Pivotal temperature for loggerhead turtles (*Caretta caretta*) from Kyparissia Bay, Greece

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Abstract: Pivotal temperature (the constant temperature giving 50% of each sex) for two clutches of loggerhead sea turtles (*Caretta caretta*) from Kyparissia Bay, Greece, was 29.3°C. Pivotal incubation duration (the time from laying to hatching giving 50% of each sex) was 52.6 days. These values are close to those obtained for this species in Brazil and the United States, providing further evidence that these characteristics are relatively conservative in different populations. Methodological differences between different experiments and limitations on accuracy of equipment make the detection of small differences problematic. Comparison of incubation durations in the field with the pivotal durations obtained here suggest that hatchling sex ratio on some Mediterranean beaches is female biased but probably varies considerably within this region.

Résumé : La température charnière (la température constante d'incubation qui produit 50 % d'individus de chaque sexe) pour deux masses d'oeufs de caouanes (*Caretta caretta*) de la baie de Kyparissia en Grèce a été estimée à 29,3°C. La durée charnière de l'incubation (le temps entre la ponte et l'éclosion qui produit 50 % de tortues de chaque sexe) est de 52,6 jours. Ces valeurs se rapprochent de celles que l'on a obtenues chez cette espèce au Brésil et aux É.-U., ce qui est une indication supplémentaire que ces caractéristiques sont relativement conservatrices dans les différentes populations. Les différences méthodologiques entre les expériences et les limites de précision des appareils rendent problématiques la détection de petites différences. La comparaison des durées de l'incubation en nature avec les durées charnières obtenues ici laisse croire que le rapport mâles : femelles chez les nouveau-nés sur certaines plages méditerranéennes favorise les femelles, mais qu'il varie probablement beaucoup dans la région.

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Introduction

The pivotal temperature (the constant incubation temperature giving 50% of each sex) is a basic piece of information about a turtle. Like size at maturity, egg dimensions and number per clutch (Tiwari and Bjorndal 2000), number of nests per season, and other such variables, the pivotal temperature may be roughly similar between different populations but should not be assumed to be exactly the same. Small differences in any of these variables may make a considerable difference in the demographic constitution of a population.

In addition to such general considerations for obtaining data on pivotal temperatures, we wished to learn more about this variable specifically for Mediterranean loggerhead turtles (*Caretta caretta*) for a number of reasons. First, as part of conservation programmes, eggs may sometimes have to be moved and reburied to save them from destruction (Margaritoulis 1998). Knowledge about functions relating sex ratio to temperature could help avoid introducing sex-ratio biases. Laboratory studies on sex ratio not only provide data on pivotal temperatures but also on pivotal incubation duration (the duration giving 50% of each sex (Mrosovsky et al. 1984*a*)). Because incubation duration correlates with temperature, it can be used to derive estimates of sex ratio. Moreover, because data on incubation duration are often collected in sea turtle conservation and management programmes, retrospective estimates of natural sex ratios can be made (Godfrey et al. 1999; Mrosovsky et al. 1999). Such estimates may provide guidance on what sex ratios to aim for in the event of global warming.

Second, to help build up an understanding of the demography of loggerhead turtles as a species, data on sex ratios from additional populations may be instructive. Previous studies on the sex ratio of this species have been surprising. The production of hatchlings at loggerhead nesting grounds in Florida, U.S.A., is extremely biased, approximately 90% female (Mrosovsky and Provancha 1992; Hanson et al. 1998). Similar strongly female-skewed hatchling sex ratios appear to occur at Bahia, Brazil, one of the principal nesting grounds for this species in the southwest Atlantic (Marcovaldi et al. 1997; Mrosovsky et al. 1999). Some males are produced at smaller nesting grounds more distant from the equator, both in the United States (Mrosovsky et al. 1984*b*; Mrosovsky 1988) and Brazil (Baptistotte et al. 1999), but no major male-producing region has yet been detected. This suggests either that the sex ratio of loggerheads may be naturally skewed toward female, something that should create selective pressures in favour of producing males (Fisher 1930; Olsson and Shine 2001), or that ratios are in disequilibrium in a number of populations. If similar female biases were found in populations in other parts of the world, it would increase confidence that these are characteristic of this species

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and not the result of selective destruction of male-producing rookeries.

