

Estimating hatchling sex ratios of loggerhead turtles in Cyprus from incubation durations

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ABSTRACT: Incubation durations for loggerhead turtles *Caretta caretta* nesting at Alagadi, in Northern Cyprus, were recorded over 6 full seasons (1993 to 1998). Because incubation duration depends on temperature, it was possible to convert data on durations to hatchling sex ratios, using extensive data from other areas on the relationship between these 2 variables. It was estimated that 89 to 99% of the hatchlings produced on Alagadi beach were females. These findings provide a further instance of highly female-skewed sex ratios in loggerhead turtles.

KEY WORDS: *Caretta caretta* · Mediterranean · Sea turtle · Temperature · Sex ratios · Sex determination

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INTRODUCTION

In many reptiles, the direction of sexual differentiation depends on the temperature prevailing during incubation. In marine turtles, warm temperatures during the middle third of incubation produce females, and cool temperatures produce males. Having phenotypic sex determined by temperature potentially allows for great flexibility in sex ratios. These could be skewed through the females choosing to nest at times or in places with particular temperatures. Temperature-dependent sex determination has been the subject of a number of studies (review in Mrosovsky 1994). The data from loggerhead turtles *Caretta caretta* appear particularly interesting.

Although it has been postulated that a 1:1 sex ratio might be the norm in species in which the costs of producing a male or female are the same (Fisher 1930), sex ratios skewed as much as 90% toward female have been found or inferred for loggerhead turtles hatching in the USA and in Brazil (Mrosovsky & Provancha 1992, Marcovaldi et al. 1997, Hanson et al. 1998, Pro-

vancha & Corsello 1998). These huge skews are theoretically challenging. However, it is conceivable that sampling biases were responsible, even though the sex ratio estimates were based on ≥ 5 yr data. Another possibility is that the females hatching on the beaches in the USA and Brazil are balanced by males originating elsewhere. Analysis of mitochondrial (mt) DNA suggests that loggerhead turtles nesting in different parts of the world are genetically distinct (Encalada et al. 1998, Laurent et al. 1998), but information on nuclear DNA is needed to determine if males produced on one beach mate with females produced at a distant site.

Given these possibilities, it is of interest to determine the sex ratio of hatchling loggerhead turtles in populations nesting in other geographic areas. If more instances of extremely biased sex ratios are found, it makes it less likely that sampling error is responsible for the skewed ratios described to date. Moreover, if more areas are shown to be female-producing, it becomes less likely that a balanced overall sex ratio can be reached through male-biased production at other sites.

Sex ratios of loggerhead turtles in the Mediterranean have been little studied. Kaska et al. (1998) found a mean sex ratio of 81.6% female in a small sample

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(n = 8) of loggerhead clutches laid at 4 sites in Cyprus and Turkey over the 1995 and 1996 nesting seasons (10 June to 2 August). However it is not possible to tell if this sample was representative of the normal thermal conditions in these areas. In a preliminary report, Broderick & Godley (2000) have drawn attention to the very short incubation durations for loggerhead turtles in Cyprus, implying warm, feminising conditions.

In this paper we estimate the sex ratios of loggerhead turtles hatching on a beach in Northern Cyprus from data on incubation durations collected there over 6 seasons. Two different methods of estimation were used.

The first method is based on a data set accumulated over several years for loggerhead turtles nesting in the USA. For these samples, sex was determined directly by histology of the gonads, and sex ratio plotted against incubation duration. The curve relating these 2 variables, based on samples from 76 clutches, has recently been summarised by Godfrey & Mrosovsky (1997). We updated this curve by the addition of data from 13 more clutches (Fig. 1).

