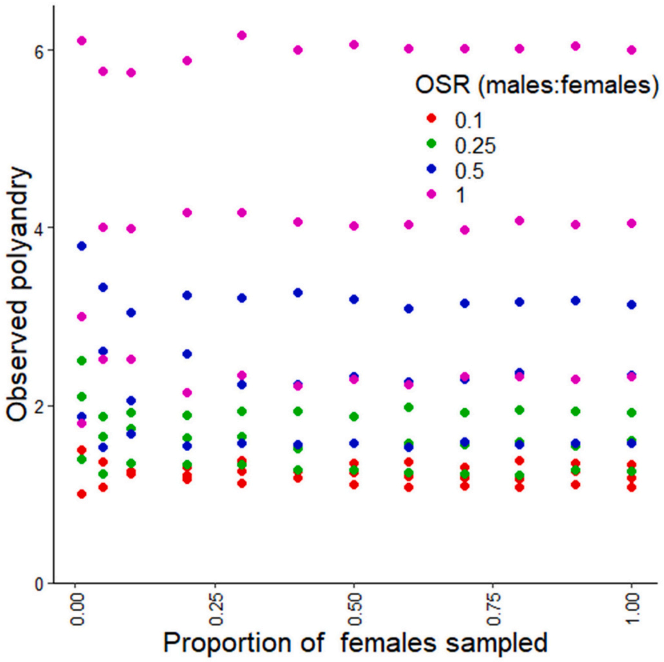

Fig. 5. Observed polyandry (number of males mating with each female) as a function of sampling effort (proportion of sea turtle female sampled) and of operational sex ratios (OSR, males: females) and polygyny (number of females mating with each male), simulated in a virtual population of 1000 sea turtle females. Four operational sex ratio values (OSR, males: females) (color) and three polygyny values (2,4,6) for each OSR value (shown as points of the same OSR color) were simulated.

In the more realistic scenario simulated in this study, in which males mate with females regardless of their prior mating status, some females may, by chance, attract disproportionate number of matings that are therefore unavailable to other females; consequently, all females would mate and be fertilised only at higher OSR or PG values ($\text{OSR} \times \text{PG} > 5$ in the simulations). If males mate repeatedly with the same female, even higher OSR or PG values would be required to fertilise all females. Consequently, unless previously mated females refuse additional copulations or unmated females solicit mating more readily that previously mated females, some females may remain unmated within a breeding season. Simulations indicate that this becomes increasingly likely when $\text{OSR} < 1$ and/or $\text{PG} < 5$. Because this study assumed random mate encounters, the resulting estimates may be conservative. If males instead encounter only a subset of females, the proportion of unfertilised females would increase as well as repeated matings with the same females, implying that the present results may underestimate the risk of female infertility.

When all potential breeders (males and females) reproduce, BSR equals OSR. Conversely, if some females fail to reproduce owing to male scarcity, BSR exceeds OSR. Thus, BSR combine the effects of OSR and female non-reproduction, with higher BSR values arising either from an increase in breeding males (higher OSR) or from an increase in unmated females. Consequently, high BSR values do not necessarily indicate high male availability and are not informative with respect to male limitation.

When nearly all females mate at least once, most females are expected to mate with more than one male. In the simulations, nearly all females mated at least once when more than 80% of females exhibited multiple paternity ($\text{MP} > 0.8$; Fig. 2).

The relationship between polyandry (PA) and PG is of particular interest because PA can be estimated relatively easily, whereas PG is more difficult to quantify directly (see the next section on the effect of sampling). $\text{PA} = \text{mates}/\text{F} = (\text{F} \times \text{OSR} \times \text{PG})/\text{F} = \text{OSR} \times \text{PG}$. This real PA, however, may include non-breeding females with $\text{PA} = 0$. Under conditions of male scarcity, where a fraction of females does not reproduce, the observed $\text{PA} = \text{BSR} \times \text{PG}$, where $\text{BSR} > \text{OSR}$. Therefore, in populations where BSR is assumed to be ≤ 1, the average observed PA can be used to infer a minimum value of the average PG.