Data on incubation duration of loggerhead turtles in Cyprus and other parts of the Mediterranean (Godley et al. 2001*a*, 2001*b*) suggest that female biases may also occur there. This supposition depends on the assumption that functions relating sex ratio to temperature in the Mediterranean are similar to those described elsewhere. But no pivotal temperature for Mediterranean loggerheads is available, other than that of 28.5–29°C based on nonrandomly selected hatchlings from eight nests, only one of which had temperatures giving <50% females (Kaska et al. 1998). A more extensive database for specification of a pivotal temperature for Mediterranean loggerheads is needed because "it would appear that with data [on incubation duration and sand temperature] already collected by workers in the region, a plausible estimate of hatchling sex ratio for the Mediterranean may be attainable once a clearly defined pivotal temperature for the Mediterranean population is generated by laboratory and/or field-based studies" (Godley et al. 2001*b*).

Laboratory studies are preferable at this initial stage because field studies depend on assumptions about lack of variability in thermosensitive period and how swings from average temperature should be treated. For instance, the mean temperature of clutches during the middle third of incubation is sometimes taken as the basis for calculating pivotal temperatures. This assumes that excursions above and below the mean are equivalent, but in fact, excursions above the mean have greater effects (Bull 1985; Georges et al. 1994). Also, the specification of the middle third of incubation as the thermosensitive period derives from studies on a small sample of clutches (Yntema and Mrosovsky 1982). These problems can be avoided by incubating eggs at constant temperatures.

Methods

Source of eggs and transport

The eggs were laid at 02:30 on 12 July 2001 at Kyparissia Bay (Fig. 1); 100 eggs from each of two clutches were taken. Straight-line carapace lengths for the turtles were 92.5 cm (tags KA086 and Y5677, 128 eggs laid, clutch T) and 78.5 cm (tags KA030 and Y5938, 117 eggs laid, clutch U); the eggs of the latter were noticeably smaller. The eggs were driven in an air-conditioned car to Athens airport and flown to Toronto, Ont. The total time from laying until the eggs were all set in the incubators in Toronto was 24.5 h. No spotting was noticed on the eggs at this time. Within a day, however, a white spot, indicating attachment of the membranes to the shell (Blanck and Sawyer 1981), had appeared on most eggs.

Incubation methods

The eggs were placed in five constant-temperature incubators (model 818; Precision Scientific, Winchester, Va.) in separate containers with sponge and vermiculite as detailed in Mrosovsky (1988). Mercury thermometers with 0.1°C graduations were placed on each shelf. These had been calibrated against a Sybron-Taylor mercury thermometer with certified calibration against platinum resistance thermometers, calibrated by the U.S. National Bureau of Standards. Temperatures on each shelf were read almost daily. In addition, maximum–minimum thermometers provided assurance that no temperature swings of appreciable magnitude had occurred between the daily readings. However, for one of the incubators, on day 19, a problem with power lasting 17.75 h resulted in a gradual drop of approximately 5.5°C from the usual range of 29.0–29.3°C. Fortunately, according to experiments with temperature pulses (Yntema and Mrosovsky 1982), a drop in temperature at this stage of development should not have affected sex ratio. It was possible to confirm this because the lower shelf of the incubator that underwent the unintended drop in temperature averaged the same as that of upper shelves in another incubator but produced a somewhat higher, not lower, percentage of females. This indicates that any possibly masculinizing temperature drop occurred before the thermosensitive period for sexual differentiation or was too short and shallow to make a difference. On days 17 and 38, 65 mL of water was added to each container to maintain moisture and high humidity (see Mrosovsky (1988) for further details).

Correction factors

In previous work, it was found that the temperature of the egg itself was slightly cooler than that of the air within the incubators. Therefore, on days 32 and 33, measurements were made within an egg and in an adjacent beaker of glycerine with thermistor needle probes (Yellow Springs Instruments, Yellow Springs, Ohio). On the basis of these measurements, a 0.4°C correction factor was subtracted from all incubator temperatures measured with the mercury thermometers. This is in line with correction factors obtained in previous experiments using the present methods: 0.3°C (Mrosovsky et al. 1984*a*), 0.5°C (Mrosovsky 1988; Marcovaldi et al. 1997), 0.5°C (Mrosovsky et al. 1992), and 0.25°C (Godfrey et al. 1999). Readers who prefer to think in terms of ambient temperatures rather than estimated egg temperatures can add 0.4°C to all values reported in this paper.