The second method has been devised for situations in which only a pivotal incubation duration (that duration giving 50% of each sex) is available from laboratory studies, and no field samples have been collected and sexed. In this method, there are 4 steps: (1) Incubation of eggs in the laboratory at various constant temperatures, followed by calculation of a pivotal incubation duration and a curve relating duration to sex ratio. (2) Adjusting this laboratory curve to one appro-

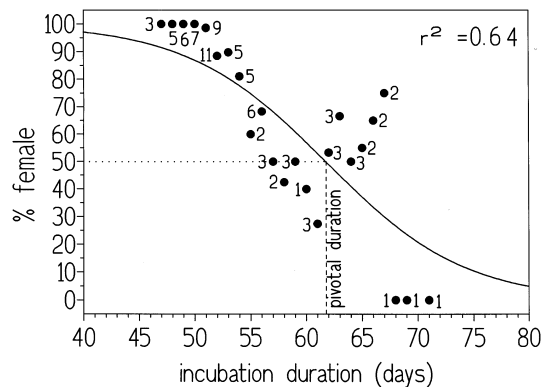


Fig. 1. *Caretta caretta*. Curve relating sex ratio and incubation duration of 89 clutches of loggerhead turtles nesting in south-eastern USA. Numbers beside points: number of clutches with that incubation duration. Sex ratio was usually based on samples of 10 hatchlings taken from a given clutch. Sources of data and further details are given in Godfrey & Mrosovsky (1997). Present curve differs from that in Godfrey & Mrosovsky in that it includes samples from 13 additional clutches from South Carolina. Horizontal dotted line: 50% level; vertical dashed line: field pivotal incubation duration which by definition is the duration producing 50% of each sex

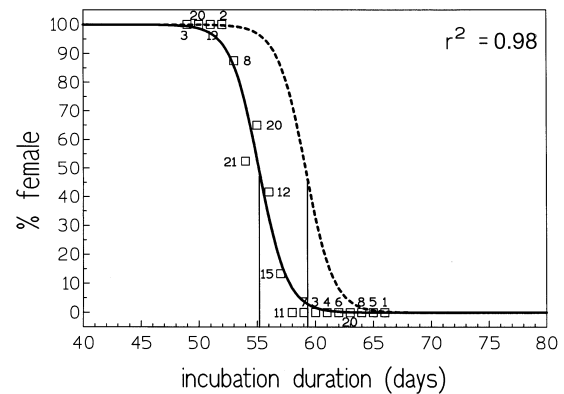


Fig. 2. *Caretta caretta*. Continuous line: relationship between sex ratio and incubation duration (laying to hatch) for Brazilian loggerhead turtle eggs studied in the laboratory (data from Marcovaldi et al. 1997). Numbers beside points: numbers of eggs at that duration (some of these n values correct transcription errors in Marcovaldi et al. 1997, but make no difference to the shape of the curve); dashed line: derived curve obtained by adding hatch-emergence interval of 4.1 d (see Godfrey & Mrosovsky 1997) to the incubation durations obtained in the laboratory (this derived curve was used to predict sex ratios from incubation duration [laying to emergence] available in the field); vertical lines: pivotal incubation durations

prate to the field by adding the hatch-emergence interval to the durations (Fig. 2). (3) Using the adjusted curve for converting values obtained in the field on incubation durations (duration from laying to hatching emergence) to the corresponding values for sex ratios; this is done separately for different time bins within the season. (4) Calculating the overall sex ratio by taking into account the number of clutches deposited at different times within the nesting season. Examples of the use of this method and its validation are given in Marcovaldi et al. (1997), Godfrey et al. (1999) and Mrosovsky et al. (1999).

