ALLOCATION OF REPRODUCTIVE OUTPUT IN THE WESTERN POND TURTLE (*Clemmys marmorata*) IN SOUTHERN CALIFORNIA

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SIGNATURE PAGE

THESIS: ALLOCATION OF REPRODUCTIVE OUTPUT IN THE WESTERN POND TURTLE (*Clemmys marmorata*) IN SOUTHERN CALIFORNIA

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ABSTRACT

This study analyzes characteristics of allocation of reproductive output in the western pond turtle (*Clemmys marmorata*) at intra- and inter-population levels, based on data from three populations in southern California. At the Santa Rosa Plateau Ecological Reserve, 24 turtles were observed producing clutches from 1998 to 2000, and a total of 21 turtles produced clutches from 1992 to 1994 at the Chino Hills State Park and the West Fork of the San Gabriel River. No significant correlation was found between clutch size and egg size. A positive correlation was found between clutch size and maternal size. Within-individual and within-population variation in clutch size were generally found to be equal. Mean clutch size did not differ among years after removing the effects of body size, despite observable variation in environmental conditions. The optimal egg size theory was useful only in providing a theoretical framework to help explain the small variation in egg size. The frequency of captures of gravid females in 2000 was smaller than in the two previous years, suggesting that many turtles defer reproduction when resource availability decreases. This study emphasizes that clutch frequency is a critical life history component in turtles and that it is likely being regulated by resource availability. It also reinforces the idea that considering behavioral components, phenotypic plasticity, and environmental variation is essential to the understanding of reproductive output characteristics. The reproductive allocation strategy described for the western pond turtle is believed to be in accordance with expectations for long-lived, iteroparous species.

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INTRODUCTION

Life histories are generally interpreted as sequences of resource allocation processes during the lifetime of an organism (Roosenburg and Dunham, 1997). The evolution of life history and reproductive strategies has received a relatively good deal of attention in both theoretical and empirical studies (Zhang and Wang, 1994; Bernardo, 1996), but life histories of long-lived organisms, such as turtles, have not been thoroughly investigated very often, mainly because of the practical and experimental difficulties long-term studies impose (Tinkle et al., 1981). Studies of life history evolution are based on the assumption that resources are limited (Cody, 1966). As a direct result of that, reproductive strategies in sexually reproducing organisms are assumed to reflect tradeoffs between resource allocation to reproduction rather than to their growth or survival: the cost of reproduction (Reznick, 1985; Zhang and Wang, 1994). The evolution of reproductive strategies relate not only to the amount of energy allocated to reproduction, but also to the way this energy is allocated, shaping reproductive effort. These "allocation units" comprise a fundamental element of an organism's life history and they should result in a strategy that will simultaneously produce successful offspring and maximize the fitness of the female (Roosenburg and Dunham, 1997).

Studies in life-history evolution have been strongly influenced by the work of David Lack, who suggested that avian clutch size is under stabilizing selection, representing the maximum number of young for which the parents can provide enough food (Krebs, 1994). Several additional studies in birds and other oviparous organisms have increased our knowledge on the reproductive tradeoffs involving the cost of reproduction and the fitness of the parents and of the offspring (Monaghan and Nager, 1997). We are now fully aware that reproductive allocation processes depend on variables such as physiological state of the organism, resource availability, environmental conditions, and survival (life expectancy), and that they might represent tradeoffs among three main factors: available energy, quality of offspring, and quantity of offspring (Roosenburg and Dunham, 1997). The presence of these tradeoffs has been offered as an explanation of why clutch sizes in natural conditions should be smaller than Lack's (maximum) clutch size (Krebs, 1996).

Optimality Models: A Brief Overview. The total level of reproductive effort and the partitioning of this effort to individual offspring are two major aspects under analysis by optimality models (Congdon and Gibbons, 1987). The quality of offspring might be controlled by egg size or egg components, and the quantity, in turn, adjusted by both clutch size and clutch frequency. Optimal egg size theory (OES) predicts that egg size is under the control of two main selective processes: 1) natural selection acting to favor females that produce the greatest number of offspring, and 2) natural selection acting to favor larger offspring, assuming that they will have greater fitness (Roosenburg and Dunham, 1997). As a result, OES states that egg size will be optimized by natural selection to allow for maximum clutch size production with the minimum investment per egg necessary to produce successful offspring (Smith and Fretwell, 1974; Brokleman, 1975).

Bernardo (1996) has presented a detailed review of the empirical literature on the concept of "optimum propagule size" and has concluded that the understanding of this life history trait is unlikely to be achieved by "stiff" models, which do not take into consideration factors such as environmental variability as well as the physiology, genetics, and development of organisms. He states that propagule size, despite being widely studied in ecology, challenges optimality theories by showing abundant unexplained variation at many hierarchical levels in nature. He also suggests that, because of the peculiarities mentioned above for each organism and population, the diversity of life history strategies will likely require more than one general model, reflecting the diversity of mechanisms found in nature.

The Optimal Egg Size Theory: Applications for Turtles. Reptiles are particularly good organisms to be used for testing hypotheses derived from the optimal egg size theory for two main reasons: they can have large clutch sizes and they usually have no postovulatory parental care. When studying the evolution of reproductive effort in reptiles, the importance of fecundity tradeoffs (such as those between offspring size and number) has been a source of much discussion (Niewiarowski and Dunham, 1992). Although variation in egg size within lizard populations generally is negligible and many groups of lizards have a fixed clutch size (Congdon and Gibbons 1987), several researchers have shown the biological significance of such tradeoffs in lizards (Niewiarowski and Dunham 1992). In turtles, however, these tradeoffs seem to have interesting peculiarities. Besides having clutches of variable size and exhibiting no postovulatory parental care, chelonians show other characteristics that make them a useful taxonomic group for a study of the evolutionary tradeoff between egg size and number: 1) female chelonians typically will retain their entire clutch before laying; 2) the volume of their body cavity limits the number of eggs they can carry; 3) their body size (more precisely, the size of their pelvic canal) will limit the size of the egg for certain species (Elgar and Heaphy, 1989). Congdon and Gibbons (1987) discuss the need to consider a pelvic constrain model when analyzing the applicability of the optimal egg size theory to smaller-bodied turtle species. Egg size is expected to be strongly related to neonate size, which, in turn, is believed to be closely related to survivorship and, thus, fitness of offspring. For these reasons, egg size in turtles is expected to be under strong normalizing selection. These relationships have received support from research on turtle populations (Congdon et al. 1983; Roosenburg and Kelley, 1996).

Elgar and Heaphy (1989), in a paper presenting comparative evidence for chelonians, describe three main lines of evidence that selection is indeed acting on egg size for turtle species. First, the intraspecific data suggesting that egg size will affect survival for turtles (larger hatchlings, emerging from larger eggs, survive better than smaller hatchlings). Second, the observed trend that variation in clutch size is greater than variation in egg size, implying an optimal egg size. Finally, a positive correlation between body size and egg shape, suggesting that smaller turtles produce more elongated eggs than larger turtles, which produce more spherical eggs (less prone to desiccation); therefore, the risk of mortality due to a very small egg is probably greater than the risk of mortality through increased desiccation as a result of a more elongated egg.

Another variable, however, is supposed to be under selection forces that are potentially opposing the forces operating on egg size: the architecture of the pelvic girdle. This architecture is crucial for various critical aspects of a turtle's life history, such as terrestrial locomotion and nesting and mating behavior. Therefore, taking the possible constraints of the pelvic girdle on egg size into consideration could help explain the cases where smaller-bodied turtles show variation in egg size as body size increases, an observation that would otherwise contradict the expectations of the optimum egg size theory. Further evidence that pelvic girdle opening is under selective pressure in turtles had been provided by Long and Rose (1989), showing that females of three species examined (*Gopherus berlandieri*, *Kinostemon flavescens*, and *Terrapene ornata*) have proportionally larger pelvic canals than do males from the same species.

The Organism. The western pond turtle, *Clemmys marmorata* (Fig.1), is currently divided into two subspecies (Seeliger, 1945; Ernst et al., 1994). The northwestern pond turtle (*C. m. marmorata*) ranges from western Washington south to San Francisco Bay, also occurring in western Nevada. The southwestern pond turtle (*C. m. pallida*) is found from San Francisco Bay south into northern Baja California; it is, therefore, the subspecies present at the Santa Rosa Plateau Ecological Reserve (Fig.2).

The southwestern pond turtle is a Forest Service Region 5 Sensitive Species and a California Species of Special Concern (CDFG, 1991; Stephenson and Calcarone, 1999). According to Holland (1991), as few as six populations with thirty or more individuals might still exist in southern California (defined here as the region south of the Santa Clara River). It is more abundant northwest of the Santa Clara River (the northern portion of its range), where it occurs throughout sites in the Los Padres National Forest and Santa Barbara and San Luis Obispo Counties (Stephenson and Calcarone, 1999). This fact, however, does not mean that these populations are less susceptible to future declines than those from southern California. Habitat destruction and alteration, the main cause of decline for pond turtle populations, show no sign of reduction throughout the southwestern pond turtle's range, and its current official status does not ensure the necessary habitat protection (Brattstrom and Messer, 1988; Brattstrom, 1988). Stephenson and Calcarone (1999) indicate that pond turtle populations in southern California are sufficiently rare to warrant site-specific management attention. More research and surveys are definitely needed to determine the viability and proper management actions for all remaining populations of this taxon.

Since the publication of Rathbun et al. (1992) on nesting behavior and movements of the western pond turtle, an increasing number of studies have been done on its reproductive ecology, in different populations, in order to clarify some aspects still not fully understood. Nevertheless, its reproductive ecology still needs to be further studied. Holland (1991) states that size and age at first reproduction vary geographically, and that secondary sexual characteristics and development of gonads are apparent throughout the range by the time the animal reaches 110mm. Many factors determine the age at which female turtles lay eggs for the first time, as well as the time of the year oviposition occurs and the number of clutches per year. These factors include, but may not be limited to, the availability of food, seasonal temperature, and location (Holland, 1994). Typically, the pond turtle will lay one clutch with one to thirteen eggs every other year, and oviposition occurs from late April to late July (Holland, 1994). Double-clutching and annual reproduction may be more common than initially suspected (Goodman, 1997b). Nests are excavated out of the watercourse, usually from 1.5 to 402 meters away (Goodman, 1997a; Holland 1991, 1994). Females leave water in the late afternoon and move upland to areas with compact, dry soils, covered with sparse vegetation (Feldman, 1982). Then, they empty the contents of the bladder onto the soil and excavate the nest with the hind limbs. The depth of the nest varies, but it usually ranges from 90 to 125mm, and the whole process may take from two to over 10 hours. (Holland, 1994)

After depositing the eggs (Fig.3), the female forms a "plug" with soil and vegetation she scrapes into the neck of the nest. During this whole time, females are very sensitive to any disturbance, and may abandon the building of the nest if slightly disturbed (Goodman, 1997a). This is the main reason why observations of such events are relatively rare. If the female is successful in building and laying the eggs, hatchlings will emerge in about 80 to 122 days (Holland, 1991, 1994; Goodman, 1997a). Hatching in fall, neonates may overwinter in the nest, leaving to enter aquatic microhabitats during spring.