Criteria for hatching and incubation duration

The date of laying was taken as day 0. Hatching was considered to have occurred when the head and at least one front flipper protruded from the egg shell (Godfrey et al. 1999). Incubators were usually inspected twice a day when hatching was expected. Date of pipping (Godfrey et al. 1999) of the shell by the egg tooth was also noted in most cases.

Histology

Sex was determined by microscopic examination of the gonads. Histology followed the methods of Yntema and Mrosovsky (1980) with slight modifications (Mrosovsky et al. 1984*a*). The principal distinguishing characteristics were the conspicuous germinal epithelium in females and immature seminiferous tubules in males.

Results

Out of the 200 eggs, 183 (91.5%) hatched (Table 1). Sexing was also possible of one late-stage embryo that appeared unlikely to hatch. Because the lower shelves of some

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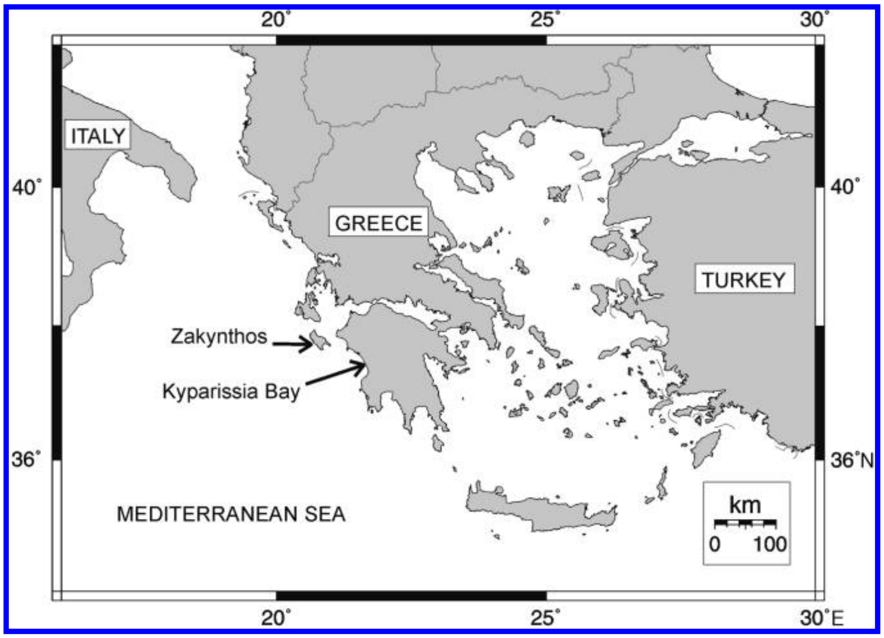
Fig. 1. Map showing location of Kyparissia Bay, and of Zakynthos, the most important loggerhead turtle (*Caretta caretta*) nesting area in Greece.



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incubators were cooler than their upper shelves, nine temperature groups were constituted by combining data from shelves in the five incubators (Table 1).

The pivotal temperature was calculated in several ways. First, to enable comparison with earlier work using this simple traditional method, a line was drawn connecting the successive sex-ratio points; the pivotal was the value at which this connecting line intersected the 50% level. Second, a sigmoidal curve was fitted to the data by the method of Girondot (1999); this provides a standard error and enables statistical comparisons with other data. We used versions 2.00 and 2.41 of Temperature Dependent Sex Determination. Third, a sigmoidal curve, shown in Fig. 2, was fitted by Prism2 (GraphPad, San Diego, Calif.) to the sex ratios for the nine temperature groups.

The pivotal values obtained by these three methods were respectively 29.37, 29.33 (±0.07 SE), and 29.25°C. For the purposes of discussion, we take 29.3°C as the pivotal temperature. The pivotal temperature of clutch T was 29.21°C (±0.09 SE) and of clutch U was 29.47°C (±0.11 SE).

The transitional range of temperature, the range between all male- and all female-producing temperatures (Mrosovsky and Pieau 1991), was only about 1.5°C. For the transitional range of temperature between 5 and 95% female, Girondot's (1999) method gives a value of 1.53°C. This steepness in the function relating sex ratio to temperature means that the pivotal temperature is a useful measure for inferring sex ratios.

The pivotal incubation duration was 52.6 days using a sigmoidal regression line (Prism2) (Fig. 2) and 52.61 ± 0.37 (SE) days using the method of Girondot (1999). The pivotal incubation duration of clutch T was 53.43 ± 0.43 days and of clutch U was 51.57 ± 0.62 days.

