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The ecology and sex determination of the pig-nosed turtle, *Carettochelys insculpta*, in the wet-dry tropics of Australia

By

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ABSTRACT

Much of what we know about temperature-dependent sex determination (TSD) in reptiles stems from constant temperature incubation studies in the laboratory. In recent years, as TSD studies moved into the field it became evident that TSD was much more complex than previously thought. The present study attempted to reveal the complexity of TSD, as it relates to other features of the species' biology and physical characteristics tractable only in the field, such as fluctuations in incubation temperature and reproductive life history. To this end I studied the ecology of the turtle *Carettochelys insculpta,* a TSD species inhabiting the wet-dry tropics of northern Australia from 1996 to 1998. I tested hypotheses associated with movements, activity, behaviour, reproduction, nest site choice, nest temperatures, embryonic survival, embryonic aestivation, hatch-ling sex ratios, and emergence in the species. Each of these was also considered in the context of the influence of the wet-dry tropics.

Compared to other turtles inhabiting lotic habitats, *C. insculpta* occupied considerably larger home ranges, covering up to 10 km of river. Of previously published factors influencing home range size, low productivity of the (micro) habitat may best explain the extensive home ranges in *C. insculpta.* Patchiness and low nutrient value of the chief food (aquatic vegetation) of *C. insculpta* may force turtles to cover large expanses of river to acquire sufficient energy for growth and reproduction. Females were more active, moved farther, and occupied larger home ranges than males. Home ranges of females comprised 1-4 activity centres, many of which were associated with thermal springs. I suggest that females may exhibit increased activity and movements relative to males because of sexual inequality in parental investment, where food is particularly limiting (e.g., in species with biennial

reproduction). Biennial reproduction in the population allowed the examination of the influence of reproductive condition on home range size, movements, and activity. Reproductive condition did not influence home range or activity, but gravid turtles moved father between successive sightings than non-gravid females. Individual data corroborate these findings, with females moving farther between successive sightings while gravid compared to while spent. Contrary to previous reports, turtles did not appear to move into estuarine areas or lowland flood plains during the wet season, but moved into the riparian forest and possibly into wetlands adjacent to the main channel in the vicinity of their dry season home ranges.

During the study I documented the turtles' use of small, localized thermal springs discharging from the river bottom. Dataloggers attached to the carapace to monitor ambient water temperatures recorded the frequency and duration of thermal spring use by individuals. Turtles used the thermal springs frequently during the winter (4-6 months) when river temperatures were lower than that of the thermal springs ($\bar{x} = 29 \pm 0.52°$ C). Turtles often utilized thermal springs for several consecutive hours, leaving the springs only to surface for air. Thermal springs may be derived from ground water (which maintains a temperature equivalent to the annual mean air temperature), rather than from a specific geothermal heat source. Nine of 19 radio-telemetered adult females were seen to use thermal springs, of which seven were gravid and two non-gravid. Thus, gravid turtles may seek thermal springs more than non-gravid turtles. Frequency, duration, and timing of usage collectively suggest active thermoregulation as the primary function of thermal spring use. Utilization of thermal springs probably permits turtles to be more active in cooler months, which may enhance growth rates and accumulation of energy for reproduction. Onset of nesting along river stretches with thermal springs preceded nesting in a stretch not

known to have thermal springs by 24 days. Thus, I speculate that by warming themselves on thermal springs in the months prior to nesting, turtles may have accelerated follicular development and nested earlier.