Because the western pond turtle is very sensitive to environmental disturbances, courtship behavior is hardly ever observed. Courtship displays occur underwater from February to November, and mating (which usually takes place underwater as well) from April to September (Holland 1991, 1994). Holland (1991) described the only observation ever recorded of courtship displays for the western pond turtle, which involved posturing and extensive limb movements by the male.

This Study. This study investigates some biological and ecological factors that might influence variation in the reproductive output of western pond turtles. Pursued in the broad context of the evolution of reproductive strategies and tradeoffs in turtles, it focuses on one particular population, from the Santa Rosa Plateau Ecological Reserve (SRPER). Questions addressing interannual variation were approached by using data for this population only, because population-specific ecological and habitat characteristics are greatly responsible for the complexity inherent in studies of allocation of reproductive output. When appropriate, in order to determine patterns within species, all other questions were approached by analyzing pooled data from this and two other southern California populations of the western pond turtle, from Chino Hills State Park (CHSP) and from the West Fork of the San Gabriel River (WFSGR). This approach was valuable for providing a greater sample size of a species whose reproduction is relatively difficult to study in the field. In addition, it helped to reveal trends at the species level with greater clarity than an approach limited to a single population. Data for these two latter populations were obtained from Robert Goodman, representing research for the reproductive seasons of 1992, 1993, and 1994 (Goodman, 1997a).

I ask in this study if, for the populations of *Clemmys marmorata* examined, egg size is optimized in accordance with expectations of the optimum egg size theory. Congdon and Gibbons (1987) stated that constraints on the architecture of the pelvic girdle existed in small emydid turtles, based on a detailed study of three species. For this reason, it was expected that such constraints would also be found in *Clemmys marmorata* and that, in this case, the observed egg size would not be optimized by natural selection. Before exploring this question, however, it is necessary to assess the role of maternal size in reproductive output, so this possibly confounding variable could be incorporated in my interpretation of the reproductive strategy of the western pond turtle. Finally, other essential components of reproductive allocation should also be considered, including a variation in reproductive output in the form of clutch size as a response to varying resource availability.

As an indicator of resource availability, I have used rainfall data from the Santa Rosa Plateau area. The effects of rainfall on the reproductive output of turtles at the SRPER is likely to be biologically important for several reasons. First, hydrological conditions at the SRPER are dependent on rainfall (Saputo, 2000). Second, these turtles are highly aquatic and most of their food is obtained in the water (Ernst et al, 1994). Third, the hydrological structure of the turtle habitat at the SRPER (deeper pools connected by shallow, seasonal creeks) indicates that their resource and habitat utilization strategies are highly dependent upon the amount of rainfall available (Pires, unpublished data). Finally, also because of the habitat characteristics and because of the number of turtles at the SRPER, it is possible that food availability, availability of basking sites, water quality, susceptibility to predation, levels of stress caused by aggressive interactions, mate competition, and availability of refugia are all affected by lower water levels due to reduced rainfall. Therefore, rainfall patterns can seriously affect the overall habitat quality and resource availability for turtles at the SRPER.

This study addressed, then, the following general questions, based on reproductive data for the western pond turtle: 1) Is total reproductive output related to maternal body size? 2) Is there evidence to support the hypothesis that natural selection has optimized egg size? 3) How do maternal size, egg size, and clutch size relate to each other in shaping total reproductive output? and 4) How does resource variation affect total reproductive output?

MATERIALS AND METHODS

The Study Site. The Santa Rosa Plateau Ecological Reserve (SRPER) is located at the southern end of the Santa Ana Mountains in southwestern Riverside County, near the city of Murrieta, California, and it covers an area of about 8,300 acres (Figures 2, 4, and 5). The USGS topographic maps of Fallbrook, Temecula, Wildomar, and Murrieta encompass the region of the Reserve. Several rather rare communities are found at the SRPER, including vernal pools, coastal sage scrub, and bunchgrass prairie. Engelmann oak (*Quercus engelmanii*) and coast live oak (*Q. agrifolia*) woodlands cover granite mounds, visible at most localities within the Reserve. The plateau is bordered by slopes covered with chaparral, which has been replaced by avocado orchards in some areas (Lathrop and Thorne, 1985). Lathrop and Thorne (1985) provide a complete account of the flora at the SRPER.

Ground water flows through silty-sandy-gravel, with cobble and bolder-sized material forming the aquifer, and is forced up by granite rock (Saputo, 2000). This geological feature creates perennial pools ("tenajas"), which comprise most of the turtle habitat at the Reserve. Creeks with seasonal water link some tenajas to each other. The Cole Creek drainage system, originating in the upper regions of the Plateau, is divided into two main parts, Sylvan Creek and the main channel, Cole Creek. Underwater vegetation and many rocks provide turtles with refugia. Descriptive data for the pools where most of the turtles were found are given in Table 1.

The Study. Turtles were captured from June 1998 to August 2000, at several sites in the SRPER. Turtles were captured by snorkeling, by the use of seine nets, or, most commonly, by the use of funnel-like nylon net traps (Legler, 1960) baited with fish (Fig.6). Holland (1991) states that, in general, trapping is a relatively inefficient method of capturing turtles of this species, giving preference to snorkeling. However, because of habitat characteristics at the Reserve, snorkeling can yield a lower capture rate per hour of effort, especially for inexperienced researchers and during dry seasons (when opacity of water increases). The type of bait had a noticeable effect on the efficacy of trapping: trapping was successful when using uncooked mackerel, mullet, or salmon, but not as successful when using canned sardines (with and without soybean oil) or canned cat and dog food. One trapping session consisted of placing up to ten traps throughout the aquatic habitats of the Reserve, and leaving them undisturbed for six to 12 hours. Trapping sessions from May to June occurred two to three times a week, and from June to August, five to 14 times a week.

Every turtle captured was sexed and marked using a standardized numerical system developed by Holland (1991) that is based on triangular notches made in the marginal scutes (Fig.7). Measurements of the carapace length (CL), from the first to the twelfth (last) right marginal scute, were recorded for all turtles captured (mm, Mitutoyo® dial caliper) (Fig. 8). Possible tooth marks, scars, or damage of any other kind in the turtles' shell and/or body also were noted. The turtles were immediately released back to the site of capture as soon as all pertinent data had been recorded. However, gravid females were first taken to a veterinary clinic to be X-rayed, or x-rayed in the field, so that clutch and egg sizes could be determined (Fig. 9). When radio transmitters (Telonics®, Mesa, Arizona) were available, they were attached with dental acrylic to the third vertebral scute of gravid females to allow for future location and observation of oviposition-related activities and habitat utilization. An adhesive, quarter-sized, white reflective dot also was attached with dental acrylic over the last vertebral scute of gravid turtles captured in 1999 and 2000, to facilitate future location and visual identification. The gravid turtles were, then, released back to the exact site of capture as soon as this process was completed. In most cases, this did not exceed 48 hours from the time of capture.

Most of the data on clutch size and egg size were obtained through x-ray radiographs of females that palpation indicated to be carrying eggs. It is pertinent, therefore, to briefly comment on the efficiency of palpation in detecting eggs, and the likelihood of failure to detect a gravid female, carrying only one or a few eggs.

X-ray radiographs have been used for several years to determine reproductive variables in turtles. It is a safe (Hinton et al., 1997) and precise (Gibbons and Greene, 1979) method that does not compromise the health of the female turtle and its offspring. Gibbons and Greene (1979) considered x-radiographs 100% accurate in revealing shelled eggs. There is a theoretical possibility that gravid females with few eggs were not detected through palpation in my study and, therefore, not x-rayed and not counted in the analyses. This would cause a bias in the data set towards females with larger clutches.

Because western pond turtles are small turtles, however, the likelihood of not detecting a gravid female is thought to be small.

Egg width for the clutch of each gravid female was determined by measurements from the radiograph to the nearest 0.01mm. Each egg was measured three times and averaged to minimize random error, and the measurements from all eggs of the clutch were averaged to determine mean egg width for a female. This value is the one reported as egg size for a female.

Statistical analyses were carried out using SYSTAT® v.9 for Windows® (SPSS Inc.) and Microsoft® Excel 2000.

Other Sources of Data. Rainfall data for the Reserve was obtained from the Burro Mesa/Santa Rosa Plateau Station (SAR), published at the website of the California Department of Water Resources, Division of Flood Management (http://cdec.water.ca.gov/), where daily and hourly precipitation measurements (in inches) are found. Monthly totals (in millimeters) calculated from these data are presented in Table 2.

Data from the West Fork of the San Gabriel River (WFSGR) and Chino Hills State Park (CHSP) populations were obtained from Goodman (1997a), where specific habitat characteristics for these populations can also be found. In all analyses with pooled data from all sites and years, the values for variables from females showing more than one clutch were averaged so that all data points were fully independent.

RESULTS

Gravid females. Table 3 summarizes all the data for the gravid females captured at the Santa Rosa Plateau Ecological Reserve (SRPER) during the period of this study. A total of 24 individual gravid females were captured at the SRPER from June 1998 to August 2000, providing a total of 31 individual clutches. Of this total, four individuals produced more than one clutch. Turtle #500 (CL = 142.9mm) was observed double-clutching in two consecutive years, 1999 and 2000. In 1999, it produced eight eggs in the first clutch and three eggs in the second; in 2000, the first and second clutches had six and five eggs, respectively. Turtle #570 (CL = 129.4mm) double-clutched in 1999 (first clutch with three eggs and second clutch with five eggs) and had at least one clutch in 2000. Turtle #586 (CL= 128.8mm) was observed with at least one clutch in 1998 and one clutch in 1999. Finally, turtle #599 (CL = 142.5mm) produced at least one clutch in 1999 and one in 2000. Out of the four females at the SRPER that were observed to produce more than one clutch, therefore, none of them had a consistent number of eggs between clutches (among or within years), the within-individual difference between clutch sizes ranging from one to five eggs (Table 3). For the two females double-clutching in 1999, one increased clutch size in the second clutch (from three to five eggs) and the other decreased (from eight to three eggs).

