To Jeff -
with much appreciation for your help, advice, and encouragement during the completion of the book
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1990

Life History and Ecology of the Slider Turtle

J. WHITFIELD GIBBONS

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The Development and Significance of Melanism in the Slider Turtle

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Abstract

Male slider turtles (*Trachemys scripta*) undergo dramatic melanic changes as they become larger and older. This transformation occurs well past the size at which most attain sexual maturity. However, the process is not strictly size-dependent. The mean body size of melanistic males varies concordantly among populations in the same region as a function of growth rate. Additionally, data do not necessarily support an age-related explanation for the phenomenon, except as predicted under population-specific growth rates. The advent of melanism is coincident with population-specific female size at maturity and with maximal development of male foreclaw length, a secondary sexual characteristic. Melanistic individuals generally form a small portion of a given population but typically predominate within larger size classes. Physiological, histological, and hormonal differences between melanistic and nonmelanistic males are demonstrated. Behavioral differences also exist and may be due to intersexual or intrasexual selection.

Introduction

The phenomenon of melanism is well known in adult male slider turtles (*Trachemys scripta;* Table 19.1). In most populations that have been studied, sexually mature males undergo dramatic melanic changes involving the shell and, later, the soft parts of the body. In spite of the familiarity of this dramatic condition, little is known regarding its onset, development, and possible significance. For ex-

Table 19.2. References to melanism in selected turtle species

Taxon	Location	Reference	Comment
Emydidae			
Batagur baska	Malaysia	23	Seasonal in males
Chinemys reevesii	Asia	27	Both sexes, plastral melanism
		1,3,13,16	--
Chrysemys picta	North America	14	--
		26	Females
	Minnesota	15	Both sexes, reticulate melanism
	North Dakota	11	Reticulate melanism
	Canada	22	Reticulate melanism
		24	Both sexes, reticulate melanism
Clemmys guttata	United States	14	--
C. muhlenbergii	United States	18	--
Graptemys ouachitensis	Wisconsin	20	Both sexes
Hieremys annandalii	Southeast Asia	21	--
Malaclemys terrapin	Louisiana	7	--
Notochelys platynota	Thailand	12	--
Pseudemys concinna mobilensis	United States	4	--
P. dorbigni[a]	South America	9,10	--
P. floridana	United States	8	--
P. nelsoni	United States	14	Both sexes
		8	--
P. rubriventris	United States	8,21,26	--
		14	"Old individuals"
Rhinoclemmys funerea	Central America	19	--
Sacalia bealei	Asia	16	--
Trachemys decorata	Hispaniola	4	Melanism not as marked as in other West Indian forms
		25	--
T. decussata	Cuba	2,4,21,28	--
	Cayman Islands	6	--
T. scripta	See Table 19.1	See Table 19.1	See Table 19.1
T. stejnegeri	Central Antilles	4	--
T. s. vicina	Hispaniola	25	Both sexes
T. terrapen felis	Bahamas	4	--
T. t. terrapen	Jamaica	4,5	--
Kinosternidae			
Kinosternon sonoriense	Arizona	17	--

Note: Scientific names for West Indian *Trachemys* and subspecific designations for *T. scripta* follow Iverson (1986).

References: 1, Gray, 1873; 2, DeSola and Greenhall, 1932; 3, Liu and Hu, 1939-40; 4, Barbour and Carr, 1940; 5, Lynn and Grant, 1940; 6, Grant, 1940; 7, Cagle, 1952; 8, Carr, 1952; 9, Freiberg, 1967a; 10, Freiberg, 1969; 11, Smith et al., 1969; 12, Taylor, 1970; 13, Mao, 1971; 14, Ernst and Barbour, 1972; 15, Ernst and Ernst, 1973; 16, Sachsse, 1975; 17, Hulse, 1976; 18, Holub and Bloomer, 1977; 19, Ernst, 1978; 20, Vogt, 1978; 21, Pritchard, 1979; 22, MacCulloch, 1981; 23, Moll et al., 1981; 24, Schueler, 1983; 25, Seidel and Inchaustegui Miranda, 1984; 26, Ward, 1984; 27, Lovich et al., 1985; 28, Sampedro et al., 1985.