Female *C. insculpta* matured at ca. 6 kg body mass (38.0 cm carapace length, 30.5 cm plastron length). Turtles produced egg sizes and clutch sizes similar to that of other turtle species of similar size. Turtles reproduced every second year, but produced two clutches in each breeding year, ca. 40 days apart. Thus, it appeared that females were energy limited, possibly due to the low available energy content of the dry season diet (aquatic vegetation). Life history theory predicts that if some costly behaviour is associated with reproduction, skipping years could reduce that cost and allow savings to be directed into future reproduction. The present study revealed no obvious accessory behaviour in the population. Within years, clutch mass did not differ between early (first) and late (second) clutches. However, earlier clutches tended to have more and smaller eggs per clutch but than later clutches, a new finding for turtles that has been demonstrated in lizards and other animals. Because the study spanned both years with 'big' and 'small' wet seasons, I was able to examine how the magnitude of the wet season influenced reproductive characteristics. Following big wet seasons turtles produced larger, heavier, and more eggs per clutch than they did after small wet seasons. Relationships among body size, egg size, and clutch size were evident after two big wet seasons but not apparent after two small wet seasons. Collectively, annual variation in reproductive characteristics and current life history theory suggest that a big wet season is a plentiful time for the turtles.

I investigated beach selection of nesting pig-nosed turtles *(Carettochelys insculpta)* along a 63 km stretch of river in 1997 and 1998. I used three classes of beaches to examine beach choice: beaches with nests, beaches with only crawls, and

beaches without nests or crawls. Across these beach types I compared aspect, solar exposure, temperature, substrate moisture, height, water depth at approach, and the height of cohesive sand. I located 82 nesting beaches with 221 nests, and identified 171 potential nesting beaches based on previously published criteria. Beaches with nests had a greater substrate moisture content and corresponding higher cohesive sand line (hereafter CSL) than beaches without nests. Beaches with nests also had a higher CSL than beaches with only crawls. Apparently, turtles could not excavate a nest chamber above the CSL due to loose substrate consistency causing sand to fall in on itself. Turtles could only nest at low elevations below the CSL on beaches with lower substrate moisture. Turtles apparently avoided nesting on these beaches due to the higher probability of nest flooding, as corroborated by a concurrent study. Beach temperatures increased with a seasonal increase in air temperatures, and were influenced by aspect and total angle of solar exposure. Temperatures did not differ among beaches with nests, beaches with only crawls, and beaches without crawls or nests. Therefore, there was no indication that turtles were manipulating offspring sex through choice of nesting beach. However, turtles may be manipulating sex by nesting in areas with particular thermal characteristics *within* beaches.

Two related aspects of hatchling emergence were studied. Using emergence phenology data, nest temperatures, historical weather data, and a developmental model, I tested the hypothesis that delayed hatching occurred in *C. insculpta,* and that such a delay would allow hatchlings to time their emergence to match the onset of the wet season. Hatchling *C. insculpta* emerged, on average, 17 days later than dates predicted from a developmental model. Combined with observations of hatchlings remaining in eggs until emergence, these results confirmed delayed hatching in nature. This delay was synchronized with initial river rises associated with the onset

of wet season rains, and is consistent with published criteria for embryonic aestivation. On a diel scale, I generated predictions of two potentially competing models for nocturnal emergence in hatchling turtles, based on the knowledge that air temperatures decrease with season during the emergence period. A test of those predictions for *C. insculpta* produced ambiguous results. However, further analysis indicated that *C. insculpta*, and probably other nocturnally emerging turtle species, respond to a decline in diel temperature rather than an absolute temperature. The former would ensure nocturnal emergence, while the latter is experienced during the day as well as at night. Nocturnal emergence may be associated with nesting in open microhabitats.

The 'decision' of when and where to nest can influence both offspring survival and hatchling sex ratios in animals with temperature-dependent sex determination (TSD). Knowledge of how these maternal attributes influence the incubation environment is an important first step in hypothesizing why TSD evolved in a particular species. 1 studied the influence of nest site choice and timing of nesting on embryonic survival and hatchling sex ratios. Predation and flooding were the major sources of embryonic mortality. Embryonic survival was influenced by both lay date and nest site choice: In one year when nesting began later, nests laid later and at lower elevations were destroyed by early wet season river rises. In other years early nesting precluded flood mortality. However, turtles did not nest at the highest available elevations. I hypothesized that turtles were unable to nest at higher elevations because the sand was dry and not cohesive. A field experiment demonstrated that turtles were constrained to nest at lower elevations where they could construct a nest chamber. A mathematical model predicting hatchling sex from fluctuating temperatures was applied to temperature data from 102 natural nests. Results