At the Chino Hills State Park (CHSP), nine individuals produced a total of 16 clutches for the reproductive seasons of 1992 to 1994 (Goodman, 1997a). Three individuals double-clutched in 1993, one of which produced an additional clutch in 1994. Of the remaining six individuals, one produced at least one clutch in all three years, one produced at least one clutch in two years, and four individuals were observed producing only one clutch (Goodman, 1997b). At the West Fork of the San Gabriel River (WFSGR), 12 individuals produced a total of 15 clutches, with two individuals producing clutches in consecutive years (1993 and 1994) and one individual observed producing one clutch in 1992 and another in 1994. The nine remaining individuals were observed producing only one clutch (Goodman, 1997a). For more specific information on the CHSP and WFGSR populations, see Goodman (1997a, 1997b).

Maternal Size. A comparative summary of the data from the three populations under study is presented in Table 4. The populations with significantly larger females (WFSGR, mean CL = 145.2mm and CHSP, mean CL = 144.4mm) also showed the highest mean clutch sizes (5.7 eggs), although this difference in clutch size was not statistically significant. The population with smallest females, from the SRPER (mean CL = 132.7mm), was the population in which turtles produced the smallest clutches (mean 4.5 eggs). In addition, the largest individual clutches (8 eggs for each of the three populations) were achieved by the largest females for two of these populations (CL = 157.5mm for the WFSGR population and CL = 153.8mm for the SRPER; at the latter population, another turtle, with CL = 149.8mm, also had a clutch of 8 eggs).

The smallest female found carrying eggs (#1605 at the SRPER) was 120.7mm in carapace length. The SRPER population in this study showed mean

CL significantly smaller (ANOVA, $F_{2,42} = 17.97$, $p<0.001$; Bonferroni adjustment, $p<0.001$) than the populations from CHSP and WFSGR. These two latter populations showed statistically identical mean CL values (Tukey's Multiple Comparison Test, $p>0.9$).

There was a weak positive linear relationship between egg size (ES) and CL ($r^2 = 0.123$, $F_{1,43}=6.04$, $p = 0.01$) and a stronger, positive linear relationship between clutch size (CS) and CL ($r^2 = 0.445$, $F_{1,43}=34.49$, $p<0.001$) (Figures 10 and 11).

Clutch Size and Egg Size. No significant difference was found in ES among all sites (ANOVA, $p = 0.941$). To examine the relationship between egg size and clutch size, I removed the confounding effect of maternal size by using a partial correlation analysis. The result indicated that the interrelationship between CS and ES was statistically equal to zero (partial correlation coefficient, $r = -0.025$; $df = 42$; $p>0.50$). An analysis of covariance, with CL as the covariate, revealed no significant differences in adjusted mean clutch size among populations ($p=0.834$).

By testing the differences between the coefficients of variation (CV) for CS and for ES ($Z_{\alpha(2)} = t_{\alpha(1),\infty}$; Zar, 1996), I found the CV for clutch size was significantly higher than the CV for egg size ($p<0.001$). Using this same test to compare the CV for clutch size within individuals with CV for clutch size within-populations, I found that, in 10 cases (out of the 12 individuals exhibiting more than one clutch, regardless of the time interval between clutches, in all populations), within-individual CV for clutch size was equal to the within-population CV (p>0.2 for eight individuals and 0.2>p>0.05 for two individuals).

Variation in Resource Availability at the Santa Rosa Plateau Ecological Reserve. Table 2 shows the total precipitation for the eight months prior to each of the three reproductive seasons under study. Despite the lack of a statistically significant difference among the means for those years, the average precipitation level for the month of February 1998 (725.93mm), during the El Niño year, was substantially higher than the average for the same month in other years (27.17mm in 1999 and 170.68mm in 2000) and for the historical data for Murrieta (60.96mm), the city near the study site. The effects of the El Niño condition on the turtle habitat at the SRPER were clearly observable: In 1998, water level was high enough for all ponds to be connected to each other by streams; it took months for the water table to be low enough to dry seasonal streams and isolate some ponds. The rainfall from February 1998 caused flooding at the SRPER and damage to the road system, with creeks overtopping their banks and stream channels being altered by the massive erosion caused by the heavy rainfall (Saputo, 2000). By the beginning of the dry 1999 year, because the water table was still filled with water from the El Niño year, the general aquatic habitat quality was decreasing until the reproductive season of the year 2000, when water level was the lowest for all years under study, even though the total precipitation for the 2000 rainy season was higher than the total for the year 1999. By the end of the 2000 reproductive season, some ponds had completely dried out, and this did not happen in 1999, thanks to the water left over from 1998. Therefore, in terms of habitat quality and resource availability for the SRPER population for the three years under study, I noticed a decrease from 1998 (when water was plentiful) to 1999 (when resources were available but at a noticeably lower level than in 1998) to 2000 (when most pools completely dried out). At the SRPER, pond turtle excrement has been observed to contain snail shell remains, aquatic adult insects (Hemiptera: Notonectidae; Coleoptera: Haliplidae and Hydrophilidae), varied aquatic vegetation, and insect larvae. These observations confirmed the information available on the feeding habits of this species, extremely dependable on water availability.

Variation in Reproductive Output Among Years. The differences in reproductive output among years for the SRPER population were analyzed in three different ways. Two analyses of covariance, holding maternal size constant, were conducted to assess the difference in CS and ES among the years 1998, 1999, and 2000. Neither CS (ANCOVA, $F = 7.603$, $p = 0.975$) nor ES (ANCOVA, $F = 5.181$, $p = 0.529$), showed a significant difference among years despite noticeable variation in total precipitation prior to each reproductive season (Table 2). In addition, the frequency of capture of non-gravid females (with $CL \geq 110mm$) was compared with the frequency of capture of gravid females in a chi-squared analysis of contingency table (Table 5). These results supported the statistical alternate hypothesis that the proportion of capture of gravid females depended on year.

DISCUSSION

The interactions of the factors involved in reproductive activities determine the adaptive value of a given strategy of allocation of reproductive output. Therefore, interpretations of life history patterns, such as the one presented below, are not complete until all of their components are looked at in a broader evolutionary context and are considered in conjunction.

Relation Between Body Size and Reproductive Output. The body size of reproductive females has been shown, in several studies of vertebrate ectotherms, to be important in relation to total reproductive output, with increased reproductive output being generally associated with increased body size (Congdon and Gibbons, 1983; Congdon and Loben Sels, 1991). It has been suggested, for example, that larger body size would increase the reproductive potential of *Clemmys guttata* by increasing its ability to store energy (Litzgus and Brooks, 1998). Despite this knowledge, it is generally accepted that there still is a lot to be learned about the relationships between maternal size and reproductive output and, more specifically, between female body size in reptiles and optimality concepts of reproductive allocation and parental investment (Congdon and Gibbons, 1985).

Because body size was observed to be confounded with other traits, the relationships among life history measures within species must be studied by first accounting for size (Buskirk and Crowder, 1994). In turtles, for instance, the maximum egg size they can produce will probably depend upon their body size

(Congdon and Gibbons, 1987). In the present study, carapace length (CL) was used as an estimate of maternal size and will be referred to interchangeably with "body size". Measuring CL is not the only way to estimate the size of a turtle. Alternative measurements include plastron length, carapace width, depth of shell, and combinations of these dimensions. Measuring and reporting analyses using CL has the advantage, however, of providing data comparable to other studies in turtle reproduction. Furthermore, in some species of turtles, body length of females (either plastron or carapace length) accounts for nearly all variation in total clutch mass (Congdon and Gibbons, 1985), and body mass and length have been found to be equally satisfactory expressions of body size (Gibbons et al., 1982). Two main parameters of reproductive output were measured: clutch size and egg size. In this first section of the discussion, I will look at their relationship to body size, independently. Later, I will look at their variation in relation to each other in order to better understand allocation of reproductive output in the western pond turtle.

Clutch Size Variation. Several lines of evidence suggest that, in *Clemmys marmorata,* maternal size has a key role in determining clutch size, the number of oviductal eggs present at the time of x-ray (Gibbons, 1982). First, the pattern observed for *Clemmys marmorata*, based on the pooled data gathered for reproductive females from the three populations under analysis, was that of a positive, significant relationship to body size (Fig.10). Second, intra-population analyses for all populations revealed a correspondence between maximum maternal sizes and maximum clutch sizes. Finally, after removing the effects of maternal size when comparing the clutch size among the three populations, we found that they were statistically equal.

When looking at results from others studies, one is better able to place this relationship in perspective. Lovich and Meyer (*in press*) observed a positive correlation between CL and clutch size in western pond turtles at the Mojave River. Other studies have also found a positive relationship between clutch size and maternal size within and across different species of turtles (Nieuwolt-Dacanay, 1997; Buskirk and Crowder, 1994; Congdon and Gibbons, 1983; Gibbons, 1982; see Congdon and Loben Sels, 1991, and Congdon and Gibbons, 1985, for more references). This relationship has also been observed in lizards (see references in Congdon et al. 1993).

Despite this large body of evidence suggesting the importance of body size in determining clutch size, other studies on turtle reproduction have pointed out that maternal size does not explain all variation in clutch size. In some cases, despite a positive correlation, a linear model is not the one that best explains the relationship between maternal size and clutch size (Gibbons et al., 1982). In other cases, it explains little of the clutch size variation (Tinkle et al., 1981) or nothing at all, such as in a study among species of marine turtles (Buskirk and Crowder, 1994). Turtle age, which might be closely associated with turtle size, has also been shown not to be a direct determinant of clutch size (Gibbons, 1982).