[a]Considered to be a subspecies of *T. scripta* by Iverson (1986) and Pritchard (1979).

Patterns of Melanization in Turtles

Several levels of melanic expression occur in turtles (Table 19.2). We recognize four basic types: permanent melanism, seasonal melanism, senile reticulate melanism, and ontogenetic melanism. Although the first three types occur principally in species other than *T. scripta* and its allies, we will present a brief review of each before proceeding to a detailed description of the process in *T. scripta*.

The type that we refer to as permanent melanism occurs in those species that are black throughout life, or at least as adults, including *Emys*, *Emydoidea*, *Clemmys guttata*, *Mauremys*, *Cuora*, *Melanochelys*, *Annamemys*, *Chinemys*, *Geoclemys*, *Heosemys*, *Siebenrockiella*, and some *Rhinoclemmys* (Ernst, 1982). Although lighter pigments may form various patterns on some of them, the above species are primarily black. Another example of this type of melanism apparently occurs in the eastern Pacific populations of *Chelonia mydas*. Hirth and Carr (1970) discussed the distribution of the "black turtle," a race of *C. mydas* characterized by heavy black pigmentation (see above). However, it is not known whether this condition is a polymorphism or a true taxonomic novelty, as suggested by Bocourt (1868) and Caldwell (1962b), because "black

matching (for review, see Porter, 1972), and the existence of melanomorphic forms in some other groups of vertebrates, including felids (Searle, 1968), fishes (Regan, 1961; Angus, 1983), and snakes (e.g., *Sistrurus catenatus*—Conant, 1951; *Crotalus horridus* and *Heterodon platyrhinos*—Conant, 1975). With the possible exception of background matching in *Chelodina longicollis* (Woolley, 1957), these forms of melanic expression have not been reported in turtles. Woolley (1957) demonstrated that *C. longicollis* melanophores contracted when live specimens were maintained over a white background and expanded when maintained over a black background. The transmutation from one state to the other required approximately 30 days. Intraperitoneal injections of melanophore-expanding pituitary hormone caused melanophore expansion in pale specimens.

Ontogenetic Melanization in *Trachemys scripta*

Ontogenetic melanization in *Trachemys scripta* has been described as a process of pattern reorganization not necessarily accompanied by an overall increase in pigmentation (McCoy, 1968). In an Oklahoma population of *T. scripta* the melanization process involves shifting of melanic pigments, in a regular sequence, between areas of the shell and the skin (McCoy, 1968). Melanic changes in the subadult pattern appear first on the plastral scutes, with subsequent involvement of the scutes of the carapace and the skin of the legs, tail, head, and neck. The first evidence of melanization is the deposition of a smudgy black spot in the center of each plastral scute, overlying and obscuring the juvenile ocellate spot (Carr, 1952). These black spots, especially those on the posterior pairs of scutes, gradually enlarge to form a continuous or almost continuous ring of black pigment around the plastron. The plastron retains a yellow center and yellow edges, and there is no melanin deposition along the scute sutures at this stage. The spots of the posterior scutes usually join, but the spots on the anterior scutes remain discrete (McCoy, 1968: Fig. 1A). As the melanization process continues, the melanin in the large, smudgy, and coalescent plastral spots is withdrawn and redeposited at other points on the plastron. In both males and females, foci of melanin redeposition occur at the junctions of the pectoral-abdominal and abdominal-femoral sutures with the central suture. Secondary foci develop where the more anterior and posterior cross-sutures intersect the central suture. Pigment transfer continues until the suture areas are broadly smudged with black, and the original central laminal spots are reduced, perhaps even light-centered (Fig. 19.1). In the population studied, the progress of ontogenetic melanization was approximately the same in males and females to this stage, but beyond this point males and females followed different patterns. In females the central plastral melanin deposits enlarge and expand in all directions and eventually wash the entire plastron with black pigment, virtually obscuring all markings. Concurrently with the development of a general blackening of the plastron from the central area, large black smudges reappear near the positions of the original central laminal spots. Remnants of the original spots may be seen as faint ringlike edgings around these new spots. The black smudges in the centers of the scutes remain visible until finally obscured by the overwash of melanin. Webb (1961) reported that the plastrons of large females from Lake Texoma, Oklahoma, were 80% blackened by melanic pigments.