confirmed a type la pattern of TSD, whereby males are produced from cooler temperatures and females from warmer temperatures. The principal determinant of hatchling sex was lay date. Clutches laid earlier in the season produced mainly males, while later clutches yielded mostly females, due to seasonal ramping of air and sand temperatures. However, nest site choice also exerted an influence on hatchling sex. Female-producing clutches were deposited at higher elevations than male-producing clutches. The onset of nesting was not influenced by water temperatures, but may have been related to the magnitude of the previous wet season(s). Turtles nested earlier after two 'big' wet seasons and later following two 'small' wet seasons. This pattern indicates that the wet season is a plentiful time for the turtles. Adaptive 'differential fitness' models for the evolution of TSD have recently been reviewed and clarified. The differential fitness model that best fits *C. insculpta* is the 'time-matching' model, whereby one sex benefits more than the other from early hatching. Male *C. insculpta* hatched 2-3 weeks earlier then females, on average. Benefit to early hatching males and, therefore, the ultimate selective mechanism (e.g., growth, time to mature) is unknown. Obtaining such data will likely prove difficult in such a long-lived species.

A recent adaptive explanation for the evolution and maintenance of temperature-dependent sex determination (TSD) in reptiles rests upon the assumption that mothers can predict or manipulate offspring sex. I postulated that four physiological and behavioural criteria must be met in order for this assumption to be valid: (1) a strong correlation must exist between substrate temperatures during nest site choice and nest temperatures during the period of development when sex is determined in the egg (thermosensitive period = TSP). (2) Assuming that (1) is possible, mothers would need to be capable of correcting for temporal factors obscuring the predictable thermal

characteristics of nest sites. This could be accomplished in two ways. By contracting nesting times mothers could assess the relative temperatures of alternate nest sites with some accuracy. A protracted distribution of nesting times could greatly reduce a mother's ability to distinguish between, for example, a cooler nest site at a warmer time and a warmer nest site at a cooler time. Alternatively, mothers would need to be able to incorporate temporal changes in nest site temperatures. (3) Sufficient variation in thermal profiles *among* nest sites, relative to the breadth of temperatures producing both sexes (pivotal temperatures), would be necessary. For example, if most nests produced both sexes, then depth of the eggs would be the deciding factor determining sex, leaving little opportunity for nest site choice to produce one sex or the other. (4) Mothers would need access to nest sites spanning a range of thermal profiles in order to produce either offspring sex. To this end, home range size relative to the number and location of nesting beaches should be important. I tested these four predictions in *Carettochelys insculpta,* a beach nesting turtle with TSD, using three years of field data on nest site choice, nesting times, thermal characteristics of nests, hatchling sex ratios, and movements of nesting turtles. A strong positive correlation existed between assessable substrate temperatures at nest site choice and mean daily TSP temperatures in all three years. However, the proportion of explained variation was highly variable among years, and low in 1998. Accordingly, the proportion of nests in which substrate temperatures at nest site choice predicted offspring sex correctly was low in 1998 (48-62 %, depending on treatment of the data). Nesting times were normally distributed, and combined with diel changes in nest site temperatures greatly reduce a turtle's ability to distinguish between sites that would produce different sexes. Considerable among-clutch variation in thermal profiles to produce variable sex ratios existed, agreeing with other studies on turtles. Radiotelemetry indicated that home ranges

encompassed several nesting beaches with differing thermal profiles, indicating scope for producing the desired sex. However, the seasonal increase in air temperatures resulted in an overriding effect of mostly males being produced in early (first) clutches and mainly females being produced in late (second) clutches. Collectively, the results suggest that *C. insculpta* mothers would find it difficult to predict, and therefore, manipulate hatchling sex, supporting the conventional notion that TSD mothers have little or no control over offspring sex.

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