A closer analysis of clutch size variation for the populations in the present study reveals that, indeed, individual variation in clutch size can be quite substantial between years (decrease of four eggs, turtle #12 at Chino Hills State Park [CHSP] between 1992 and 1994; Goodman, 1997a) or within multiple clutches in the same year (decrease of five eggs, turtle #500 from SRPER in 1999) (Table 3). In addition, the minimum clutch size per site was not associated with the smallest turtles. Discovering and understanding the sources of variation in clutch size within a species is one of the objectives of life-history studies (Gibbons, 1982). It is, therefore, pertinent to search for this understanding through studies of the variation in clutch size within individuals and for the whole population, so that unexplained variation can be reduced. Because I have very limited data on multiple clutches from the same individual pond turtles (within and among years, maximum sample size is four clutches), it is difficult to adequately compare clutch size variation within individuals with variation within the population. My analyses seem to indicate that the intrinsic variability of clutch within-individuals is equal to the intrinsic variability of clutch size for the whole population. This same pattern was found in other freshwater turtles (Gibbons, 1982), implying that there might be a large effect of microenvironmental conditions on clutch size (Gibbons, 1982). These results are consistent with the optimal egg size theory prediction for turtles (that clutch size, rather than egg size, varies with varying environmental conditions), but this issue should not be so easily confirmed, since individual microhabitat and resource acquisition variables are very difficult to obtain and measure under natural conditions. An understanding of these factors, when available, will more clearly define the role of body size in clutch size variation for pond turtles.

At this point, it seems safe to conclude only that maternal size definitely plays a role in the reproductive allocation of pond turtles, but factors other than size also account for the observed variability (Tinkle et al., 1981). Gibbons et al. (1982) hypothesized that the variability and inconsistency in the body size - clutch size relationship in turtles would be a function of the upper limit of clutch size imposed by the female's body size as well as of the varying resource availability at different levels. The direct implication of this hypothesis, as they also point out, is that the maximum clutch size for a turtle species would vary among individuals and would depend on resource conditions on both time and spatial scales.

Egg Size Variation. Egg size (width) has also been measured as a parameter of reproductive output, and its lack of significant variation at various levels will be analyzed in more detail in the next section of this discussion. The measurement of egg width, in contrast with egg length, as an estimator of egg size has the advantage that it can be determined precisely from x-ray photographs (Gibbons and Greene, 1979). Besides this advantage, egg width has been experimentally shown to be a better estimator of egg mass than egg length (Congdon and Gibbons, 1983; Congdon and Tinkle, 1982; Gibbons and Greene, 1979). The weak correlation between maternal size and eggs size, observed in this study, was not surprising, based on expectations of the Optimal Egg Size theory (OES) and based on published analyses from several other turtle populations. The general pattern found in turtles is that increase in egg number, rather than size, is the usual way reproductive output is increased (Congdon and Gibbons, 1987; Congdon and Tinkle, 1982; Congdon et al. 1983). Egg size in turtles is generally found to be positively correlated with maternal size (Congdon and Gibbons, 1983; see Congdon and Gibbons, 1985, for more references), but this relationship may be weak and/or weaker than the relationship between clutch size and maternal size (Congdon and Loben Sels, 1991). Mean x-ray egg width was not significantly correlated with CL in western pond turtle populations studied by Lovich and Meyer (*in press*). Likewise, for other turtle species, egg size was not found to increase with maternal size at all (Congdon and Gibbons, 1983; Nieuwolt-Dacanay, 1997).

Because the relationship between egg size and maternal size is unclear, due to the results reported here and to the variable (but generally weak) relationships reported from other studies in turtle reproduction, the issue of egg size variation and its role in reproductive allocation strategies is better explored in the present study by attempting to answer the question of whether egg size is optimized in the western pond turtle and, perhaps, subject to a tradeoff with clutch size.

Optimization and Tradeoffs in Reproductive Allocation. Egg size is expected to be under strong selection, because it is an important determinant in offspring growth rate and survival in several vertebrate ectotherms (Chambers and Legget, 1996; Thorbjarnarson and Hernandez, 1993). Additionally, there is a minimum egg size, below which the offspring would not be able to survive (Elgar and Heaphy, 1989). Because of its biological significance, egg (in broader terms, propagule) size has been widely studied in ecology. There is still, nonetheless, a lot to be understood about its evolution, as abundant unexplained variation is found at many levels, imposing a great challenge to the optimal egg size theory (OES) (Bernardo, 1996).

The OES theory predicts that most of the variation in reproductive output should result in variation in the number of offspring, rather than size (Smith and Fretwell, 1974; Brockelman, 1975). This prediction has been emphasized by theoretical studies evaluating effects of several variables (competition, predation, survival, environmental variation, etc) on the evolution of egg size (Roosenburg and Dunham, 1997). Hence, whenever little variation in egg size is found in nature, attempts to explain this observation usually point to the OES theory. In their influential paper, Congdon and Gibbons (1987) point out that care must be taken when making use of the OES theory to explain low variation in egg size of turtles because of a possible morphological constraint (namely, the pelvic girdle aperture) to egg size (however, this is not to say that egg size in turtles is expected to be under weaker selection than clutch size [Iverson et al., 1993]). Thus, constancy of turtle egg size on spatial and/or time scales might be a direct consequence of a morphological constraint rather than an indication of the existence of an optimal egg size, determined by natural selection. The hypothesis that turtle egg size is primarily determined by morphological constraints, and not by a result of tradeoffs between size and number (that is, by selection for the optimal balance between the cost of reproduction and offspring fitness) can be tested experimentally by analyzing the variation of egg size as a function of body size: If egg size does not change as a function of female size, while pelvic aperture width does, this would indicate that egg size is optimized and not primarily constrained by turtle morphology.

Egg size in turtles, then, is predicted to be constrained in small species and in smaller individuals of all species (Long and Rose, 1989; Congdon et al., 1987; Congdon and Gibbons, 1987; Congdon and Tinkle, 1982). Ideally, when considering relationships between reproductive variables of turtles, it would be important to assess whether (or to what extent) pelvic constraints are operating in the population under study (Nieuwolt-Dacanay, 1997); an equal relationship of pelvic opening width and egg width to maternal body size would suggest, indirectly, that there is a morphological constraint to the maximum width of the egg for a given body size (Congdon et al. 1983; Congdon and Tinkle, 1982). In the present study, measurements of the pelvic aperture using the radiographs were not considered reliable. However, maternal size can be used as an indicator of the width of the pelvic aperture in the western pond turtle, for these variables have been shown to be positively related in the painted turtle, another small emydid turtle, with a slope equal to that of the relationship between egg size and maternal size (Congdon and Tinkle, 1982).

Analyses of the data for the western pond turtle revealed that, despite the significant difference in size among females from the SRPER population and the other two populations, the average egg size was found to be statistically equal for all populations, whereas the average clutch size was significantly smaller at the SRPER. These analyses, by pointing out a possible trend among populations of *Clemmys marmorata*, provide directions for future investigation, but are not capable of determining reasons for differences and similarities among populations (Elgar and Heaphy, 1989).

Another piece of evidence for optimization of egg size in western pond turtles, as discussed earlier, was that the relationship between egg size and maternal size was found to be weak when looking at pooled data for all populations as well as for intra-population data. These results lead me to believe, in general terms, that morphological constraints are not the only (or primary) factors determining egg size for the western pond turtle. Alternately, they tend to support the hypothesis that egg size has been optimized, as also seen in other turtle populations where no correlation between maternal size and egg size was found (Congdon and Gibbons, 1987; Congdon and Gibbons, 1985).

Similar to results for the western pond turtle presented here, studies on spotted turtles (*Clemmys guttata*) reported two populations with different mean body sizes showing relatively low variation in egg size, when compared to variation in clutch size, implying that egg size has been optimized in this species (Litzgus and Brooks, 1998). The significant difference between the coefficient of variation for clutch size when compared to the coefficient of variation for egg size for the western pond turtle, as presented here, was also observed in additional studies of reproductive allocation in turtles (Roosenburg and Dunham, 1997;

Nieuwolt-Dacanay,1997), and it supports the predictions of the OES theory, that clutch size variation should be much higher than egg size variation.

Another way to explore the applicability of the OES theory to the reproductive output of the western pond turtle is by further analyzing the relationship between clutch size and egg size. Studies of number and size tradeoffs are important components of understanding life history evolution. Finding a tradeoff (that is, a significant negative relationship) between egg size and number would support the expectations of the OES theory, because it assumes that energy for reproduction is limited and that the optimum egg size is adjusted, based on varying conditions and different optimum relationships between the cost of reproduction and offspring fitness (although this is not the only possible explanation; see Roosenburg and Dunham, 1997).

Very few comparative studies have provided evidence for a tradeoff between size and number (Elgar and Heaphy, 1989), but this result has been observed experimentally in some turtle populations (Roosenburg and Dunham, 1997; Buskirk and Crowder, 1994; Elgar and Heaphy, 1989). None of these studies, however, considered this negative relationship between size and number as a strong evidence supporting the optimality model, mainly because contrasting results were found at other levels within the same studies. Interestingly, one reported relationship between clutch size and egg size for the western pond turtle has suggested a tradeoff of this kind (Congdon and Gibbons, 1985). This study, however, was based on a very small sample size and the authors did not consider it supportive of the OES theory, because it was based solely on individuals from different populations and it was unable to assess within-population variability.

Another possible relationship between egg size and number is a positive correlation (that is, egg size increases along with clutch size). Some turtle populations have been reported to exhibit this relationship (Congdon and Loben Sels, 1991; Congdon and Gibbons, 1985; Congdon and Gibbons, 1983). This type of evidence supports the model of "developmental plasticity" (not very commonly analyzed for turtles, perhaps because it requires data on within-individual variation; see references in Roosenburg and Dunham, 1997). According to this model, females exhibit plasticity in their reproductive output, adjusting it based on environmental conditions (Roosenburg and Dunham, 1997).

A final possible relationship between clutch size and egg size is that of complete independence (that is, there is no observable tradeoff), as found in the present study. This is possibly the most common result reported for turtle reproductive patterns (Litzgus and Brooks, 1998; Congdon and Tinkle, 1982; Congdon et al., 1983; Nieuwolt-Dacanay, 1997) and it has been reported for the western pond turtle (Lovich and Meyer, *in press*). These results suggest that, as with several other turtle populations, no tradeoff exists between the number of eggs a female produces and the size of these eggs. As Flint et al. (1996) very appropriately observe, however, the lack of tradeoffs observed in studies of reproductive allocation can have different biological interpretations, depending on the physiology and the correlations between body size and reproductive variables for the organism under study. The data presented here indicate that reproductive output of the western pond turtle might be shaped by factors other than maternal size and the relationship between clutch size and egg size.