Adult females retain the bright carapace pattern of juveniles virtually throughout life. In the population studied, the carapace pattern of some very old females was slightly obscured by a thin overwash of melanin. The striped pattern of the skin of the head, neck, legs, and tail remains unaffected by melanization in adult females. It is important to note that although slight melanic changes can be demonstrated in females of the *scripta* subgroup (sensu Weaver and Rose, 1967), these changes are only superficially similar to those typical of males. In fact, of the more than 9,000 *T. scripta* that have been collected on the Savannah River Plant in South Carolina during the past 20 years, none of the females were melanistic.

In males the transfer of pigment to the plastral sutures at the expense of the spots continues until the spots are completely lost or are only ring-shaped, and the pigment is concentrated along the sutures. The centers of the scutes are yellow or slightly vermiculated with melanin, but both the juvenile ocelli and the melanic smudges that replaced them are lost (McCoy, 1968: Fig. 1D).

At an early stage the bright juvenile pattern of the carapace scutes in males is obscured by general deposition of melanin over the carapace. Subsequently, there is a progressive depigmentation of the carapace scutes, with the melanin moving to and concentrating along the sutures. Ultimately, the sutures of the carapace scutes are narrowly and vividly outlined in black, and the centers of the scutes are greenish yellow and without dark markings. This is the classic *"troostii"* or *"rugosa"* phase that confounded early naturalists.

A further and final stage in the melanization of adult males involves complete obliteration of the striped pattern of the head, neck, legs, and tail and replacement with a gradually darkening, black-mottled melanic pattern on an olive ground color (Fig. 19.2). Carr (1952) reported that a further stage involves a secondary wash of black pigment over the plastron, obscuring the pattern of melanin along the sutures.

Evidence of melanic change in male *T. scripta* from Alabama consists of (1) an obscuring of the yellow and black rosette or swirl pattern on the carapace, (2) a similar obscuring on the skin of neck, limbs, and tail accompanied by a breakup of the juvenile and female head stripe pat-