4.2. *Effects of sampling on sex-ratio and behavioural estimates*

The results indicate that any degree of sampling introduces artefacts, leading to an overestimation of BSR (observed $\text{BSR} > \text{BSR}$) and an underestimation of polygyny (observed polygyny $<$ real polygyny). This arises because sampling is asymmetric and is conducted at the clutch (female) level: a clutch has exactly one mother but may have one or more fathers, and it is unlikely that all clutches sired by the same male are sampled. Consequently, BSR and polygyny cannot be estimated through partial sampling. These parameters could only be assessed by sampling all nesting females of a population, defined as a closed group of males and females breeding exclusively among themselves. Sampling only a subset of females, while males also mate with females outside the sampled group, does not allow estimation of BSR and PG (see Fig. 6 for a graphical explanation). Since males mate with females nesting across wide spatial areas (Hays et al., 2022), estimating BSR and polygyny becomes practically impossible. Only sampling intensity affects observed BSR and polygyny, not absolute population size, except in cases where both population size and sampling intensity are so low that the absolute number of sampled clutches is very small (<50–100 clutches), leading to additional sampling bias.

By contrast, polyandry can be estimated reliably through sampling, except at very low sample sizes, because polyandry is a female parameter. Observed polyandry is consistently higher than observed BSR because polyandry is calculated at the individual clutch level and does not account for males shared among different clutches. At low sampling intensity, observed polygyny tends towards 1, and consequently observed BSR converges towards observed polyandry. When observed polyandry >1, the number of males represented in the sample exceeds the number of females (clutches). This implies that if males are less numerous than females in the population ($\text{OSR} < 1$), the proportion of males sampled is higher than the proportion of females sampled.

It is important to note that the effects of sampling on the estimation of BSR, polygyny, and polyandry described above depend exclusively on the asymmetry of sampling at the female level through clutches, in a biological context in which each clutch has exactly one mother but may have one or more fathers. The assumptions underlying the simulations can affect only the magnitude of these effects, not their occurrence.

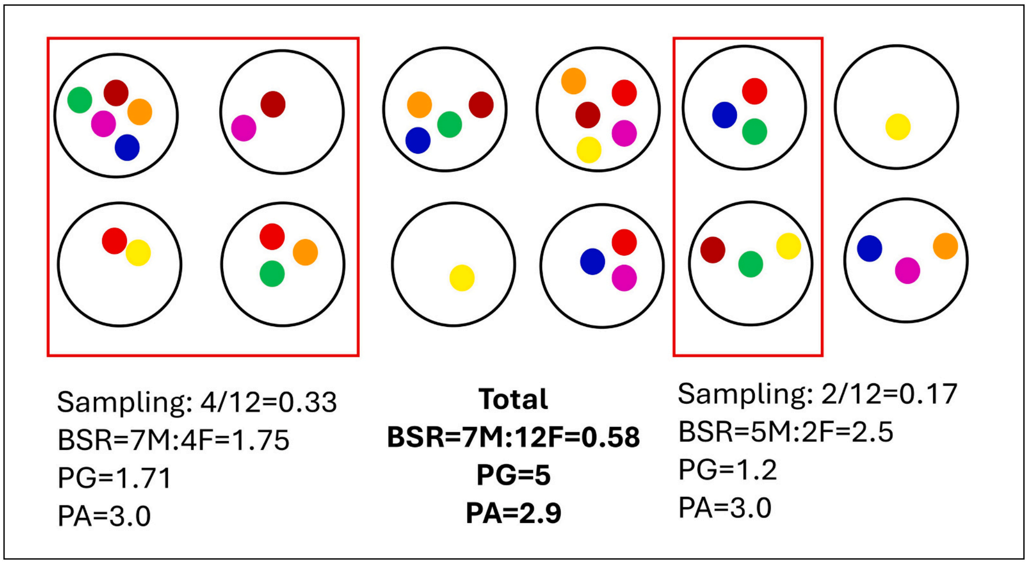

Fig. 6. Graphical representation of the effect of sampling on estimates of breeding sex ratio (BSR, M:F), polygyny (PG) and polyandry (PA). In this simplified example with a very low absolute sample size, the breeding population consists of 12 females and 7 males, with a $\text{BRS} = 0.58$. PG is 5 and the resulting PA is 2.9. Clutches (one per female) are represented by large empty circles and male contributions to individual clutches are represented by colored circles (each male has a different color). From this population, two samples of 4 and 2 clutches are taken, resulting in overestimates of BSR and underestimates of polygyny.

4.3. Approaches for assessing male limitation in sea turtle populations

Infertility resulting from insufficient male availability is the primary concern associated with climate-change–driven shifts in sex ratios, and declining egg fertility has been proposed as an indicator of male scarcity (Hays et al., 2022). However, this approach requires that egg infertility is both detectable and that infertile clutches are available for investigation.

