Climatic Change (2022) 175:15
https://doi.org/10.1007/s10584-022-03470-4

When population-advantageous primary sex ratios are female-biased: changing concepts to facilitate climate change management in sea turtles

Pilar Santidrián Tomillo[1,2]

Received: 2 March 2022 / Accepted: 8 December 2022 / Published online: 21 December 2022

Abstract

Sea turtles have temperature-dependent sex determination. Because females are produced at high temperatures, increasing global temperature may lead to population feminization. Primary sex ratios (PSR) of sea turtle hatchlings are naturally female-biased, but this translates into a more balanced operational sex ratio because male turtles reproduce more often than females. As a consequence, a balanced PSR and the temperature that produces it (pivotal temperature) are of limited use to guide climate mitigation management because an equal PSR may be demographically suboptimal. Here, I define population-advantageous primary sex ratios (PA-PSR) as the PSR that will tend to be in equilibrium in a population and that will result in balanced operational sex ratios; I then estimate PA-PSR for different reproductive frequencies (years elapsed between reproductive seasons) of adult female and male turtles. I also define population equilibrium temperature (PET) as the temperature that would result in the equilibrium PSR of hatchlings (i.e., PA-PSR). These concepts may help assess the influence of rising temperatures on populations, as they can better indicate if PSRs depart from those at equilibrium. I compared PA-PSR and beach PSR for two populations of sea turtles for which male and female remigration intervals were known and found that a mild or no feminization over the PA-PSR may be occurring. Because PSR varies inter-annually, and hatchlings coming from beaches of different thermal conditions could recruit to the same population, it is critical to estimate beach PSR at the right temporal and spatial scales. Climate mitigation strategies based on these concepts could provide better management guidance for conservation practitioners. Similar approaches could be considered for other female-biased species with temperature-dependent sex determination.

Keywords Population-advantageous sex ratios · Pivotal temperature · Population equilibrium temperature · TSD · Sea turtles · PA-PSR · New concepts · OSR

✉ Pilar Santidrián Tomillo
psantidrian@imedea.uib-csic.es

[1] Animal Demography and Ecology Unit, GEDA, Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Miquèl Marques 21, 01790 Esporles, Spain

[2] The Leatherback Trust, Goldring-Gund Marine Biology Station, Playa Grande, Costa Rica

1 Introduction

Natural populations tend to have balanced sex ratios (Fisher 1930). This seemingly universal principle has resulted in a whole body of literature discussing its meaning, likely advantages and exceptions (Hamilton 1967; Bull and Charnov 1988; Clutton-Brock 2017). Although balanced sex ratios are generally the rule, these may vary between life stages (Trivers and Willard 1973). The probability of reproduction seems to be the selective pressure for producing one sex over the other (Fisher 1930). Thus, balanced sex ratios are more likely to be found in adult reproductive individuals and may or may not be found in new-born ones (Trivers and Willard 1973; Jennions and Fromhage 2017).

In sea turtles, the primary sex ratio (PSR) of hatchlings is typically female-biased (Godfrey et al. 1996, 1999; Sieg et al. 2011) or highly female-biased (> 90% female, Broderick et al. 2000) (see Table 1 for a list of the acronyms used throughout the text). However, unbalanced PSR translates into a more balanced operational sex ratio that is normally close to the 1:1 Fisherian ratio (Hays et al. 2010; Wright et al. 2012; Stewart and Dutton 2014; Gaos et al. 2018). Because there is differential reproductive frequency by sex (i.e., males reproduce more often than females), an adult population that is female-biased can have equal numbers of reproductive individuals of each sex in a given year (Hays et al. 2010, 2014; Stewart and Dutton 2014).

Sea turtles have temperature-dependent sex determination (TSD) with the percentage of female hatchlings increasing along with incubation temperatures (Yntema and Mrosovsky 1980; Standora and Spotila 1985). The temperature that results in 50/50 PSR is known as the pivotal temperature (PT), and the range of temperatures over which both sexes are produced is the transitional range of temperatures (TRT) (Pieau and Mrosovsky 1991). Both PT and TRT are frequently used and have been helpful to compare TSD curves (i.e., population-specific curve that describes the relationship between mean temperature and sex ratio) of different populations of sea turtles (Chevalier et al. 1999; Wibbels et al. 2003; Bentley et al. 2020).

Because the percentage of female hatchlings in sea turtles increases at high temperatures and global air temperatures are rising, there is some concern about the potential over-feminization of populations (Jensen et al. 2018; Tanner et al. 2019). Highly skewed sex ratios from climate warming could reduce genetic diversity, the effective population size and increase the potential for inbreeding (Heppell et al. 2022; Maurer et al. 2021; Lockley and Eizaguirre 2021). On the other hand, high temperatures also increase egg failure and hatchling mortality, which are therefore threatened by climate change (Santidrián Tomillo et al. 2009; Valverde et al. 2010).