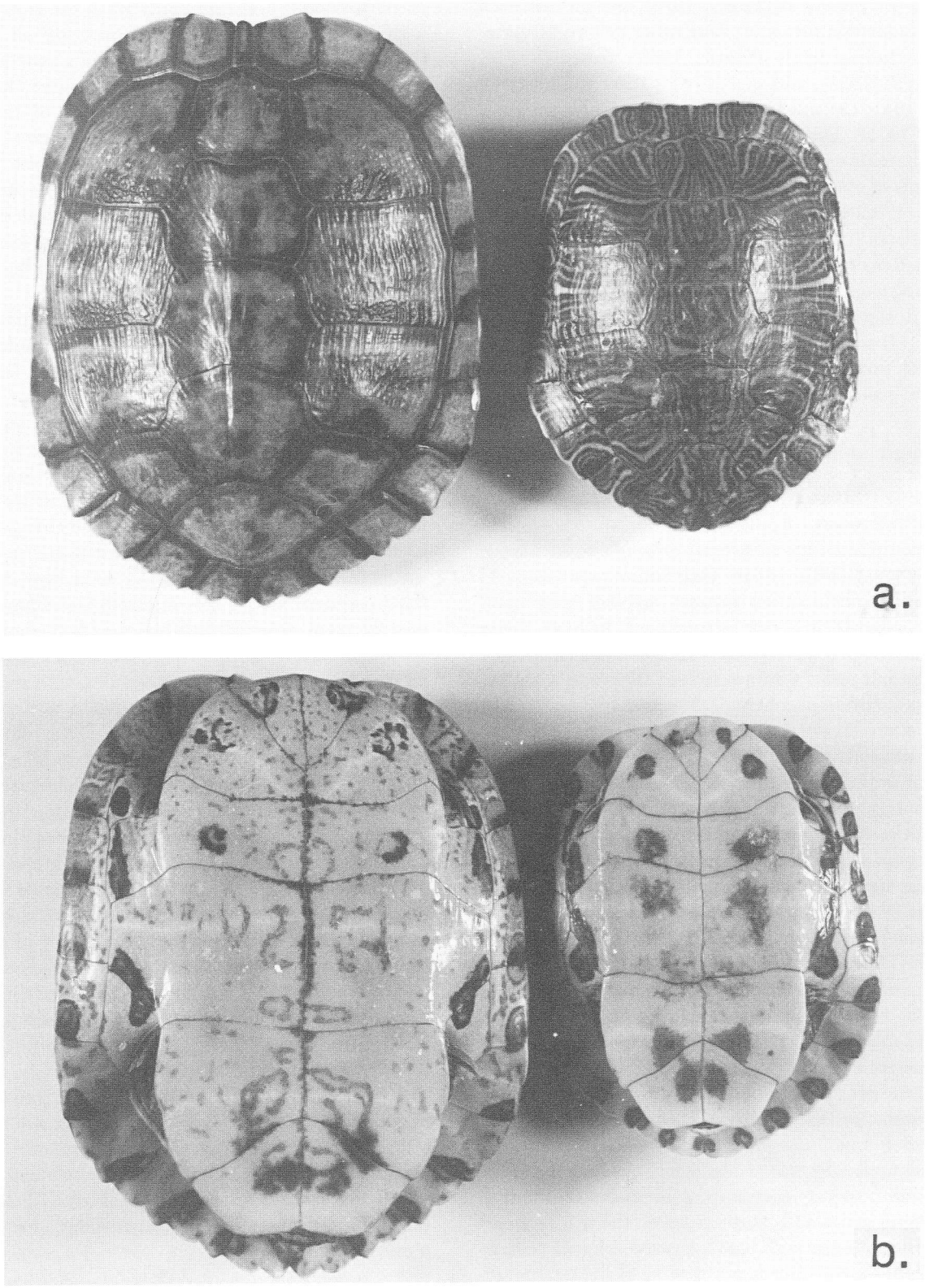

FIGURE 19.1. Color pattern of melanistic (left) and nonmelanistic (right) male *Trachemys scripta* collected in northern Alabama. Turtles were collected monthly by drag seine, trap, or trammel net from drainage canals in the White Springs Unit, Harris-Sweetwater dewatering area, Wheeler National Wildlife Refuge, Limestone County, Alabama. *a*, carapace color pattern; *b*, plastron color pattern. Note the concentration of black color along the scute margins and the disappearance of pattern from the scute centers in both views of melanistic specimens.