Regarding detectability, two studies (Phillott and Godfrey, 2020; Lavigne et al., 2025) provided detailed analyses of the methods and challenges associated with assessing infertility, concluding that determining whether an egg clutch is infertile (i.e. no eggs have been fertilised) is not straightforward. Infertility is difficult to distinguish from early embryonic mortality, and reliable assessment requires advanced and preferably multiple diagnostic approaches. Phillott and Godfrey (2020) identified only six studies that applied appropriate methods, none of which reported infertility, and emphasized that "researchers must assume a greater burden of proof before designating unhatched eggs without signs of egg development as infertile". Similar limitations apply to the detection of partial infertility within clutches. For example, low hatching success observed at a major nesting site was attributed primarily to embryonic mortality rather than infertility (Bell et al., 2004).

Regarding availability, approaches based on infertility assessment implicitly assume that unmated females lay clutches in a manner comparable to mated females. This assumption is, at best, uncertain given current knowledge. Observations reported by Sakaoka et al. (2013) instead suggest that unmated females may avoid laying clutches of unfertilised eggs or may lay only a single clutch during the breeding season, rather than multiple clutches as is typical for sea turtles (Miller, 1997). Such a behaviour would be consistent with biological expectations, because the energetic cost of producing multiple clutches is substantial and unmated females would benefit from conserving energy; the first clutch may already be initiated during the mating period and therefore may no longer be avoidable. As a consequence, the proportion of unfertilised nests relative to the total number of nests may be much lower than the proportion of unmated females relative to the total number of females, thereby making the identification of non-hatching nests particularly difficult. Furthermore, depending on the monitoring programme, such non-hatching clutches may not be sampled for genetic analyses or might not be detected at all and not inventoried.

One empirically testable prediction of an increased proportion of unfertilised females is an apparent increase in the observed remigration interval, arising not from a true change in remigration behaviour but from an observational effect, whereby females present in the breeding area are not detected in years in which they are not fertilised. However, estimating remigration intervals is challenging (Casale and Ceriani, 2020) and detecting such a phenomenon would require an high level of sampling. Moreover, in case of a fraction of females that remain unfertilized, the abundance of females estimated from remigration intervals would represent an underestimate of the real population.

A necessary consequence of a declining proportion of males is a reduction in the average number of males with which each female mates. Accordingly, the present results suggest that polyandry represents a potentially useful indicator of male scarcity and it can be reliably estimated through sampling. However, observed polyandry is calculated exclusively from fertilised nests and therefore reflects only females that successfully reproduced, excluding potentially breeding females that did not reproduce owing to insufficient male availability. As a result, polyandry cannot provide a direct estimate of the proportion of unmated females, but only indirect indications. Accurate estimation of polyandry would require most or a large part of a clutch, depending on the number of fathers and the possible dominance (see also Quennessen et al., 2025), in order to detect all contributing fathers. This is often unfeasible and genetic sampling typically involves only a subset of eggs from each clutch. Multiple paternity (a simplified proxy for polyandry defined as the proportion of clutches fertilised by more than one male) may therefore represent a more practical indicator, because it requires detecting only the first two fathers and can thus be achieved with sampling of a subset of eggs. In this respect, the general guideline of sampling 20 eggs or hatchlings per clutch (Lasala et al., 2020) appears to be adequate for detecting multiple paternity, because it would detect the presence of at least one additional father when the combined contribution of all secondary fathers is as low as 13% of the clutch, i.e. even if the primary father fertilised up to 87% of the eggs. However, an alternative method has been recently developed that requires only one fresh egg to detect multiple paternity in a clutch, through genetic identification of sperm from different males in the perivitelline membrane (Shamblin et al., 2026).

Under scenarios in which infertility is negligible (i.e. almost all females are fertilised), most females are expected to mate with multiple males. Consequently, a warning threshold for multiple paternity should not be set at zero (i.e. all sampled females mating with a single male) (Hays et al., 2023), because any female producing a fertilised clutch must have mated with at least one male and the incidence of multiple paternity cannot be less than zero, at any level of infertility, because unfertilized females are just not sampled. A zero incidence of multiple paternity is instead expected when only a small fraction of females are fertilised, that is, when male scarcity is already severe. Hays et al. (2023) estimated, on the basis of primary sex ratios, that populations with negligible male scarcity would have an average incidence of multiple paternity of 0.74. Notably, this value closely approximates the threshold identified in the present simulations above which the majority ($\approx$95%) of females are fertilised (Fig. 2), and it may therefore represent a more appropriate warning threshold for real male scarcity and decreased female fertility, with values below 0.5 being particularly concerning. The latter consideration is based on simulations and should therefore be interpreted in light of the underlying assumptions and their associated uncertainties.