Management strategies, such as nest shading and irrigation, have been proposed to mitigate the impact of high temperatures on eggs and hatchlings and PSRs (Hill et al. 2015; Jourdan and Fuentes 2015). However, the need to artificially control PSRs is questionable unless the sex ratio of hatchlings reaches extremely female-biased levels (Patrício et al. 2021; Santidrián Tomillo et al. 2021). Although very useful concept, the pivotal temperature has sometimes been used to assess the occurrence of feminization (DeGregorio and Williard 2011; Tanabe et al. 2020). This could be problematic because PSRs in sea turtles are not normally balanced and female-biased sex ratios are most commonly found. At the same time, there is a knowledge gap because there have been no attempts to determine what PSR (i.e., female percentage) could be advantageous at the population level, around which a sex ratio equilibrium could be expected.

Table 1 Terms and acronyms used in this study and their definition

Acronym	Term	Definition
ASR	Adult sex ratio	Sex ratio of the adult individuals (reproductive and non-reproductive) in a population
OSR	Operational sex ratio	Sex ratio of reproductive individuals during a reproductive season
PA-PSR*	Population-advantageous primary sex ratio*	Primary sex ratio that will tend to be in equilibrium in a population because it results in a balanced OSR
PSR	Primary sex ratio	Sex ratio of newborn individuals or hatchlings
PET*	Population equilibrium temperature*	Temperature during development that results in the PA-PSR
PT	Pivotal temperature	Temperature during development that results in 50% female: 50% male offspring in species with TSD
RI	Remigration interval	Time elapsed between two reproductive seasons
TRT	Transitional range of temperatures	Range of temperatures over which both sexes are produced in species with TSD
TSD	Temperature-dependent sex determination	Process by which sex is determined by temperature during embryonic development

*Concepts defined in this study

Sea turtles are migratory and exhibit high seasonal fecundity (Wallace et al. 2007). During the nesting season, and depending on the species, female turtles may nest ~ 2 to 7 times every 9 to 20 days and lay ~ 50 to 130 eggs in each clutch (Miller 1997). Female turtles are believed to fast during the nesting period at least at some nesting sites (Hays et al. 2002), making the energetic cost of reproduction even more demanding. This large reproductive output makes female turtles unable to reproduce every year typically skipping 1 to several years before returning to a beach to nest (Miller 1997). Male turtles also migrate from their foraging grounds to the areas around the nesting beaches, where they encounter females to mate. Males normally leave the nesting area earlier than the females (Schofield et al. 2017), probably lowering their energy expenditure in comparison with females. As the cost of reproduction may be disproportionally larger in females, male turtles could reproduce more often (Limpus 1993; Miller 1997; Hays et al. 2010).

Operational sex ratios may play a central role in life history evolution, because competition for mates tends to balance sex ratio biases (Jennions and Fromhage 2017). As mentioned above, female-biased PSR are the norm in sea turtles and operational sex ratios tend to be more balanced. Consequently, the temperature that provides 1:1 hatchling sex ratios is of limited use to assess population over-feminization. I propose that identifying the PSR that results in a balanced operational sex ratio, as well as the temperature that produces that PSR, would be beneficial for the management of threatened sea turtle populations. Here, I define and estimate population-advantageous PSR (PA-PSR) in sea turtles, based on the reproductive frequency of adult individuals. As an example, I calculated the PA-PSR for two populations of sea turtles for which, both male and female reproductive frequencies were known. Then, I compared the estimated PA-PSR to their beach PSR, which had been previously reported for these populations, to assess the occurrence of population feminization. I considered feminization as any departure from the PA-PSR toward more females. I also define the temperature during incubation that result in the PA-PSR (population equilibrium temperature, PET) at the nest level to provide a more practical concept for sea turtle management than the pivotal temperature. Finally, I compared PET to the pivotal temperatures of different populations of sea turtles around the world for which a TSD-curve had been described. Moving beyond the seminal concept of the pivotal temperature and embracing the PA-PSR could help to better assess the impact of climate change on sea turtle populations in the long run.

2 Methods

2.1 Definitions and considerations

Operational sex ratios are the sex ratios of sexually active females and males at a given time (Emlen and Oring 1977). In sea turtles, operational sex ratio has been considered as the ratio of adult turtles that are ready to mate in a season (Maurer et al. 2021). Based on the estimations of operational sex ratios obtained at different nesting beaches around the world, these tend to be relatively balanced in sea turtle populations (reviewed in Santidrián Tomillo and Spotila 2020). Because female and male turtles have different reproductive frequencies, balanced operational sex ratios indicate that the adult sex ratio (ASR) in the population is unbalanced. Knowing the operational sex ratio (in this case, 50% female: 50% male) and the reproductive frequencies of each sex, the ASR can be calculated.