Discussion

The pivotal temperature (29.3°C) for these clutches from Kyparissia Bay was slightly higher than those obtained for loggerhead eggs from the southeastern United States (approximately 29.0°C) and Brazil (29.2°C) incubated by the same methods (Table 2). However, there was some overlap; some of the clutches from the United States had pivotals equal to that of clutch T from Greece in the present work. Moreover, even if statistical significance could be extracted from such data, with differences being a few tenths of a degree Celsius, caution about comparing results from different experiments is advised. A variety of methodological differences might affect the results.

Despite attempts at standardization, the exact moisture and amount of the vermiculite substrate may not have been same in each container. Correction factors for evaporative cooling (which might vary among eggs in different positions in an incubator) have been based on measurements of one or two eggs only. The exact temperature of each egg in a large incubator is not known. And when it comes to comparing work with the present methods with that with other methods, there are further differences; for example, in the way lines are fitted to the data, the accuracy of calibration, the resolution of thermometer scales, and the range of temperature variation. Therefore, with the present technology, when differences are only fractions of a degree Celsius and only few clutches are studied, there is danger of overinterpretation.

An example of overinterpretation is the conclusion of Chevalier et al. (1999) that leatherback turtles (*Dermochelys coriacea*) nesting on the west coast of Costa Rica and at French Guiana have a different transitional range of temperature, which is the range between male- and female-producing temperatures within which both sexes may differentiate (definitions in Mrosovsky and Pieau 1991). Because the functions relating sex ratio to temperature were determined on relatively few eggs, and not by the same experimenters, it would be more appropriate to emphasize that transitional range of temperature differed between particular

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Table 1. Details of samples and comparison of the two clutches of loggerhead turtles (*Caretta caretta*).

	Temperature (°C)								
Clutch	31.0±0.2	30.8±0.2	30.5±0.3	29.2±0.2	29.0±0.2	28.5±0.2	28.3±0.2	27.3±0.3	27.1±0.2
Number of eggs set									
T	4	8	8	12	20	20	8	12	8
U	4	8	8	12	20	20	8	12	8
Number hatched									
T	2	8	8	11	20	18	7	11	8
U	4	8	8	10	19	17	6	12	6
Hatchling mass (g)									
T	19.50±0.33	19.26±1.18	19.72±0.80	19.54±0.70	19.19±0.99	20.24±0.70	19.98±0.74	20.46±1.09	19.71±1.28
U	13.68±0.48	13.63±1.01	13.41±0.67	14.19±0.62	13.83±0.96	13.69±0.92	14.28±0.55	13.95±0.63	14.07±0.88
Number sexed									
T	2	8	8	11	20	18	7	11	8
U	4	8	8	10	19	18[a]	6	12	6
Percent female									
T	100.0	100.0	100.0	54.5	25.0[b]	11.1	0.0	0.0	0.0
U	100.0	100.0	100.0	30.0	5.3	5.6	0.0	0.0	0.0
All	100.0	100.0	100.0	42.9	15.4	8.6	0.0	0.0	0.0
Incubation duration (days)									
T	46.5±0.71	47.1±0.35	47.3±0.46	53.2±0.75	54.9±1.46	56.7±0.96	57.7±1.98	65.6±0.92	65.9±1.46
U	46.3±0.50	47.0±0.76	46.9±0.64	53.1±0.88	54.7±1.16	56.4±1.06	58.2±1.60	65.1±1.31	65.2±1.17
All	46.3±0.52	47.1±0.57	47.1±0.57	53.1±0.79	54.8±1.31	56.5±1.01	57.9±1.75	65.3±1.15	65.6±1.34

Note: Values are given as the mean ± SD.
[a]One embryo was removed before hatching.
[b]One animal was diagnosed as male but with slight signs of intersexuality.

Table 2. Pivotal temperatures of loggerheads.