4.4. Reinterpreting existing data: Artefacts, misinterpretations, and male scarcity

Several studies have interpreted observed BSR values greater than 1 as an indicator of population health, in terms of a relatively high proportion of reproductive males (Wright et al., 2012; Lasala et al., 2013; Stewart and Dutton, 2014; Lasala et al., 2018; Hatase et al., 2024; Silver-Gorges et al., 2024; Amorim et al., 2025; Kaska et al., 2025) (Table 1). These BSR values have been assumed to correspond to OSR, which would be more balanced than PSR owing to higher breeding periodicity in males than in females (Hays et al., 2022). However, two observations raise substantial doubts about this interpretation. First, no BSR values below 1 have been reported to date (Table 1), despite suspected male scarcity in some populations. Second, only PG values equal or very close to 1 have been reported (Table 1), which is inconsistent with the well-documented polygynous behaviour of males, particularly in contexts where BSR is presumed to be high.

In contrast, the present results show that BSR > 1 and low polygyny values are expected artefacts of sampling only a small fraction of the population. This is inherent to BSR studies, in which only a subset of clutches (i.e. females) laid at a given nesting site is sampled, while the nesting site itself represents only a small portion of the overall breeding area shared by the pool of breeding males and females. Individual females may nest across spatial extents of hundreds to more than one thousand kilometres (Shamblin et al., 2021), and males may cover, on average, a wider nesting area than females because they can visit multiple nesting sites (Wright et al., 2012; Casale et al., 2013) or might mate opportunistically during migrations (FitzSimmons et al., 1997). For these considerations, substantial overestimation of BSR and underestimation of polygyny are likely to have occurred in those studies. With an observed polygyny $= 1$, the observed BSR of those studies was simply equal to polyandry, adding no information.

Moreover, BSR values exceeding OSR are expected whenever some females fail to reproduce owing to male scarcity—precisely the condition of interest in such studies—because BSR is calculated exclusively from fertilised females. Consequently, observed BSR values cannot be used to infer true BSR, OSR, or male availability more generally, and conclusions regarding population status drawn from observed BSR values are invalid and should be disregarded.

Known multiple paternity (MP) values span wide ranges even within the same species (Table 1), indicating that low MP values are not caused by some species-specific reproductive behavioural patterns, but are more likely due to population-specific OSRs. Importantly, the several low MP values observed so far, including very low values <0.5 (Table 1), were obtained using adequate sampling intensity ($\geq$20 hatchlings per clutch; Table 1) and therefore cannot be attributed to methodological artefacts. Interestingly, the highest MP ($MP = 1$) was reported from Zakynthos (Greece), a *Caretta caretta* breeding site, where a balanced OSR was estimated through direct observations (Schofield et al., 2017). Based on the arguments outlined in the previous section, populations exhibiting an incidence of multiple paternity below 0.74 (Hays et al., 2023), and especially those with values below 0.5, are instead suspected to already experience male scarcity, with a fraction of females remaining unfertilised during a breeding season. Such a pessimistic scenario could be mitigated only if unmated females could increase their chances to encounter a male or if mated females refused subsequent copulations, neither of which is supported by current empirical evidence.

4.5. Conclusions and recommendations

The present study shows that the most concerning effect of climate change on sea turtle populations—namely, altered sex ratios leading to an insufficient number of males to fertilise all females—is inherently elusive and cannot be assessed using current approaches such as estimation of BSR and may be insufficiently assessed through detection of infertile clutches. These approaches may generate false optimism as a result of methodological artefacts and are therefore not recommended. First, unfertilized females might remain undetected if they lay no clutches or fewer clutches with all unfertilized eggs, and are not considered by BSR which, by definition, considers only fertilised females. Second, BSR cannot be estimated through sampling, that generates uninformative overestimates due to sampling asymmetry (i.e., sampling females through their clutches).

On the contrary, multiple paternity regards females only and is not affected by the asymmetric sampling like BSR. Therefore, the incidence of multiple paternity (defined as the proportion of clutches fertilised by more than one male) represents an useful indirect indicator of male limitation and potential infertility at the population level. In a simulated scenario with negligible infertility and random mating, the majority of females are expected to mate with multiple males. On this basis, the present results suggest that some sea turtle populations may already have an insufficient number of males to fertilise all females available for reproduction, a hypothesis that requires further investigation.

CRediT authorship contribution statement

Paolo Casale: Writing – original draft, Visualization, Resources, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111925.

Data availability

No data was used for the research described in the article.

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