Sex-specific immature survival rates are largely unresolved (Chalopka and Limpus 2005). Because I was unaware of any differences between sexes, I assumed equal survival probabilities for male and female turtles in the water. Under natural conditions, equal survival probabilities by sex would mean that the ASR mirrored the PSR of hatchlings coming from the beach. As mentioned before, the PA-PSR is the sex ratio of hatchlings that will result in a balanced operational sex ratio. Thus, if beach PSRs departed from the PA-PSR toward more females or males, it could indicate the occurrence of population feminization or masculinization respectively.

In order to assess population feminization by comparing the PA-PSR to the beach PSR, it is necessary to obtain a good approximation to the beach PSR. Because sea turtles have temperature-dependent sex determination, PSRs are affected by the prevailing climatic conditions (Godfrey et al. 1996). To be representative at the population level, the estimation of beach PSR must capture climate-driven intra- and inter-annual variabilities in sex ratio (Godfrey et al. 1996; Laloë et al. 2016). Thus, sampling duration and sample size are key considerations to estimate beach PSRs accurately. For instance, estimations over approximately one decade have been used to average PSRs at some sites (Godfrey et al. 1996; Sieg 2010; Fuller et al. 2013) and one male-biased year was estimated to occur at that frequency in some areas (Sieg 2010; Heredero-Saura et al. 2022).

The effect of temperature on hatching and emergence successes should also be taken into account when estimating beach PSRs. As mentioned above, high temperatures reduce hatching and emergence successes (Santidrián Tomillo et al. 2009; Valverde et al. 2010), while increasing the percentage of female hatchlings (Standora and Spotila 1985). Averaging the PSR estimated for a number of nests (i.e., averaging percentages) could infer incorrect results because some nests have more viable hatchlings than others. Thus, weighting PSR by hatching/emergence success would provide a more accurate estimation (see Santidrián Tomillo et al. 2014).

2.2 Remigration intervals and calculation of population-advantageous PSR

I estimated the PSR that would be advantageous at the population level (PA-PSR), based on different combinations of female and male remigration intervals (RIs). For female turtles, I considered mean RIs between 1 and 6 years to account for variability among populations. There is extensive literature on the RIs of female sea turtles based on capture-mark-recapture data obtained on the nesting beaches (Limpus et al. 1984; Troëng and Chaloupka 2007; Hatase and Tsukamoto 2008). Remigration intervals vary interannually and among populations because they are affected by ocean primary and secondary productivities and by the species-specific trophic status (Broderick et al. 2003; Saba et al. 2007). Mean RIs between 2 and 3 years are the most common intervals (Limpus et al. 1984; Miller 1997; Troëng and Chaloupka 2007). However, although mean RIs over 4 years are infrequent in sea turtle populations, RIs are highly variable and have been estimated to be as long as 5–7 years in green turtles (*Chelonia mydas*) in Australia (Limpus et al. 1994, reviewed in Troëng and Chaloupka 2007). Exploring these higher RIs would also allow us to account for the extremes that could occur under climate change or due to changes in resource availability (Stubbs et al. 2020). I also considered RIs as short as 1 year, because such a short frequency has been recorded for some individuals (Miller 1997). Moreover, since RIs depend on ocean productivity and conditions could change through time (Hays 2000; Saba et al. 2007), it was important to include both short and long RIs in the analysis.

Less information is available on male RI due to the difficulty of capturing and/or recapturing male turtles at sea. The few studies that have attempted to estimate male RIs, either by satellite telemetry or by in-water capture, indicated that male loggerhead and green turtles had higher reproductive frequencies than females with RIs being normally as short as 1 year (or slightly longer than that) (Hays et al. 2010; Limpus 1993; Casale et al. 2012). Based on this information, I considered that male RIs could be between 1 and 3 years. For each combination of male and female RIs, I estimated the population-advantageous primary sex ratio (PA-PSR).

The average number of reproductive female and male turtles per season could be calculated as: $R_f = N_f/RI_f$ and $R_m = N_m/RI_m$, where R_f and R_m correspond to the mean number of reproducing female and male turtles respectively in a season, N_f and N_m are the numbers of adult females and males in the population (reproductive and non-reproductive) and RI_f and RI_m correspond to the mean remigration intervals for each sex in the population. Since we assume that operational sex ratios are balanced ($R_f = R_m$), we can substitute the terms of the previous equation:

$$N_f/RI_f = N_m/RI_m$$

therefore, the total number of females would be as follows:

$$N_f = \frac{RI_f}{RI_m} * N_m$$

Since the adult sex ratio (ASR) is calculated as female percentage, this is as follows:

$$ASR = \frac{N_f}{N_f + N_m}$$

, which translates into the following:

$$ASR = \frac{\frac{RI_f}{RI_m} * N_m}{\frac{RI_f}{RI_m} * N_m + N_m}$$

and can be summarized as follows:

$$ASR = (\frac{RI_f}{RI_m})/(\left(\frac{RI_f}{RI}\right) + 1)$$

Because we assumed an equal survival probability for all age classes from hatchlings to breeding adults for both sexes, the adult sex ratio (ASR) was set to equal the PSR of hatchlings coming from the beach. Thus, the equation we used to estimate PA-PSR was as follows:

$$PA\_PSR = (\frac{RI_f}{RI_m})/(\left(\frac{RI_f}{RI_m}\right) + 1)$$

Finally, I estimated PA-PSRs and compared it to beach PSRs for two example sea turtle populations for which male and female RIs have been previously reported:

loggerhead turtles (*Caretta caretta*) that nest in Greece (Hays et al. 2010, 2014) and green turtles that nest in Heron Island, Australia (Limpus 1993). In the case of the loggerhead turtles from Greece, Hays et al. (2014) estimated that the probability of male loggerhead turtles returning to reproduce to Zakynthos National Park after 1 year was 76.4%. If we assumed that the remaining 23.6% of turtles that did not return in year one, did so in year two, the male remigration interval would be 1.24 years. If instead, those turtles came back in year three, the RI would be 1.47 years. Hays et al. (2010) estimated that the mean female remigration interval for loggerhead turtles nesting in the nearby island of Cephalonia was 2.3 years. In the case of green turtles from Heron Island, Limpus et al. (1993) estimated that male and female reproductive frequencies were 1–2 years and 4.7 years respectively, based on capture-mark-recapture of turtles at foraging grounds. Estimations of beach PSR were previously reported as 68–81% for loggerhead turtles nesting in Greece (Zbinden et al. 2007; Katselidis et al. 2012) and 73–87% for green turtles nesting in Heron Island (Booth and Freeman 2006).

2.3 Population equilibrium temperature

I define population equilibrium temperature (PET) as the temperature that results in the PSR that is advantageous at the population level (PA-PSR). For example, if PA-PSR is 70% female, the PET would be the temperature along the TSD curve of the population of study that will result in a sex ratio that is 70% female. To compare PET to PT for different populations of sea turtles, I selected all populations I could find from published records for which a TSD curve had been depicted. I found 12 populations of sea turtles, including three populations of green turtles (one population from Suriname, Godfrey and Mrosovsky 2006 and two populations from Australia, Bentley et al. 2020), three populations of loggerhead turtles (one population from Greece, Rees and Margaritoulis 2004, one population from USA, LeBlanc et al. 2012a and one population from Australia, Woolgar et al. 2013), three populations of flatback turtles (*Natator depressus*) from Australia (Bentley et al. 2020), one population of leatherback turtles (*Dermochelys coriacea*) from Costa Rica (Binckley et al. 1998), one population of olive ridley turtles (*Lepidochelys olivacea*) from Brazil (Castheloge et al. 2018), and one population of Kemp's Ridley turtles (*Lepidochelys kempii*) from the USA (LeBlanc et al. 2012b). I used the TSD-curve of each population to estimate PET. Then, I compared PETs and PTs for a range of PA-PSRs.

3 Results

3.1 Population-advantageous PSR

Population-advantageous PSR (PA-PSR) increased along with the female remigration interval (RI) for any given male RI (Fig. 1). The longer female turtles take to return to the beach to nest, the greater the female bias in PA-PSR. On the contrary, the longer male turtles take to migrate to reproduce again, the lower the proportion of females required to produce a PA-PSR for a given female RI (Fig. 1, Table 2).

Based on the previously described RIs of female and male turtles, I estimated that the PA-PSRs of green turtles from Heron Island were between 70 and 82% female and PA-PSR of loggerheads from Greece were 61–65% female. Beach PSRs for Heron Island were reported as 73% and 87% female in 2002 and 2003 respectively (Booth and Freeman,