Location	Pivotal temperature (°C)	Clutches represented[a]	Reference
Laboratory studies			
Southeastern United States	30.0	5	Yntema and Mrosovsky 1982
Southeastern United States	29.0[b]	6	Mrosovsky 1988
Queensland, Australia	28.6	6	Limpus et al. 1985
Queensland, Australia	29.0	?	Georges et al. 1994
Bahia, Brazil	29.2[b]	2	Marcovaldi et al. 1997
Japan	29.7	4?	Matsuzawa et al. 1998[c]
Greece	29.3[b]	2	This study
Field studies			
Turkey and Cyprus	28.5–29.0	8	Kaska et al. 1998
South Africa	~29.1	17	Maxwell et al. 1988

[a]Usually only a subsample of a clutch was studied.
[b]Same methods used in these experiments; see text for some methodological differences between other experiments.
[c]Abstract only, no details given.

clutches in particular experiments. Whether these findings stem from true regional differences or are individual differences or are methodologically derived is not yet established.

Ideally, to demonstrate differences in pivotals from different regions, larger samples of eggs from the two areas should be incubated simultaneously in alternating positions within the same incubator (cf. Mrosovsky 1988). With such a procedure, differences in pivotal of as much as 1°C have sometimes been detected between clutches laid on the same night in the same area (Mrosovsky 1988, 1994). The difference between the two clutches studied here was only a quarter of a degree. However, the difference in pivotal incubation duration was almost 2 days and significant. Possibly, the smaller size of clutch U eggs and hatchlings (Table 1) promoted faster incubation (also see Hewavisenthi and Parmenter 2000).

Caution is also appropriate for comparisons of pivotal incubation durations. For instance, the temperature during the days of transport from beach to incubator may differ between experiments and so affect overall incubation duration. When eggs were taken from Brazil to Canada, they were kept in air-conditioned rooms as much as possible during the interval between hatching and arrival in the laboratory (Marcovaldi et al. 1997). Other procedures that may affect the specification of incubation duration are the criteria for

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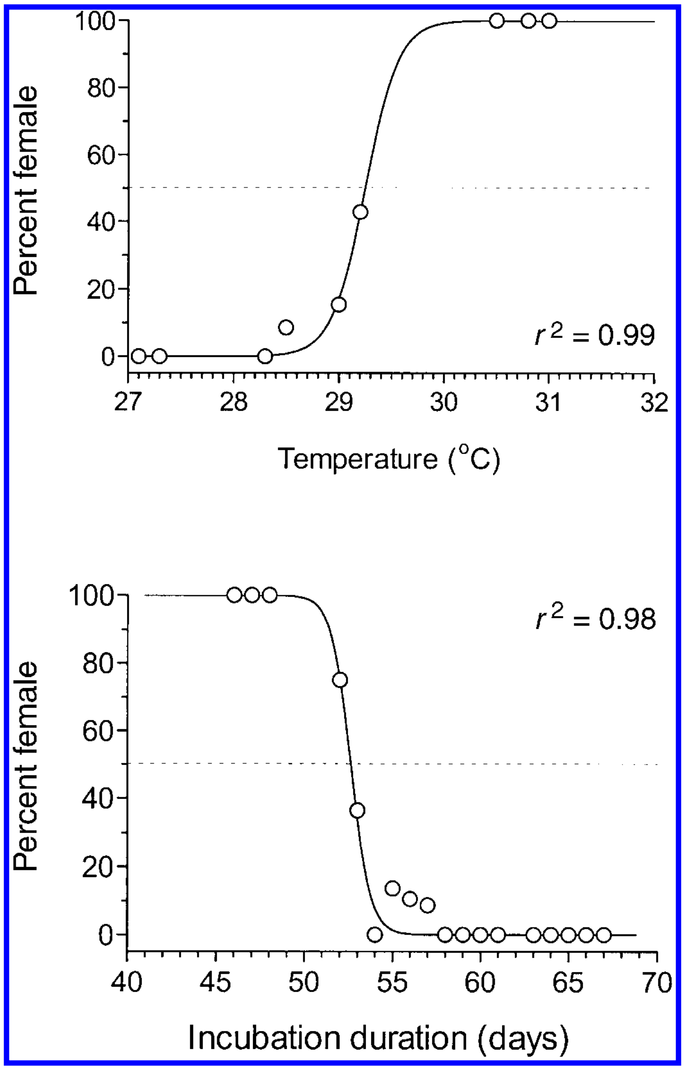
Fig. 2. Percent female as a function of temperature (top) and incubation duration (bottom). Sigmoidal curves fitted by Prism2 (GraphPad).



hatching and the frequency with which incubators are inspected for hatching. These variables have not been explicitly standardized in experiments.