An extremely important component of turtle reproductive output that has been left out of this discussion and may be responsible for the lack of a comprehensive model to explain the variation encountered in turtle reproduction is clutch frequency. Clutch frequency is the number of egg clutches produced by an individual over the course of a single nesting season (Johnson and Ehrhart, 1996). Clutch frequency is one of the most challenging problems in reptile life history studies and is a critical variable for the understanding of reproductive effort in iteroparous animals (Bull and Shine, 1979; Gibbons, 1982). It has been emphasized as the dominant influence on variation in annual reproductive output in turtles (Elgar and Heaphy, 1989; Gibbons, 1992) and as an alternative for reproductive investment when there is an increase in reproductive potential, such as when body size increases (Congdon and Gibbons, 1983). Perhaps because clutch frequency is so variable, however, and because this variability is probably dependent upon ecological variables and individual differences, not much information is available about it in large, comparative studies. In comparison with single clutches, multiple clutches have the advantage of increasing fitness by distributing the annual reproductive effort in time and space, reducing the risk of nest predation as a consequence (Christiansen and Moll, 1973).

As pointed out by Gibbons (1982), "future challenges in the study of reproductive variation and ecology of turtles include relating environmental factors to the observed changes in clutch frequency, determining what microenvironmental factors or nutritional features affect clutch size of individual turtles, and incorporating egg size, along with clutch size and frequency, into the overall model for reproductive output." I will incorporate all of these reproductive variables when interpreting interannual variation of the reproductive effort of the western pond turtle at the SRPER in the final section of this discussion.

Other Sources of Variation. Although clutch size, egg size, and clutch frequency are definitely important measures of reproductive output, other variables of parental investment and resource allocation into reproduction are known to exist and should be mentioned. For example, the energy and time spent in search of an oviposition site possibly represent a very important component of life history evolution for turtles, perhaps under equally strong selection with egg size, egg number and other "hard components" in shaping life histories (Resetarits, 1996). Several behavioral components associated with oviposition, such as nest site choice and oviposition timing, have been studied (Crick et al., 1993; see Resetarits, 1996, for more references). Likewise, studies of parental investment in the form of the amount of material and energy invested per egg (Nagle et al., 1998; Congdon and Gibbons, 1985), and of use of oviductal sperm storage (Gist and Congdon, 1998), will help us understand life history evolution in turtles. Another related area of research is that of the evolution of egg volume and shape as a variable in reproductive tradeoffs. Some researchers have already looked at these aspects of turtle reproduction (Litzgus and Brooks, 1998; Rose et al., 1996; Iverson et al. 1993; Congdon et al. 1983), and these results certainly contribute immensely to our general understanding of reproductive allocation in turtles, by directing us towards more accurate ways of assessing reproductive effort. As discussed by Niewiarowski and Dunham (1994), a complete understanding of the evolution of reproductive effort can only come from theories that not only deal with the tradeoffs and optimization issues discussed earlier, but also with system-specific constraints on the allocation of energy to growth, maintenance storage, and reproduction.

All of the above-mentioned factors, however, were beyond the scope of the present study. A comprehensive model for reproductive allocation will need to incorporate our knowledge of behavioral, physiological, ecological, and evolutionary aspects of the life history of the organism(s) under study. The investigation of propagule size and number tradeoffs represents but a piece in the puzzle of life history evolution.

Effects of Resource Variation on Reproductive Output. Gibbons and Greene (1979) stated that one of the most intriguing evolutionary and ecological questions concerns the relationship between environmental characteristics and the amount of time, effort, or nutrients invested in reproduction. This broad question is still intriguing today, and I will explore parts of it here.

Because one of the basic assumption of the OES theory is that energy available to reproduction is limited (Smith and Fretwell, 1974; Brokleman, 1975), fluctuations in resource levels are important variables to be incorporated in studies of reproductive output. Resource availability and demographic environment are believed to be two major selective factors determining total reproductive effort and investment per offspring and, ultimately, shaping life-history evolution (Congdon and Tinkle, 1982). These observations are believed to be particularly relevant in the case of species that live and reproduce for many years, such as turtles (Tinkle et al., 1981). Comprehensive models of life history evolution, and more specifically of the evolution of reproductive strategies, are not likely to be described without incorporating environmental factors in them. Bernardo (1996) emphasizes that the understanding of egg size variation, under a broad evolutionary context, requires consideration of the ecological environment in which a mother is producing eggs as well as the one the offspring will enter. Environmental stability has been experimentally pointed to as a possible selective force influencing among-habitat variation in both clutch size and egg size in lizards (Rand, 1982). In birds, both egg and clutch sizes were observed to increase when resources were abundant, showing no tradeoff between quantity and quality of eggs as a response to environmental variation (Hakkarainen and Korpimäki, 1994). Remarkably, despite the understanding that resource variability needs to be incorporated in investigations of life history evolution, analyses including direct and objective use of resource variability have not been commonly reported in studies of allocation of reproductive output in turtles (Nieuwolt-Dacanay, 1997). The following discussion will compare my results with those of the published research on this aspect of turtle reproductive strategies.

In turtle populations, variability in critical life history traits, such as clutch size and clutch frequency, has been pointed out as presumably being a consequence of variation in nutrient availability and other environmental factors (Congdon and Gibbons, 1993). These factors would include rainfall, water level, area of the habitat, water temperature, seasonal timing, and interactions among these factors (Gibbons, 1982). The basic prediction for turtles, derived from the OES theory, is that clutch size will decrease under low resource conditions and increase with abundant resource availability (Iverson et al., 1993; Nieuwolt-Dacanay, 1997)—a prediction that has been supported by several theoretical studies of egg size evolution (Roosenburg and Dunham, 1997). This rationale has been used to suggest an explanation for observed natural variation in clutch size among years for turtles (Congdon and Loben Sels, 1991).

Gibbons et al. (1982) presented three main lines of evidence, based on large data sets for five freshwater turtle species, that extrinsic environmental factors govern annual reproductive output of individual turtles. First, they found that within-individual variation in clutch size was high. Secondly, annual variation for the number of reproductive females was high. Finally, they found that interannual timing of egg laying also was highly variable. These data, however, do not support the idea that annual variation in resource acquisitions or environmental factors has an *immediate* impact on individual clutch size in turtles. As a matter of fact, they were presented along with evidence that mean clutch size did not vary among years despite an "obvious year to year variation in measurable environmental factors" (Gibbons et al. 1982; Gibbons, 1982). Other studies also have shown evidence of constancy in clutch size among years, despite variations in resource availability (Lovich et al., 1999; Nieuwolt-Dacanay, 1997).

For pond turtles at the SRPER, when the effects of body size were removed for all females, neither clutch size nor egg size varied among years, despite the obvious variation in habitat quality and resource availability. These results, like those reported by the researchers mentioned above, do not support the hypothesis of variation in clutch size as an immediate response to variation in resource availability.

It seems that microhabitat conditions, and not necessarily large-scale resource variation, might be playing a determinant role in total reproductive output for individual turtles, and this would help explain the high within-individual variation in clutch size (as mentioned earlier) and the lack of variation of mean clutch size among years. This reasoning assumes that the maximum clutch size for an individual may not be realized at each reproductive season (or at each clutch within the same season, in the case of turtles with multiple clutches) because resources are limited and variable. Therefore, turtles are expected to show high variability in reproductive output (specially in clutch frequency and size, due to expectations about constancy in egg size, discussed earlier) because environmental conditions can vary greatly, both seasonally and annually. As a consequence, reproductive patterns in freshwater turtles may be very difficult to determine, especially in short-term studies.

Adding analyses of clutch frequency could help in the understanding of these patterns, even in short term studies like the one presented here. As discussed earlier, clutch frequency has been considered to be the most important reproductive variable in turtles and, perhaps, other iteroparous organisms (Gibbons, 1982). Because some individuals may reproduce for 25 years or more, the outcome of a single reproductive season or event is not as vital for the individual's fitness as it is for a short-lived organism, like most other reptiles that have been the subject of studies of reproductive allocation (Tinkle et al., 1981). The best available data for one of the most studied turtle populations in North America (painted turtles in southeast Michigan) suggest that many females, perhaps as many as 50% or as few as 30%, fail to reproduce every year (Tinkle et al., 1981). Clutch frequency of western pond turtles is poorly studied and understood (Goodman, 1997b). It has been suggested that the majority of the female western pond turtles reproduce in alternate years, with a small percentage producing clutches every year (Holland, 1994). The significance, frequency, and biology of double-clutching (producing two clutches in the same year) in pond turtles is not clear (Goodman, 1997b). Only one instance of double-clutching has been observed in the northern subspecies and three females were reported to double clutch in southern California (Goodman, 1997b). More recently, circumstantial evidence has suggested double-clutching for two female western pond turtles at the Mojave River (Lovich and Meyer, *in press*). In the SRPER, two individuals were observed to double clutch, and one of them (#500) did so twice, in consecutive years (Table 03). Goodman (1997b) has suggested that the increase in rainfall (and, consequently, in available resources) due to the 1992 and 1993 El Niño condition in southern California could have been a factor contributing to the observed double clutches.

Comparing the number of reproductive females among years, it seems reasonable to expect variation as a result of different environmental conditions. A few studies have confirmed this expectation. In box turtles (*Terrapene ornata)* reproductive data indicated that dry springs might cause turtles to defer laying eggs completely, rather than reducing annual output (Nieuwolt-Dacanay, 1997). This life history feature is not unusual in long-lived iteroparous organisms, particularly ectotherms (Bull and Shine, 1979). Desert tortoises (*Gopherus agassizii*) also have been observed responding to varying levels of rainfall in the same pattern: in years with an abundance of food plants, more tortoises reproduced and produced more clutches, with a relatively constant clutch sizes between years (Lovich et al., 1999). A four-year study on spotted turtles (*Clemmys guttata*) suggested that females may not have regular reproductive cycles, but instead produce eggs when sufficient stores of energy are available (Litzgus and Brooks, 1998). Likewise, painted turtle (*Chrysemys picta*) populations have been observed to forego reproduction in years when there were insufficient resources at the time females make reproductive commitments (Tinkle et al., 1981). Gibbons (1982) found that, indeed, the general pattern for freshwater turtles was to vary clutch frequency, rather than clutch size, as a response to varying conditions.