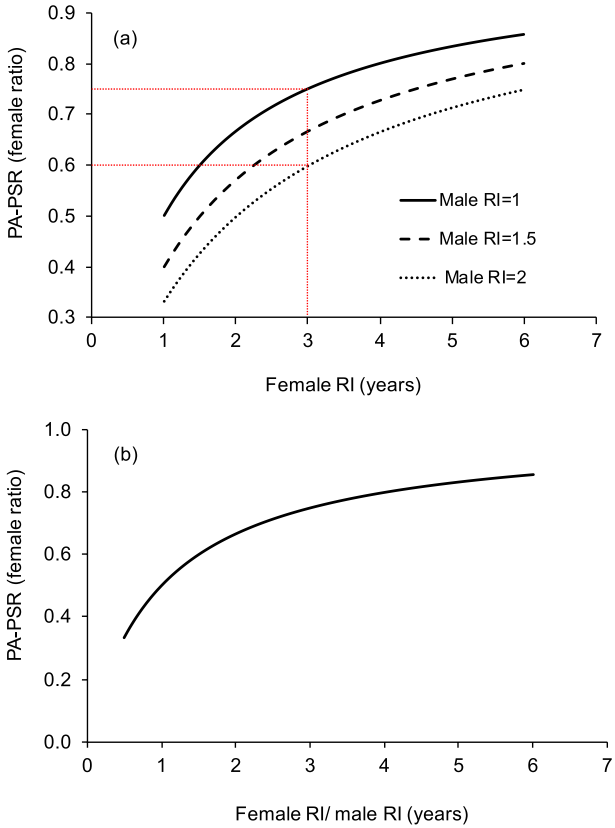

Fig. 1 Population-advantageous primary sex ratio (PA-PSR) of hatchling sea turtles to reach balanced operational sex ratios (1:1) depending on (**a**) the remigration intervals (RI) of female and male turtles and (**b**) the ratio between female and male remigration intervals. Red-dashed lines indicate the PA-PSRs corresponding to a female RI of 3 years and male RIs of 1 and 2 years. The longer that female turtles take to return to nest, the greater the proportion of females needed to produce a population-advantageous sex ratio. However, as males take longer to return to nest, the opposite effect occurs, so that less females are required to produce a population-advantageous sex ratio

2006), which is only slightly above the estimated PA-PSR. Beach PSRs for Zakynthos were reported by Zbinden et al. (2007) as 68% and 75% female in 2002 and 2003 respectively, and by Katselidis et al. (2012) as 77%, 80.6%, and 73.2% in 2007, 2008, and 2009 respectively. Average beach PSRs for all those years would be 74.7% female, which is 9.7–13.7% above the PA-PSR estimated. Thus, if beach PSRs were accurately estimated, the percentage of female hatchlings coming from the beaches would be slightly above the levels that are advantageous for the populations suggesting that a mild feminization may be occurring, especially in Greece.

3.2 Population equilibrium temperature

As the PA-PSR increased in female percentage, the difference between PET and PT became larger (Fig. 3), but the rate of change varied among populations due to the variability in the shape of TSD curves (Figs. 2 and 3). In particular, the largest differences between PET and PT were found in the green turtle nesting population of Suriname, followed by one green turtle population nesting in Australia and by one of the flatback populations (Figs. 2 and 3). On the contrary, the smallest differences between PET and PT were found in the population of loggerhead turtles that nest in Australia, followed by one of the flatback populations and by the loggerhead turtles that nest in Greece (Figs. 2 and 3). Generally, the populations with the smallest differences between PET

Table 2 Mean remigration intervals (RI) (number of years elapsed between nesting seasons), the corresponding adult sex ratio (ASR), and the population-advantageous primary sex ratios (PA-PSR) (% female) that would result in a balanced operational sex ratio (OSR) in the population. Notice that the PA-PSR equals the ASR

Mean RI (years)		ASR (female:male)	OSR (female:male)	PA-PSR (female %)
Female	Male			
2.0	1.0	2:1	1:1	67%
2.5	1.0	2.5:1	1:1	71%
3.0	1.0	3:1	1:1	75%
3.5	1.0	3.5:1	1:1	78%
4.0	1.0	4:1	1:1	80%
4.5	1.0	4.5:1	1:1	82%
5.0	1.0	5:1	1:1	83%
5.5	1.0	5.5:1	1:1	85%
6.0	1.0	6:1	1:1	86%
2.0	1.5	1.3:1	1:1	57%
2.5	1.5	1.7:1	1:1	63%
3.0	1.5	2:1	1:1	67%
3.5	1.5	2.3:1	1:1	70%
4.0	1.5	2.7:1	1:1	73%
4.5	1.5	3.0:1	1:1	75%
5.0	1.5	3.3:1	1:1	77%
5.5	1.5	3.7:1	1:1	79%
6.0	1.5	4:1	1:1	80%
2.0	2.0	1:1	1:1	50%
2.5	2.0	1.3:1	1:1	56%
3.0	2.0	1.5:1	1:1	60%
3.5	2.0	1.8:1	1:1	64%
4.0	2.0	2:1	1:1	67%
4.5	2.0	2.3:1	1:1	69%
5.0	2.0	2.5:1	1:1	71%
5.5	2.0	2.8:1	1:1	73%
6.0	2.0	3:1	1:1	75%