In the present case, no suitable data from laboratory work are available for Mediterranean loggerhead turtles. However, the physiology of sex determination appears to be a conservative characteristic in sea turtles (Mrosovsky 1994). The pivotal temperatures (those giving 50% of each sex) in studies of loggerhead turtles reported so far all cluster within a degree of 29°C (Mrosovsky 1994, Marcovaldi et al. 1997). Some limited data suggest that this is true of loggerhead turtles nesting in the Mediterranean. Although the sample of Kaska et al. (1998) from the eastern Mediterranean was too small to specify sex ratio in nature, it does provide an indication of pivotal temperature because temperatures in the nests were measured. Using the means of temperatures taken in the middle third of incubation (the thermosensitive period for sexual dif-

ferentiation), the pivotal temperature was just below 29°C. This is similar to the values of 29.2°C for Brazil (Marcovaldi et al. 1997), and 29°C for the USA (Mrosovsky 1994). Also, the pivotal incubation duration calculated by fitting a line to the data of Kaska et al. (1998) is 59.9 d, which is close to the values of 59.3 and 61.7 d for Brazil and the USA, respectively. Although Kaska et al. did not take random samples of hatchlings from nests, their data indicate that the physiology of loggerhead turtles in the Mediterranean is quite similar to that of loggerhead turtles in the Americas with respect to thermal influences on sexual differentiation. The more extensive data sets from the latter areas can therefore be used to provide an estimate of the sex ratio of hatchling loggerhead turtles produced in Cyprus.

MATERIALS AND METHODS

Study site. The work took place at Alagadi (35° 33' N, 33° 47' E) in Northern Cyprus in the eastern Mediterranean. This is one of the main nesting areas in Cyprus for *Caretta caretta* (range in seasonal total of nests = 38 to 95 per season from 1993 to 1998). The beach consists of 2 short coves, 0.8 and 1.2 km long, separated by a rocky headland. Extensive dunes and low scrub lie behind the beach itself. There is no shade on the beach. The climate is typical of the eastern Mediterranean, with virtually no rain from May to October and mean daily air temperatures during this period in the region of 20 to 30°C. For further description of the study site, see Broderick & Godley (1996) and Broderick (1997).

Data collection. From 1993 to 1998, nesting was recorded during nightly patrols, and emergences of hatchlings during early morning patrols. Data were collected from May to October each year, encompassing all nesting and hatching on this beach. Emergence was taken as the first day on which >20 hatchling tracks were seen at a nest. At Alagadi, 54% of nests had emergences confined to 1 night; of all hatchlings produced, more than 80% had emerged by the end of the first night (Glen et al. 2000). For analysis, data were grouped into half-month time bins by laying date.

RESULTS

Incubation periods

Incubation periods for *Caretta caretta* at Alagadi were short in all years (Table 1) with an overall mean incubation period of 48.0 d (SE = 0.7, range = 42 to 58, n = 227).

Sex ratios calculated using Method 1, based on USA field data

Mean incubation durations for the main nesting season, June and July, were ≤ 50 d (Fig. 3). With such short durations, it is evident from the curve in Fig. 1 that sex ratios must be highly skewed toward females. After calculating the sex ratio for each incubation duration from this curve, and taking the nesting distribution into account, the overall sex ratio, based on 227 recordings of incubation durations over the 6 yr, is 89.2% female.