Raising such caution is not the same as saying that small differences are unimportant. When nest temperatures are near the pivotal levels, small differences in pivotals could have sizeable effects on sex ratio. But to make progress in specifying small geographic differences, if they exist, what is needed are incubators that reliably control ambient temperature throughout to within 0.1°C or more experiments with eggs from different regions incubated simultaneously. Until such experiments have been carried out, we prefer to emphasize the general similarity in pivotal temperatures of loggerheads from regions of the world as far apart as Greece, the United States, and Brazil.

With these pivotals close to 29°C, given the high beach temperatures prevailing in the United States and Brazil and the corresponding short incubation durations, female-skewed production of hatchlings is to be expected (Mrosovsky and Provancha 1992; Marcovaldi et al. 1997; Hanson et al. 1998; Naro-Maciel et al. 1999). With the present provision of a pivotal temperature for a Mediterranean population of loggerheads, the previous inferences (based on short incubation durations and warm temperatures) of highly female-skewed sex ratios in Cyprus are now better justified. Nest temperatures in Cyprus can reach as high as 33°C and generally exceed 30°C, and incubation durations in the field often are lower than 50 days (Godley et al. 2001*a*, 2001*b*). Although the present pivotal temperature is slightly higher and the pivotal incubation duration slightly lower than the values assumed in those previous calculations, in Cyprus the sand is so warm and the incubation duration so short that a small adjustment in the pivotal can barely affect the estimated approximately 90% production of females there.

For other parts of the Mediterranean, there are some indications that temperatures may be closer to pivotal levels. For instance, at Kyparissia Bay in 1987, a mean incubation duration of 55.5 days was obtained with a sample of 50 (Margaritoulis 1989). These values are for field incubation durations that include the interval between hatching and the emergence at the sand surface a few days later. This interval has not been adequately researched but is probably about 4 days for loggerheads (Godfrey and Mrosovsky 1997). If 4 days is added to the 52.6 days obtained here for pivotal duration to hatching, then it gives an estimated field pivotal of 56.6 days. This is similar to the 55.5 days for Kyparissia Bay in 1987, suggesting that in some years, appreciable numbers of males might be produced there. More generally, female biases at other beaches in the Mediterranean may not be as extreme as those in Cyprus, which has the shortest recorded incubation durations in the region (Godley et al. 2001*a*, 2001*b*; Ilgaz and Baran 2001). At Zakynthos (Fig. 1), the largest documented loggerhead nesting aggregation in the Mediterranean, mean seasonal (n = 4) incubation durations ranging between 57.4 and 61.9 days have been found (D. Margaritoulis and K. Katselidis, unpublished data). Nevertheless, there are other Mediterranean beaches on which incubation durations appear to be several days less than the estimated field pivotal of 56.6 (Türkozan 2000; Godley et al. 2001*b*). Taken together, the available reports giving data on incubation duration lead one to believe that hatchling sex ratio in the Mediterranean may vary considerably among beaches.

This conclusion, however, should be qualified as tentative. Most papers with values for incubation duration provide few details of how the sample was constituted. For example, if some nests near the water are moved to save them from inundation, the remaining natural nests available for sampling might comprise an undue proportion of nests higher up the beach where it might be slightly warmer. This is not the only reason why any attempt to estimate sex ratio throughout the Mediterranean would be premature. To do this properly would require considerable additional information, such as data on incubation durations for different parts of the season, together with the number of turtles nesting in those different parts. This would be needed for all of the principal nesting beaches. At present for Libya, which may host an appreciable number of loggerheads (Laurent et al. 1997), adequate information is lacking even on the number nesting there, let alone on incubation durations. Moreover, emergence of loggerhead hatchlings in the Mediterranean is often asynchron-

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ous (Kaska et al. 1998; Türkozan 2000; Houghton and Hays 2001; Rees 2003). Differences of as much as a week can exist between the first and the last emergence. Reports in the literature do not always state how incubation duration for a clutch emerging over several days is specified. Estimates of sex ratio made from incubation duration could be improved by taking the extent of asynchronous emergence into account and by better knowledge of the variability in the hatch–emergence interval.

Finally, it would also be desirable to determine pivotals and transitional ranges of temperatures of clutches from other parts of the Mediterranean and not base too much on the present limited sample. The data given here for Kyparissia do, however, provide at least some start. The pivotal value near 29.3°C reinforces the impression of a worldwide conservatism in pivotal temperatures in loggerheads.

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