and PT also had the narrowest ranges of temperatures over which both sexes are produced (i.e., TRTs, see for example Fig. 2e), with some exceptions. For example, one of the flatback populations had a very small difference between PET and PT, despite having a relatively wide TRT (Fig. 2h). For all populations, the difference between PET and PT was also proportionally larger at higher PA-PSRs than at lower ones (Fig. 3). At the PA-PSR of 75% female, PET ranged between 29.1 and 31.1 °C and PT between 29.0 and 31.0 °C (Fig. 2). However, there was considerable intra-specific variability in TSD curves, and therefore in the PTs and PETs, in those species for which there was more than one population (Figs. 2 and 3). For example, at a 75% female PA-PSR, PET ranged between 29.6 and 30.5 °C in green turtles, 29.1 and 29.9 °C in loggerhead turtles and 29.9 and 31.1 °C in flatback turtles.

As mentioned above, the estimated PA-PSR of loggerhead turtles nesting in Greece was 61–65% female. Using the TSD-curve for this population, the corresponding PET

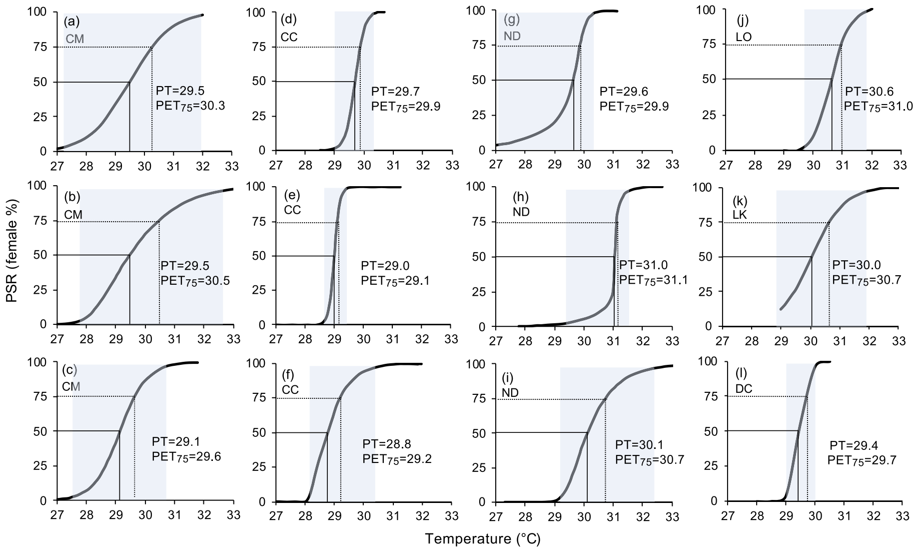

Fig. 2 Temperature-dependent sex determination (TSD) curves for several populations of sea turtles showing the pivotal temperature (PT) (solid lines), population equilibrium temperature (PET_{75}) (dashed lines), and transitional range of temperatures (TRT) (gray area) (see definitions in Table 1). In this example, PET_{75} corresponded to a 75% female PA-PSR. The TSD-curves belong to green turtles (*Chelonia mydas*, CM in figure) that nest in (**a**) Suriname and (**b**, **c**) Australia; loggerhead turtles (*Caretta caretta*, CC) that nest in (**d**) Greece, (**e**) Australia, and (**f**) Georgia, USA; (**g**, **h**, **i**) flatback turtles (*Natator depressus*, ND) that nest in Australia; (**j**) olive ridley turtles (*Lepidochelys olivacea,* LO) that nest in Brazil, (**k**) Kemp's ridleys (*Lepidochelys kempii,* LK) that nest in Texas, USA, and (**l**) leatherback turtles (*Dermochelys coriacea,* DC) that nest in Costa Rica. References are cited in methods section

for a 65% female would be 29.8 °C. Because this population has a narrow TSD-curve

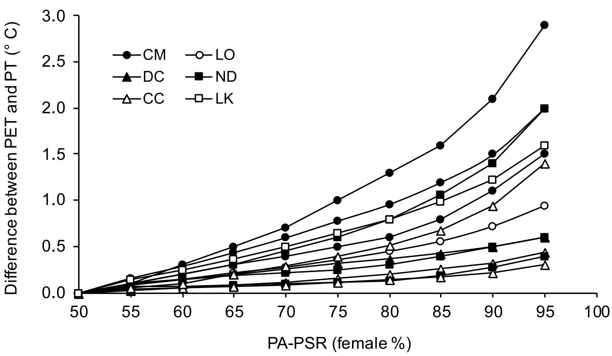

Fig. 3 Difference between the population equilibrium temperature (PET) and the pivotal temperature (PT) for 12 populations of sea turtles for which TSD curves had been previously described. PET was estimated for different population-advantageous primary sex ratios (PA-PSR). Populations included green turtles (CM in figure) that nest in Suriname and Australia (2 populations); loggerhead turtles (CC) that nest in Greece, Georgia, USA (and Australia; flatback turtles (ND) that nest in Australia (3 populations); olive ridley turtles (LO) that nest in Brazil; Kemp's ridley turtles (LK) that nest in Texas, USA and leatherback turtles (DC) that nest in Costa Rica. References are cited in methods section

(Fig. 2d), PET would only be 0.1 °C above the PT (29.7 °C, Rees and Margaritoulis 2004) at 65% female PA-PSR.