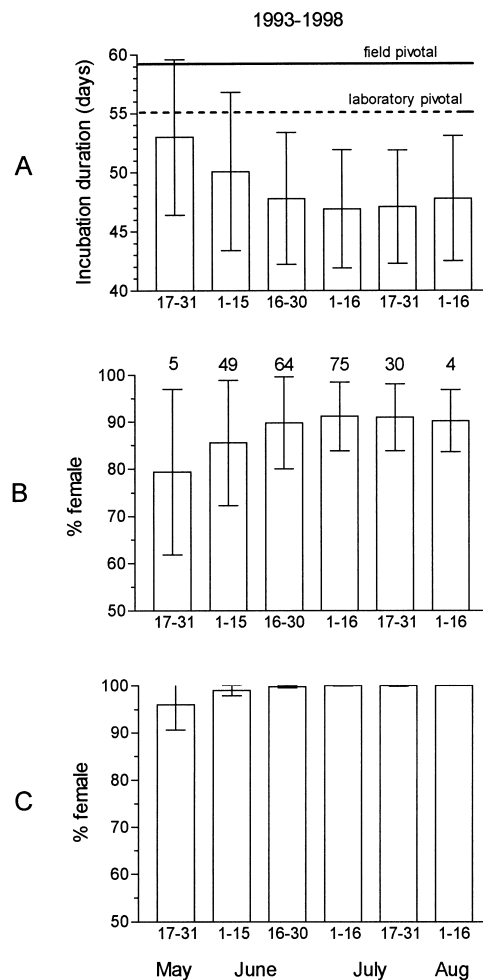


Fig. 3. *Caretta caretta*. (A) Incubation durations (mean \pm 2 SD) for combined data set for 6 yr at Alagadi, Northern Cyprus. Dashed horizontal line: pivotal incubation duration obtained in laboratory incubation of Brazilian loggerhead turtle eggs; continuous horizontal line: derived field pivotal incubation duration for Brazilian loggerhead turtles (see Fig. 2). (B) Sex ratios (mean \pm 2 SD) for the combined data set for the 6 yr, as estimated using the curve in Fig. 1 for USA loggerhead turtles; numbers above each bar: sample sizes for each half-month bin. (C) Sex ratios (mean \pm 2 SD) for the 6 yr combined, estimated using the derived curve for Brazilian loggerhead turtles in Fig. 2 and the 4.1 hatch-emergence interval; sample sizes as in (A) and (B)

Table 1. *Caretta caretta*. Incubation periods of *in situ* nests recorded at Alagadi and elsewhere in the Mediterranean

Beach	Year	Mean	SE	(n)	Total nests in season of study	Source
Cyprus						
Alagadi	1993	47.9	0.6	(17)	41	This study
Alagadi	1994	47.9	0.4	(58)	95	This study
Alagadi	1995	47.7	0.5	(39)	95	This study
Alagadi	1996	48.1	0.5	(45)	60	This study
Alagadi	1997	47.8	0.5	(41)	57	This study
Alagadi	1998	48.7	0.7	(27)	38	This study
Greece						
Kiparissia	1987	55.5	0.9	(50)	598	Margaritoulis (1989)
Zakynthos	1980	50.7	–	(3)	–	Margaritoulis (1985)
Zakynthos	1983	57.5	2.8	(6)	2460	Sutherland (1985)
Crete	1998	49.4	–	(30)	345	Ireland (1998)
Turkey						
Dalyan	1989	59.3	0.6	(47)	235	Erk'akan (1993)
Fethiye	1993	56.9	1.0	(67)	118	Turkozan & Baran (1996)
Fethiye	1994	55.0	–	(75)	158	Baran & Turkozan (1996)
Göksu	1992	57.0	1.2	(25)	89	van Pigglen (1993)
Göksu	1991	54.8	1.2	(33)	117	Peters & Verhoeven (1992)
Kizilot	1990	59.6	–	(70)	143	Kaska (1993)
Patara	1992	60.0	–	(25)	52	Kaska (1993)

Sex ratios calculated using Method 2, based on laboratory data and derived curve for Brazil

Incubation durations were considerably shorter than the derived field pivotal duration of 59.2 d obtained for loggerhead turtles nesting in Brazil (Fig. 3). In fact the