When analyzing the reproductive data for the SRPER population, the expectations described above were confirmed. The differences in frequencies of capture of non-gravid and gravid females found among years, possibly as a direct result of resource availability variation among years, imply that whenever resources are scarce, turtles will defer reproduction, rather than produce smaller clutches or smaller eggs (Table 2 and Figure 12). This result is not only consistent with the theoretical and empirical expectations, but also with our current knowledge of the reproductive biology of the western pond turtle and with natural selection processes. Oviposition-related activities for this species represent an enormous effort and risk. Turtles at the SRPER exhibited nesting behavior similar to that reported for other populations (Pires, unpublished data; Goodman, 1997a; Rathbun et al., 1992). Especially at the SRPER, where they find no natural predators in the water but are heavily harassed by large mammals when out of the water, nesting behavior represents a significant risk to their survival. If resources, at the time a female needs to make reproductive commitments, are such that it could only produce a clutch size substantially below its maximum (or optimal), natural selection would tend to favor the strategy to forego reproduction rather than be to exposed to a significant survival risk for a very low possibility of successful reproduction. This interpretation of the reproductive strategy of the western pond turtle may be an example of the incorporation of knowledge of oviposition-related activities and "hard components" (namely, clutch and egg sizes) to describe the adaptive value of reproductive outputs.

The OES theory describes some aspects of the reproductive output of the western pond turtle at the SRPER. For instance, the lack of significant variation in egg size among years, with and without taking maternal size into account. Clutch size variation among years, however, was not explained by the OES theory, since it did not vary when maternal size was accounted for, despite variation in environmental conditions. Current evidence appears to confirm the hypothesis that output adjustment to environmental conditions is partially accomplished by changes in clutch frequency. It would be important to understand the exact cues female pond turtles use to assess environmental condition. Finally, future and long-term studies of this population and species can substantially increase the sample size (especially for within-individual analyses) for investigating reproductive strategies and tradeoffs. These studies would help us achieve a better understanding of reproduction in the western pond turtle in the context of broader ecological and evolutionary questions.

CONCLUSIONS

The analyses presented here support the hypothesis that maternal size plays a role in shaping the reproductive output (particularly clutch size) of turtles, as shown in several other studies, but it cannot explain large portion of the variability in reproductive output. In the present study, carapace length was used as an estimate of body size and it was found to have a significant, positive effect on the number of eggs produced in a clutch. Moreover, when the effects of maternal size were removed, no difference in mean clutch size was observed among populations. These results were somewhat expected because of trends found in other species, because the reproductive potential of a turtle is expected to increase with its body size, and because this effect of size is expected to be more clearly noticeable in small-sized turtle species such as the western pond turtle. Nevertheless, clutch size was highly variable within individuals. In addition, egg size was only weakly related to maternal size and did not vary among populations, despite significant differences in body size.

The morphology of the pelvic girdle imposes an interesting challenge to optimality theories of egg size in turtles, and some studies have shown, directly or indirectly, that egg width is expected to increase with maternal body size, particularly in small-sized emydid turtles such as the western pond turtle. This expectation was not confirmed in this study. Two main lines of evidence apparently support the idea that egg size is optimized in the western pond turtle. First, turtles at different sites, despite their significant difference in carapace length, produced eggs within a very narrow size range. In addition, a comparison of the variability in egg size and clutch size also suggested that only egg size has been optimized by natural selection.

There was no clear relationship between egg size and number of eggs produced per clutch, in accordance with a common pattern found in other turtle species. The interactions between the number and size of eggs, like maternal size, do not seem to regulate reproductive output in western pond turtles. The absence of a tradeoff between size and number is not predicted by the optimal egg size theory. This result is consistent with the conclusion of other researchers that there is no comprehensive theoretical framework in which reproductive allocation processes in turtles can be accommodated.

The optimal egg size theory predicts that clutch size variation should be explained by variation in resource availability, but the present study, in accordance with several other studies of turtle reproduction, did not confirm this prediction in the exact terms proposed by the theory. It is still possible that resource availability affects clutch size, but the effects are not likely to be immediate and/or are difficult to measure because they occur at small scales and are subject to individual variation.

By incorporating the analysis of clutch frequency variation in the present study, the possible effects of resource availability on reproductive output could be observed. Turtles at the Santa Rosa Plateau Ecological Reserve responded to variation in resource availability by tending to defer reproduction in a season following a period of low resource availability. This result is consistent with a few studies conducted on other chelonians, and it certainly emphasizes the importance of clutch frequency in the reproductive biology of turtles, as other researchers have noted. In an evolutionary context, this "all or nothing" strategy (in contrast with producing fewer and/or smaller eggs in a reproductive season following a period of low resources) is supposedly a strategy of higher selective advantage for long-lived, iteroparous organisms. This hypothesis is strengthened when taking into consideration specific behavioral and ecological characteristics of the reproductive biology of the western pond turtle, specially regarding oviposition-related activities.

This study is but a limited attempt to interpret the reproductive characteristics of the western pond turtle in evolutionary and ecological contexts. Only long-term studies and large data sets, focusing on different levels, can more precisely help to address the topics that are still unclear in the evolution of turtle reproductive strategies, such as the specific biological and ecological variables controlling the number of eggs produced per clutch. More robust studies of within-individual variation, although constrained by practical difficulties, should be emphasized because they have the potential to elucidate several aspects of reproductive allocation strategies in turtles. In addition, by focusing on physiological and microhabitat variation within and among individuals, future studies are expected to start revealing more factors that influence reproductive allocation processes.

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Figure 1: Southwestern pond turtle (*Clemmys marmorata pallida*) at the Santa Rosa Plateau Ecological Reserve

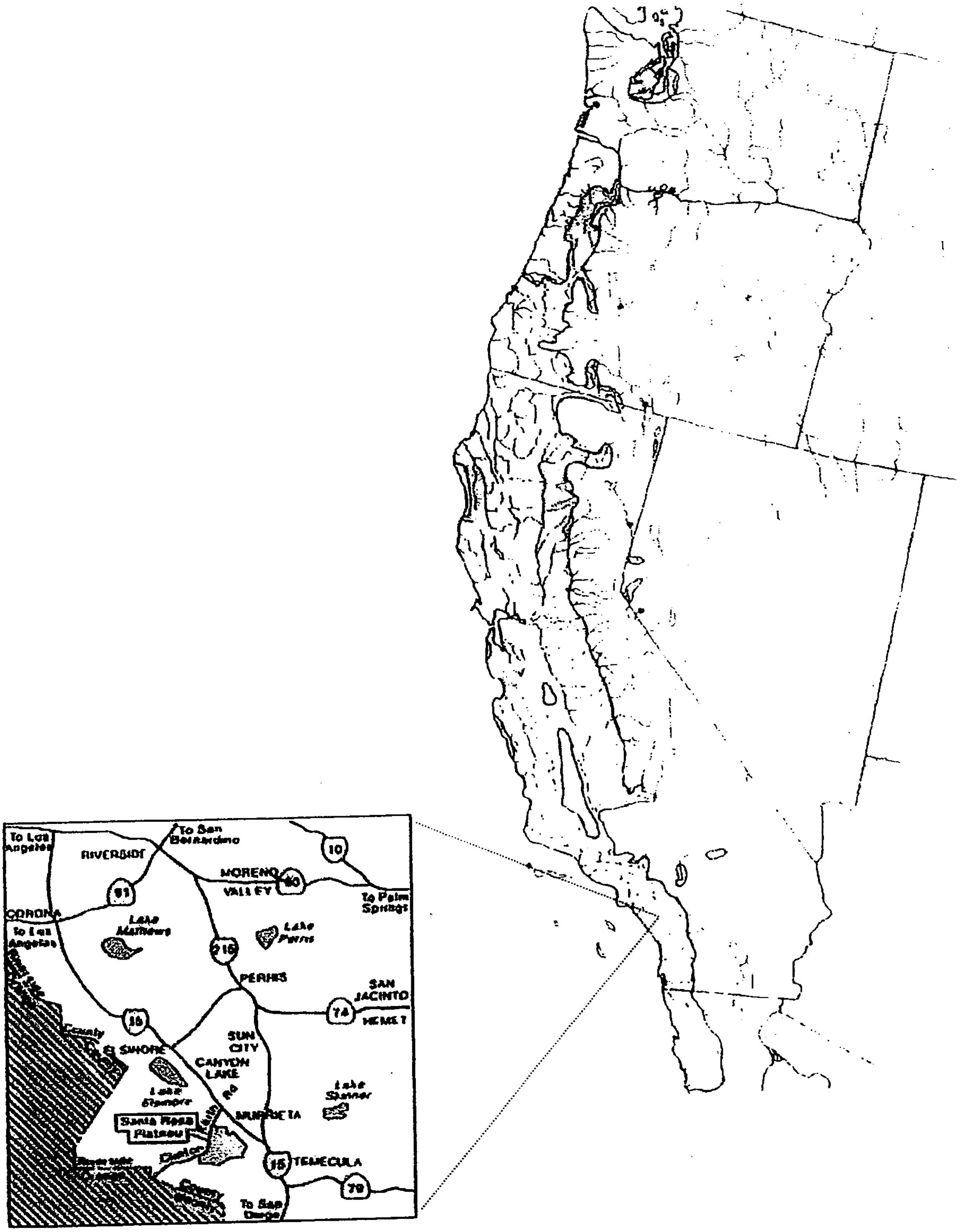


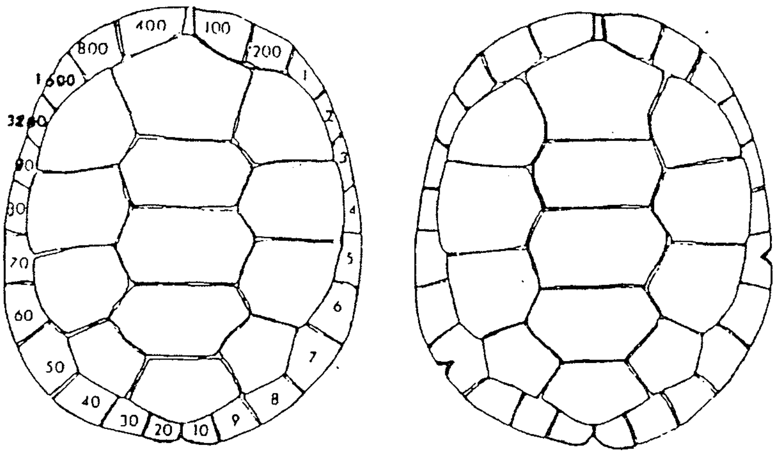
Figure 2: Historical Range of the Western Pond Turtle, *Clemmys marmorata* (by Dan Holland) and the study site, Santa Rosa Plateau Ecological Reserve, California