4 Discussion

Warming temperatures threaten to cause unsustainable levels of feminization in sea turtle populations (Patrício et al. 2021). Extremely biased sex ratios (> 90% female) are not common but have already been detected on some nesting beaches (Broderick et al. 2000) and foraging grounds (Jensen et al. 2018). This suggests that some populations may already be feminizing over their equilibrium levels and interventions could be recommended if males became a limiting factor. However, to properly assess the occurrence and extent of feminization, it would be useful to have an idea of the PSR that would be at equilibrium in the population (PA-PSR). Because the temperature that results in 50/50 sex ratio makes a poor indicator of feminization, any approximations to the actual PA-PSR, as proposed in this study, would help assess a more accurate level of population feminization. Using the PA-PSR concept could also move us closer toward understanding true climate vulnerability of nesting populations, while management of sea turtle nests would be more demographically appropriate.

In addition, it is important to obtain a good approximation to the mean beach primary sex ratio of a population. I found that PA-PSR could be ~ 3 to 5% and 10–14% lower than the beach PSR in green and loggerhead turtles that nest in Heron Island and Greece respectively. This suggests that a mild feminization could be undergoing, particularly in Greece. However, this result must be taken with caution, as beach PSR was estimated by averaging the percentage of sex ratios reported for different years, which could be problematic because it may not account for differences in hatching success under various thermal conditions. For example, the estimation of PSR in leatherback hatchlings decreased from 85% female to 79% female when it was estimated based on the total number of hatchlings of each sex that emerged over multiple years (Santidrián Tomillo et al. 2014). A similar difference between methodologies in the studied populations would indicate that population feminization was milder than estimated or that it was not occurring.

The estimation of PA-PSR also presents some practical problems because the reproductive frequency of adult individuals may be difficult to obtain and/or it may change over time. A good approximation to the RI of female turtles can be obtained from mark-recapture data. Although this is much easier to be inferred than in the case of male turtles, there may still be some inaccuracies. For example, a high level of nest-site fidelity is common in most sea turtle populations, but some individuals may place their nests over long distances, causing some turtles to go undetected during some nesting events (Miller et al. 2003; Bowen and Karl 2007). In addition, if the level of nest-site fidelity is low in a population, or beach coverage is poor, the RI of female turtles would be overestimated (Casale and Ceriani 2020; Pfaller et al. 2022). Because some beaches are difficult to be accessed or covered due to their extension, the probability of encountering a turtle could be low, ultimately affecting the estimation of RIs. Satellite telemetry for instance, has indicated that turtles can often go undetected, affecting the estimation of population parameters (Tucker 2010; Santos et al. 2021).

While the estimation of female RIs may have some inaccuracies, the estimation of RI of males is comparatively at its infancy. Since male turtles do not emerge to the nesting beaches, remigration intervals can only be obtained from capture-mark-recapture of turtles at sea (Limpus 1993), or from tracking male turtles in their movements from and to the nesting beaches (Hays et al. 2010, 2014). The latter may be more reliable as turtles can be followed for the entire period between nesting seasons (Hays et al. 2014). Limpus (1993) estimated a RI of 1–2 years for male turtles based on recaptures of green turtles around courtship areas, but intervals were shorter (~ 1 year) in other populations when inferred from satellite tracking (Van Dam et al. 2008; Hays et al. 2010, 2014). However, estimations could also be explained by differences among species and rookeries. Because of the difficulties and low reliability associated with capturing turtles at sea, and the high expenses associated with satellite telemetry, male RIs are unknown for most populations. Consequently, the application of the PA-PSR concept will be more valuable in the future, as population-specific male remigration intervals are refined.

I assumed equal survival for both sexes from the time hatchlings enter the water until turtles reach sexual maturity. However, some studies have found smaller sizes and poorer locomotor performance in hatchlings emerging from warmer nests that were potentially female hatchlings (Booth 2017; Staines et al. 2019). We cannot be certain that survival in the ocean does not differ between sexes. However, if this was the case, these estimations would need to be recalculated. Considering the most common male (1.0–1.5 years) and female (2–3 years) RIs for sea turtle populations in natural conditions, the PA-PSR would be ~ 70 to 75% female. This approximately coincides with the estimated PSR for sea turtle populations around the world (reviewed in Hays et al. 2017), suggesting that the beach sex ratios for many populations may be close to optimal for sustaining relatively balanced OSRs.