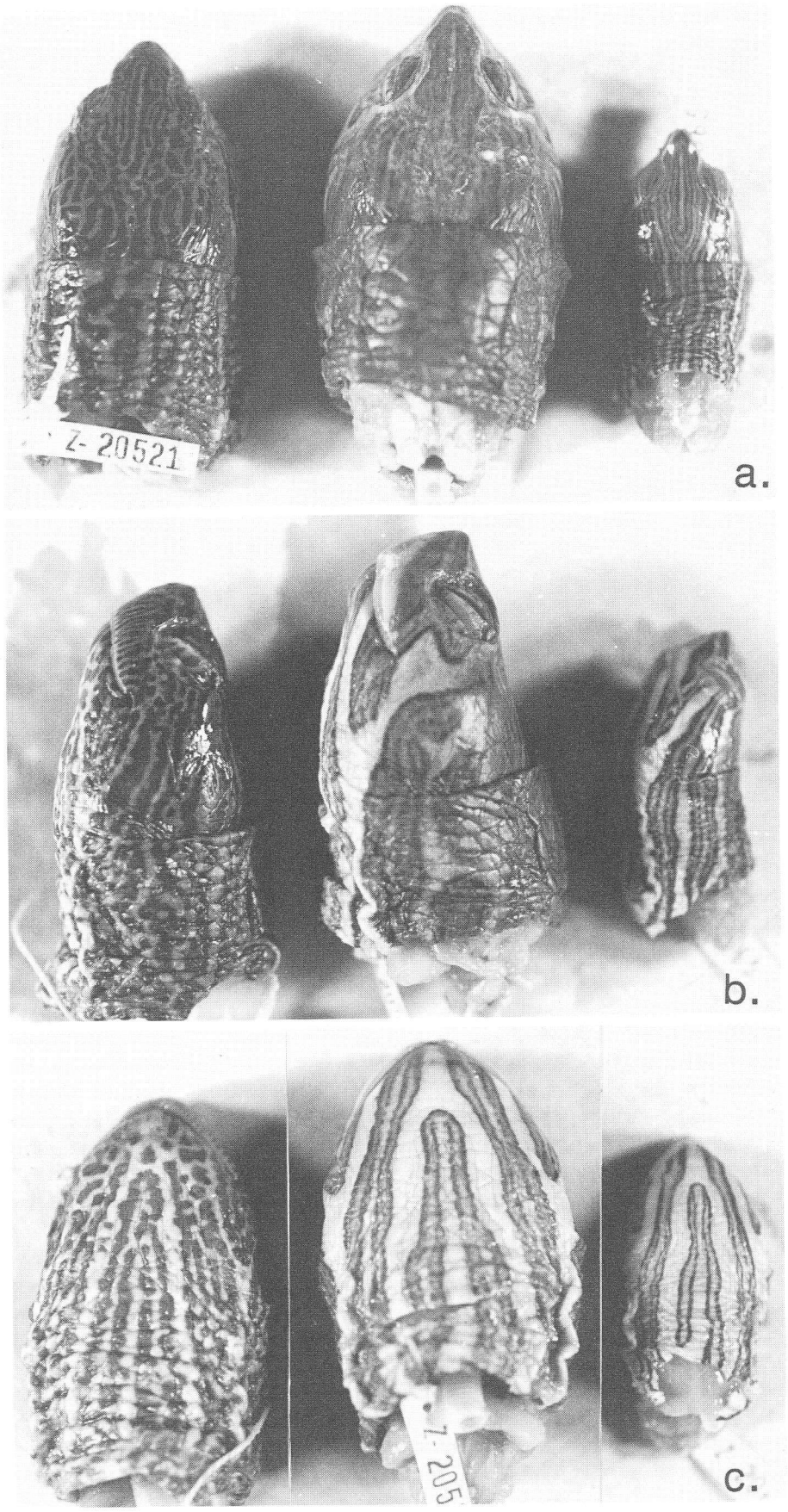

FIGURE 19.2. Comparison of the head color pattern of a melanistic male (left), a female (center), and a nonmelanistic male (right) from northern Alabama. *a*, dorsal view; *b*, lateral view; *c*, ventral view. Note the breakup of the striping pattern in the melanistic male to short wavy lines and dots.

tern into series of dots, and (3) the appearance of dark pigmentation at the scute margins of both carapace and plastron (Figs. 19.1 and 19.2). Few males in the Alabama population attained a uniformly black carapace, but all males in that population with a plastron length greater than 160 mm exhibited clear evidence of changes in color pattern. However, in other populations adult males may retain the juvenile pattern throughout life (Cahn, 1937; Barbour and Carr, 1940). Because overall darkening does not always occur, the condition in male slider turtles may not be strictly melanism. However, we will continue to use the term because of its precedence in describing this phenomenon. The preceding description of the melanization process is based on the assumption that less melanic patterns undergo a transition to more-melanic patterns. To the best of our knowledge, no one has ever studied the process over time with known individuals in a controlled experiment.