Figure 3: Southwestern pond turtle egg

Figure 4: The Santa Rosa Plateau Ecological Reserve: Cole Creek

Figure 5: The Santa Rosa Plateau Ecological Reserve: Sylvan Meadows

Figure 6: Nylon funnel-like trap



MARKING SYSTEM

NUMBER 55

Figure 7: Marking system (Holland, 1991)

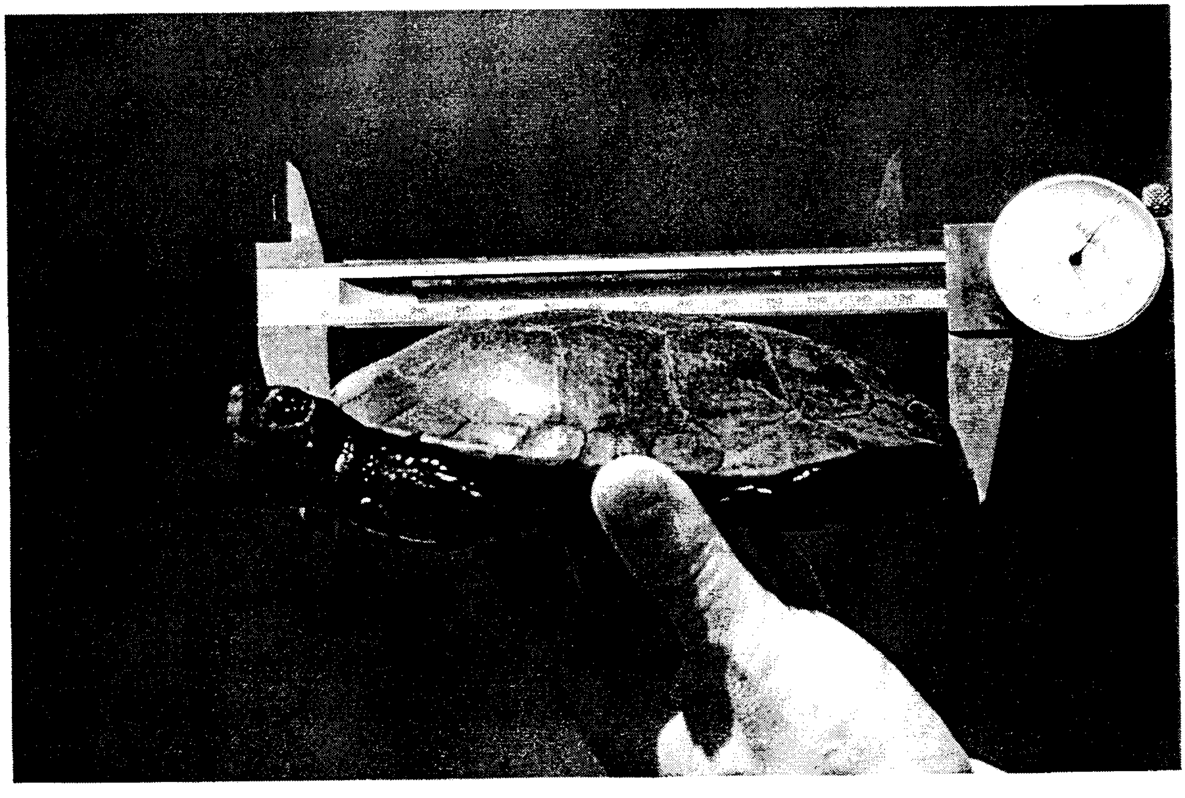


Figure 8: Carapace Length (CL) measurement

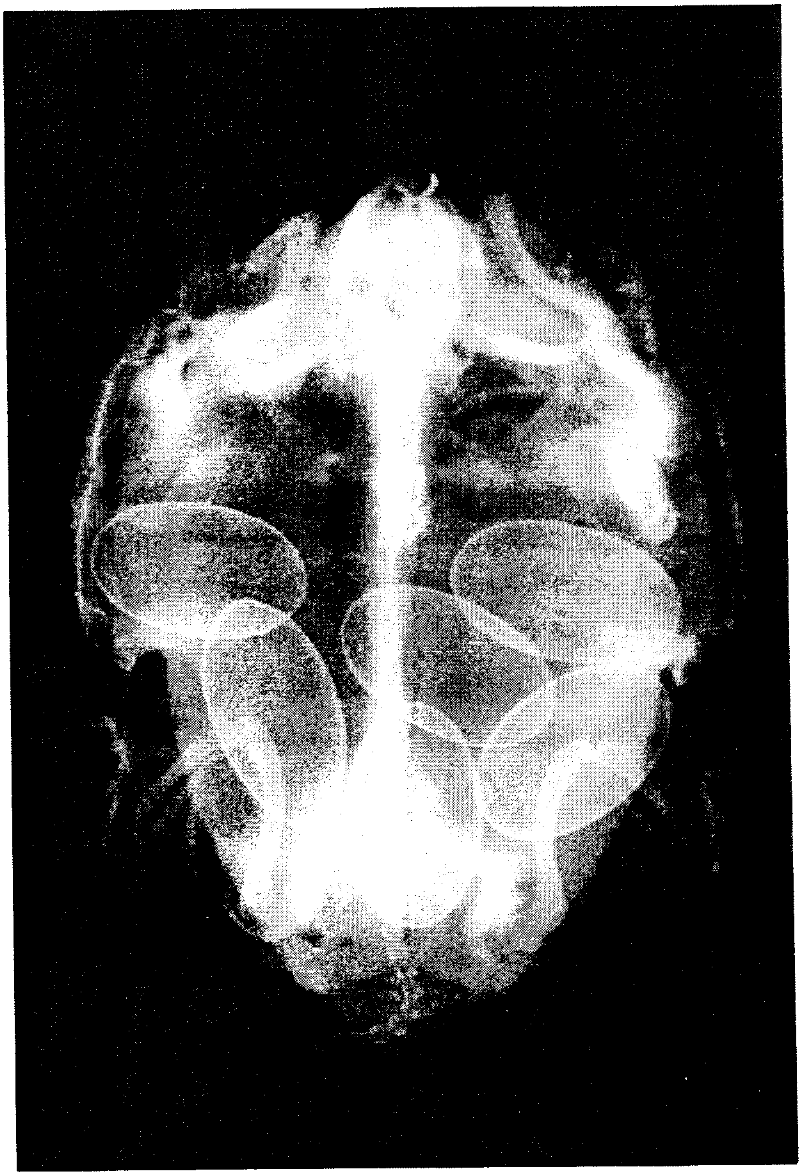


Figure 9: X-ray of gravid southwestern pond turtle

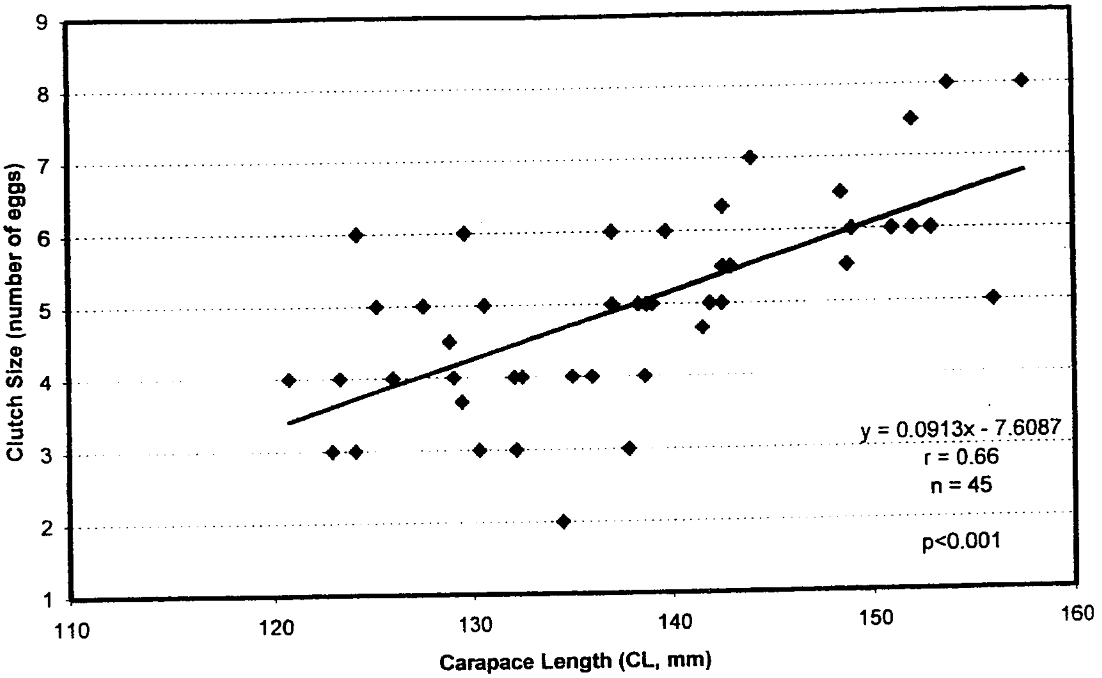


Figure 10: Clutch size versus carapace length for females from the Santa Rosa Plateau Ecological Reserve (n=24), Chino Hills State Park (n=9), and West Fork of the San Gabriel River (n=12); pooled data.