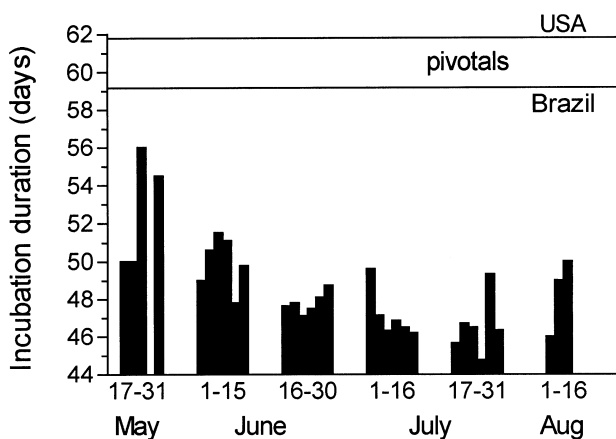


Fig. 4. *Caretta caretta*. Incubation durations for each year. Data are shown in groups of 6 bars, representing from left to right the years 1993 to 1998 for each time bin. However, sample sizes for May and August bins are 0 to 2; therefore, any differences at these times are unreliable. The figure illustrates the similarity in incubation durations between the 6 yr for the main nesting season (June and July) and the shortness of these durations compared to the field pivotal duration for the USA (Fig. 1) and the derived field pivotal incubation duration for Brazil (Fig. 2)

durations were even less on average than 59.2 – 4.1 = 55.1 d, the pivotal incubation duration in the laboratory. In other words, even if turtles emerged on the day they hatched (hatch-emergence interval = 0), there would be a skew toward female, because the average incubation durations were shorter than the laboratory pivotal value (Fig. 3). When more reasonable hatch-emergence intervals are assumed, the overall sex ratio is highly female-biased: 99.6% assuming a 4.1 d hatch-emergence interval, and 98.4% assuming a 2 d hatch-emergence interval.

Comparisons among years

As a result of the similarity in incubation duration among different years (Fig. 4), sex ratios are highly biased toward females in all years.

Seasonal pattern of hatch rate and hatching success

Were the hatch rate (i.e. the proportion of nests which hatched) or hatching success (i.e. the mean proportion of eggs hatched per nest) to vary much across the nesting season, then the sex ratios for turtles hatched might differ from those calculated on the basis of clutches laid. However, a comparable proportion of clutches hatched from each time bin (Fig. 5), and there was no obvious seasonal pattern in hatching success in any year.

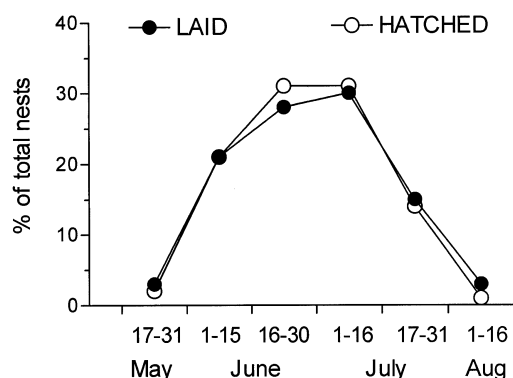


Fig. 5. *Caretta caretta*. Temporal distributions of clutches laid and hatched. Data are means of percentages for half-month bins for each season. Curves are also closely similar for individual years (data not shown)

DISCUSSION

Because incubation durations for *Caretta caretta* were so short, both methods of converting duration to sex ratios gave high skews toward female. It is interesting, especially in cases where the incubation duration is generally close to the pivotal value, to consider which method is superior. The pivotal value (that giving 50% of each sex) is not the only important aspect of the relationship between incubation duration and sex ratio. The extent of the transitional range of temperatures between 100% female and 100% male, where a mixed sex ratio is likely to be produced, is also important. If the curves are not steep, then even though temperatures (and associated incubation durations) are well on the female side of the pivotal value, they may nevertheless still not only produce females (for further discussion of transitional ranges of temperature see Mrosovsky 1994 and Chevalier et al. 1999).

The curve for loggerhead turtles in the USA (Fig. 1) may be too flat: few data points for long incubation durations contribute to this curve, and if such durations produced all males, the curve would become steeper. On the other hand, the curve for loggerhead turtles in Brazil (Fig. 2) may be too steep. It is based on only 2 clutches of eggs. If there is variability in pivotal durations between different clutches, even if the shape of the curves is similarly steep for all individual clutches, an average of several clutches would produce a flatter curve.