The duration of the RI is environmentally driven, with the intervals of female turtles being longer when sea surface temperatures are warmer (Solow et al. 2002; Saba et al. 2007). It has been suggested that ocean sea surface warming from climate change could increase the RI of female turtles due to a decrease in food supply from a reduction of marine net primary productivity (Saba et al. 2007; Chaloupka et al. 2008). Changes in oceanographic conditions toward warming conditions, could also affect male turtles because males and females display similar migration patterns and forage in similar areas (Godley et al. 2008; Schofield et al. 2010).

The PA-PSR of sea turtles is likely complex and affected by other factors than RIs. For instance, good or bad years in fecundity or survival that coincide with male- or female-producing years could also eventually affect the adult sex ratio. Some areas that are highly influenced by El Niño Southern Oscillation, for example, are characterized by large inter-annual variability in hatchling production and sex ratios (Santidrián Tomillo et al. 2012; Sieg 2010). Likewise, trade-offs between RIs and other life history traits such as fecundity or survival could also ultimately influence population sex ratio. At the same time, RIs could also change in response to other pressures to increase chances of finding mating partners or caused by better foraging conditions that would allow them to reproduce more often. Consequently, RIs could be more dynamic than what has been presented here, likely affecting the PA-PSR.

On the other hand, populations could possibly have different PA-PSRs under various thermal conditions. The advantage of producing males or females in the offspring could change along with the thermal conditions, making PA-PSRs more dynamic. Temperature-dependent sex determination provides some resilience to rising air temperatures because more females are produced at the high temperatures that increase embryo and hatchling mortalities (Santidrián Tomillo et al. 2015). By increasing the percentage of female hatchlings, the future number of nesting turtles increases as well, which can offset the detrimental effect of high temperatures at the population level (Santidrián Tomillo et al. 2015; Hays et al. 2017). Thus, the PA-PSR could change under different thermal conditions because the chances of future reproduction for each sex could vary. Thus, interventions based on punctual estimations of PSR to artificially target them may not be a good practice as these may change.

For management, however, and considering that temperatures can relatively quickly reach critically high levels (Fuentes et al. 2009), it is useful to have an approximation to the PSR that would be advantageous with the information that we have today. Although in most places interventions are not needed, in areas where most egg clutches are already incubated in hatcheries due to a number of threats (e.g., high risk of egg poaching or tidal inundation; Chacón-Chaverri and Eckert 2007; Mutalib and Fadzly 2015), PA-PSR and PET could guide management actions. For example, nest shading and irrigation have been proposed to lower nest temperatures and increase hatching success (Hill et al. 2015; Jourdan and Fuentes 2015; Lolavar and Wyneken 2021; Smith et al. 2021), but this could also reduce the number of female hatchlings and cause population declines in the long term (Santidrián Tomillo et al. 2021). Thus, using PET to reach current PA-PSRs would be a better strategy than using the PT to reach equal sex ratios in hatchlings, where the environmental conditions of nests are already being controlled.

At this time, it does not seem reasonable to intervene with nests that can successfully incubate on the beach, as the impact of mitigation actions is not yet fully understood (Patrício et al. 2021). But we have to be ready in the event of feminization levels becoming detrimental for sustained population growth. So how can we know when the time to act has come? Some sea turtle populations may be highly female-biased, but as long as there are males in the population and eggs are fertilized, intervention may not be needed. A drop in the fertility rate of eggs over time, however, could be a red flag (Phillot and Godfrey 2020). Additionally, sea turtles are known to have multiple paternity, as a consequence of several males mating with a single female (Lee et al. 2018). A decrease in the level of multiple paternity, if accompanied by a decrease in fitness, could also indicate that the population is becoming feminized over equilibrium levels.

On the other hand, some beaches produce extremely female-biased sex ratios, but there may be male-producing beaches nearby, and hatchlings from both sites could recruit to the same nesting population, lowering the overall female percentage of hatchlings (Baptistotte et al. 1999; Zbinden et al. 2007; Marcovaldi et al. 2016). Thus, estimations of PSR would be better if done at the population (regional) level and not at the beach (local) level, which is sometimes complex, as different research groups may work on different nesting beaches. Ideally, current conservation efforts should focus on better understanding the fluctuations of the sex ratios of hatchlings and adult sea turtles at a regional level so that sea turtles can be adequately protected at the right spatial scale when necessary.

Acknowledgements I am grateful to A. Martínez-Abraín, Graeme Hays and three anonymous reviewers for providing comments on the manuscript P.S.T. was funded by the Vicenç Mut program of the Govern Balear.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature.

Data availability Data will be made available on a reasonable request.

Materials availability Data will be made available on a reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

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