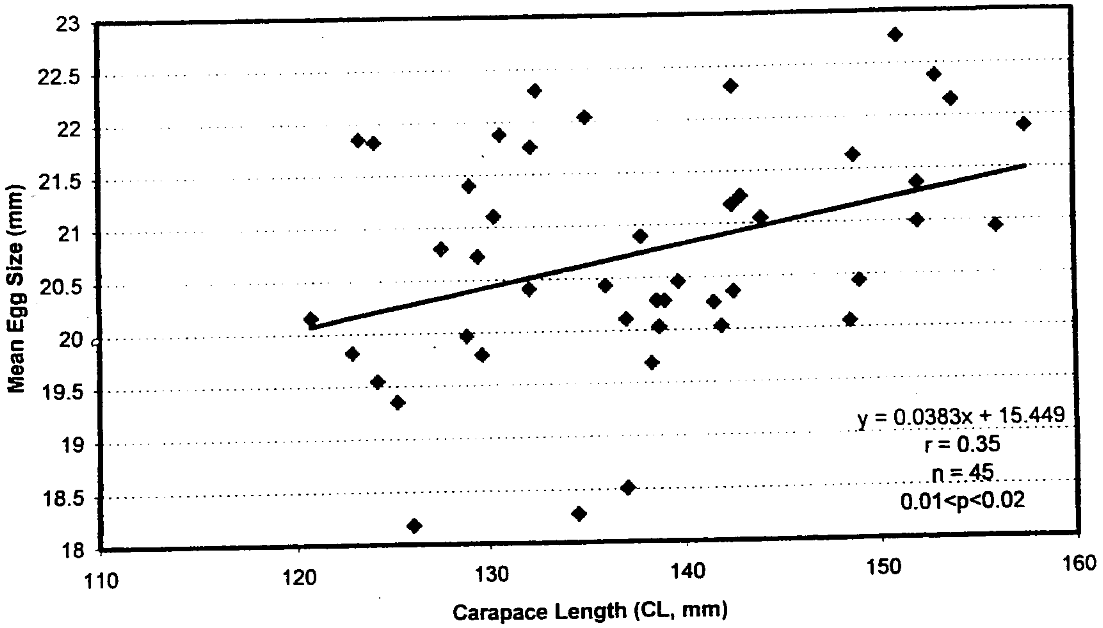


Figure 11: Egg size versus carapace length for females from the Santa Rosa Plateau Ecological Reserve (n=24), Chino Hills State Park (n=9), and West Fork of the San Gabriel River (n=12); pooled data.

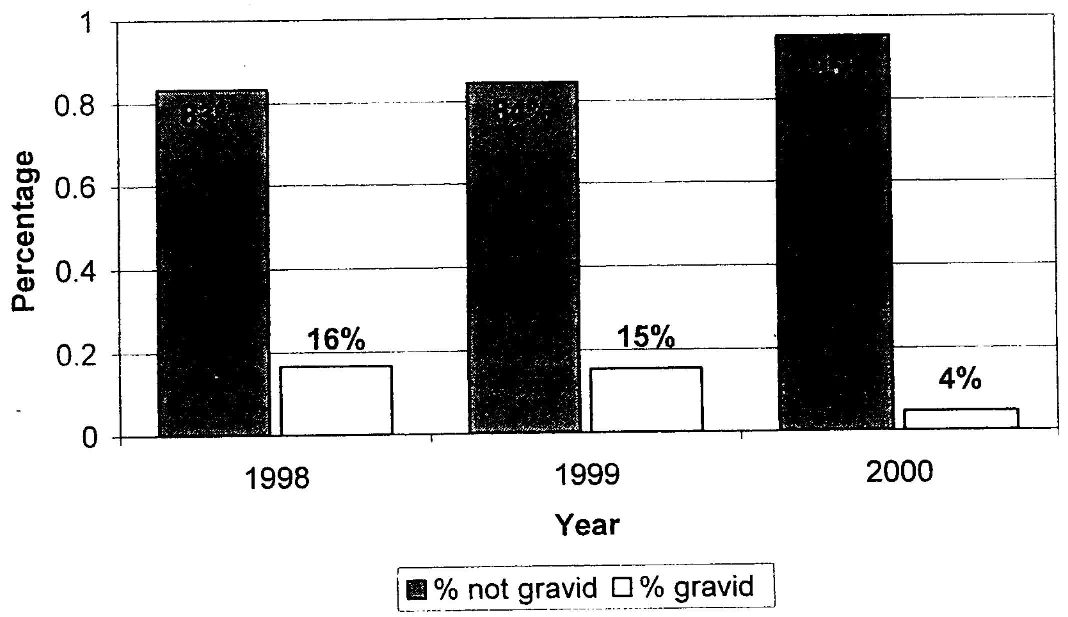


Figure 12: Comparison of percentages of gravid and non-gravid captures among years

Table 1: Descriptive data for pools where most turtles were found at the Santa Rosa Plateau Ecological Reserve

US = Upper Sylvan Pond; PDS = Pond with Dead Sycamore; TP = Turtle Pond; RP = Restoration (De Luz) Pond; CP = Ceremonial Pond; HP = Hidden Pond; OP = Owl Pond.

*Measures do not represent the actual pond area at any given time; they represent an <u>approximate value</u>, based on the average water level throughout the months of May, June, and July of 1998, 1999, and 2000.

SITE	US	PDS	TP (#01)	RP	CP	HP(#30)	OP(#02)
Location (GPS data)	N 33° 31.753'	N 33° 31.753'	N 33°31.663'	N 33°31.449'	N 33°31.849'	N 33°31.331'	N 33°31.775'
	W 117° 17.146'	W 117° 16.711'	W 117°16.346'	W 117°15.219'	W 117°16.169'	W 117°17.196'	W 117°16.239'
	EPE 13ft 3.96 m	EPE 18ft 5.48m	EPE 21ft 6.40m	EPE 15ft 4.57m	EPE 18ft 5.48m	EPE 24ft 7.31m	EPE 22ft 6.70m
	Alt 1903 ft 580.03m	Alt 1890 ft 576.07m	Alt 1831ft 558.08m	Alt 1859ft 566.62m	Alt 1812ft 552.29m	Alt 1962ft 598.01m	Alt 1824ft 555.95m
Approximate dimensions*	150 x 96 ft 45.72 x 29.26m	96 x 72 ft 29.26 x 21.94m	60 x 42 ft 18.28 x 12.80m	42 x 42ft 12.80 x 12.80m	54 x 54ft 16.45 x 16.45m	108 x 30ft 32.91 x 9.1m	48 x 24ft 14.63 x 7.31m

Table 2: Monthly precipitation (mm) at the Santa Rosa Plateau Ecological Reserve from September to April prior to the reproductive seasons of 1998, 1999, and 2000. Source: California Department of Water Resources, Division of Flood Management.

Month	**1997-1998**	**1998-1999**	**1999-2000**
Sep	25.65	7.87	1.01
Oct	1.01	0.76	0.00
Nov	52.32	42.67	0.76
Dec	92.45	27.94	6.09
Jan	121.66	42.92	14.98
Feb	725.93	27.17	170.68
Mar	154.94	17.52	62.73
Apr	69.85	32.00	29.46
Total precipitation (Sep. to Apr.)	1243.81	198.85	285.71

Table 3: Gravid females captured at the Santa Rosa Plateau Ecological Reserve from June 1998 to August 2000. Carapace Length (CL, mm); Clutch Size (CS, number of eggs); and Egg Size (ES, mean egg width per clutch, mm). *individuals that produced more than one clutch throughout these three reproductive seasons.

Year	Turtle number	CL	CS	ES
1998	586*	129.0	5	19.70
1998	503	124.2	6	19.55
1998	515	124.1	3	21.82
1998	526	130.3	3	21.10
1998	527	132.1	4	20.41
1998	595	135.0	4	22.04
1999	500*	142.8	8	21.86
1999	500*	142.8	3	20.68
1999	570*	129.5	3	21.65
1999	570*	129.5	5	20.03
1999	586*	129.0	4	20.24
1999	599*	142.2	6	22.53
1999	1676	130.6	5	21.88
1999	571	132.5	4	22.30
1999	6363	123.3	4	21.85
1999	1681	153.8	8	22.15
1999	592	127.5	5	20.80
1999	1631	125.2	5	19.35
1999	104	129.0	4	21.40
1999	603	141.9	5	20.03
1999	537	134.5	2	18.27
1999	5949	122.9	3	19.82
1999	1705	132.2	3	21.76
2000	500*	143.1	6	21.48
2000	500*	143.1	5	21.04
2000	570*	129.5	3	20.49
2000	599*	142.9	5	22.10
2000	613	129.6	6	19.79
2000	1616	137.8	3	20.89
2000	615	126.0	4	18.18
2000	1605	120.7	4	20.16

Table 4: Comparison of reproductive variables among Santa Rosa Plateau Ecological Reserve (SRPER), Chino Hills State Park (CHSP; Goodman, 1997a) and West Fork of the San Gabriel River (WFSGR; Goodman, 1997a) western pond turtle populations. Entries represent mean values and (standard deviation). Sample size (n) represents number of individual females in the case of body size comparisons (carapace length, CL, mm) and number of clutches in the case of mean clutch size (CS, number of eggs per clutch) and mean egg width (ES, mm) comparisons. The number of observations of double clutching (DC) in a year is also shown (the percentage of the total number of clutches) for all years. SRPER values for CS, ES, and DC are based on x-rays of 31 clutches from 24 individuals from 1998 to 2000. *differences were significant (ANOVA for CL and ES; ANCOVA for CS, with CL as covariate)

Variable	**SRP**	**CHSP**	**WFSGR**	**P-value**
Carapace Length (CL)	132.7 (7.9) range: 120.7-153.8 n=24	144.4 (6.4) range: 135.0-156.0 n=9	145.2(6.5) range: 137.0-156.5 n=12	P<0.001*
Clutch Size (CS)	4.5 (1.4) range: 2-8 n=31	5.7 (1.7) range: 2-8 n=16	5.7 (1.0) range: 4-8 n=17	P = 0.834
Mean Egg Width (ES)	20.8 (1.1) range: 18.18-22.53 n=31	20.5 (0.5) range: 19.68-21.36 n=16	20.9 (1.2) range: 18.51-22.76 n=17	P = 0.941

Table 5: Numbers of captures (and percentage of total) of female western pond turtles determined to be gravid from June 1998 to August 2000 at the Santa Rosa Plateau Ecological Reserve. Reproductive condition was assessed by palpation and confirmed with x-rays for all individuals.

	Reproductive Season		
	1998	**1999**	**2000**
not gravid	30 (83.3%)	93 (84.5%)	165 (95.3%)
gravid	6 (16.6%)	17 (15.4%)	8 (4.6%)
Total number of captures	*36*	*110*	*173*

Chi-Square = 11.22
Chi-Square critical (0.05,2) = 5.99
$0.001<p<0.005$