On this basis, we tentatively suggest that the true value for Alagadi may lie somewhere between the 89 and 99% female estimates provided by the 2 methods. In either case, the ratios are highly skewed toward female turtles. This fits with data we have on nest tem-

peratures at Alagadi. Temperatures recorded within nests by data-loggers (Orion Components, Chichester, UK) indicate that clutches rarely incubate at temperatures $<29^{\circ}\text{C}$. Mean temperature throughout the incubation ranged from 29.5 to 33.2°C (mean = 31.6°C , SE = 0.2, n = 23 nests; Broderick 1997, Broderick & Godley unpubl. data), with the mean temperature experienced during the middle third of incubation by these same nests ranging from 29.3 to 33.7°C (mean = 31.6 , SE = 0.3, n = 23).

Despite the extreme skews toward females, there is no indication that there are insufficient males for fertilisation at Alagadi. Mean annual hatching success of nests which were followed to completion (i.e. excluding those lost to predation or inundation by waves) ranged from 75 to 83% (Broderick & Godley 1996). Assuming that similar sex ratios have been produced over a generation time or more, either the few males produced on Alagadi are sufficient to ensure fertilisation, or males originating elsewhere assume this role.

Comparisons between mitochondrial and nuclear DNA in another marine turtle species, the green turtle *Chelonia mydas* (Karl et al. 1992, FitzSimmons et al. 1997), are consistent with the idea that, although males show some degree of fidelity to courtship grounds in their natal area, they may move among sites more than females (or intercept females in overlying feeding grounds or en route to breeding grounds). A similar study on loggerhead turtles in Turkey and Cyprus suggested a low level of male-mediated gene-flow (Schroth et al. 1996). However, from what information we have been able to collate, there does not appear to be any large known rookery in the Mediterranean that is likely to produce mostly males, as judged by incubation durations (Table 1). In addition, on beaches other than Alagadi in Northern Cyprus, the mean incubation duration of 70 nests in 1998 was 48.8 d (SE = 0.6; Broderick & Godley unpubl. data). This is similar to the values for Alagadi (Fig. 3), suggesting a similar, female-biased sex ratio.

In other parts of the Mediterranean, incubation durations are mostly reported to be shorter than 59 d (Table 1). In addition, in Israel and Egypt, where all nests have been relocated to hatcheries which attempt to mimic natural nest conditions, short incubation durations have been recorded (Israel: mean = 52.7 d, SE = 0.4, n = 175, Z. Kuller pers. comm.; Egypt: mean = 49.3, SE = 1.1, n = 11, M. Clarke pers. comm.). Regrettably, for the largest known loggerhead turtle nesting site in the Mediterranean, Zakynthos, with about 1000 to 2000 nests yr^{-1} , there are very few data available, even though this beach has been extensively monitored for over a decade. However, the mean incubation duration for Kiparissia, which is very close to Zakyn-

thos (<100 km), is <56 d, suggesting a female-biased hatchling production in this region of Greece (cf. Table 1, Fig. 3). It is possible that there is a large aggregation of loggerhead turtles nesting in Libya (Laurent et al. 1997, 1998). We presume that the sand at such a southern location would not be appreciably cooler than elsewhere in the Mediterranean.

Whatever the situation with respect to movement of males, there are implications for sea turtle conservation. If there is a sizeable genetic interchange between male- and female-producing beaches, producing relatively balanced sex ratios overall, then a macro-ecological perspective must be taken to preserve the appropriate sex ratios in the population as a whole (Baptistotte et al. 1999). But if, as seems more likely, the sex ratio is highly female-biased on a number of beaches in the Mediterranean, it would seem wise to pay particular attention to protection of the few male-producing clutches laid at the start of the seasons (Mrosovsky et al. 1984).

The proximate and ultimate causes for highly female-biased sex ratios in loggerhead turtles remain unknown. The more often such ratios are found, the less likely it is for sampling error to be the explanation. The present analysis adds the Mediterranean to the USA and Brazil as places where loggerhead turtles are producing some highly skewed hatchling sex ratios. Why frequency-dependent pressures (Fisher 1930) have not led to more balanced sex ratios in loggerhead turtles remains puzzling.

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