Quantifying Melanism

A major problem with reviewing the phenomenon of melanism in slider turtles is that a quantitative method for measuring the degree of melanization has not been employed or even suggested. Thus, a condition defined as partially melanistic by one researcher may be considered fully melanistic by others. The situation is complicated by differential involvement of the shell and soft parts in the melanization process. A partial solution would be to measure qualitatively the degree or pattern of melanization exhibited by a given structure such as the plastron. In *Chinemys reevesii*, for example, several plastral patterns appear to form a continuum toward complete melanism (Lovich et al., 1985; also see Table 19.4); however, involvement of the soft parts is difficult to predict from the level of plastral melanism observed. A shortcoming of this approach is the loss of information regarding the concomitant involvement of other anatomical units.

Another technique is to use a photo coordinate grid overlay (Forestry Suppliers, stock no. 45026). This is a clear acetate sheet printed with a dot matrix that can be placed over photographs or photocopies of a turtle's carapace or plastron. By counting the numbers of grid points that are superimposed on light and dark areas, an estimate of the percentage of area that is black can be calculated. Flat surfaces such as the plastron can be analyzed directly without the use of photocopies. The relative area of the carapace that was black was measured in a sample of nonmelanistic males (N = 14; 100–158 mm plastron length, or PL), melanistic males (N = 23; 154–197 mm PL), and females (N = 14; 108–212 mm PL) from northern Alabama using the grid overlay technique (Terrell and Garstka, 1984). The extent of carapace darkening differed significantly between groups: Nonmelanistic male carapaces were 30% (± 3.8%) black, melanistic males were 58% (± 3.2%) black, and females were 37% (± 4.1%) black (F = 17.35, df = 2/48, p < .001). However, there was considerable overlap between nonmelanistic and melanistic males: Nonmelanistic carapace black ranged to 68% (132 mm PL), and melanistic carapace black was as low as 36% (162 mm PL). Although some very large females may exhibit a darkened carapace (to 74% black in a 212 mm PL female), none of the more than 300 females examined in the northern Alabama population showed evidence of color pattern reorganization on the carapace scute margins or of neck skin stripe reorganization characteristic of the male morphological color change. Thus, even this preliminary quantitative approach may not be sufficient to indicate color pattern changes.

Table 19.4. Relationship between size and plastral melanism in *Chinemys reevesii*

Amount of pigmentation	Mean plastron length (mm)			
	Male	Female	Juveniles	Total sample
Light	62.5 (10)	83.9 (5)	46.7 (1)	68.2 (16)
Intermediate	77.2 (49)	94.5 (46)	45.2 (13)	80.7 (108)
Dark	75.4 (27)	107.6 (48)	43.8 (10)	89.9 (85)
Melanistic	107.1 (30)	144.7 (7)	-- --	114.2 (37)

Source: Lovich and Ernst, pers. com.

Note: Sample size is given in parentheses after each mean. Pigmentation categories follow Lovich et al. (1985). There is a significant difference in plastron lengths between pigmentation categories (ANOVA, juveniles excluded; F = 9.45, p < .0001, df = 3, 218).

A more precise approach would involve the use of a digitizer to scan turtle shells or photographs. This technique evaluates and quantifies the degree of lightness or darkness in small areas (pixels) of the image, thus greatly increasing resolution of minute pigment differences. An overall value reflecting the degree of melanization can be obtained and easily compared with other values. This technique is presently being evaluated for detailed analysis and quantification of melanic changes in *T. scripta* (Lovich, unpub. data).

We also investigated the microscopic structure of the skin of melanistic and nonmelanistic male *T. scripta*. This comparison of sections of the neck skin of 21 nonmelanistic and 34 melanistic males revealed that the melanophores in the dark stripes of nonmelanistic males were principally dermal and that the melanophores of melanistic males were principally epidermal (Fig. 19.3). Cytocrine deposition by the epidermal melanophores is clearly indicated. Furthermore, the expansions of the nonmelanistic dermal and of the melanistic epidermal melanophores were noticeably different from each other.

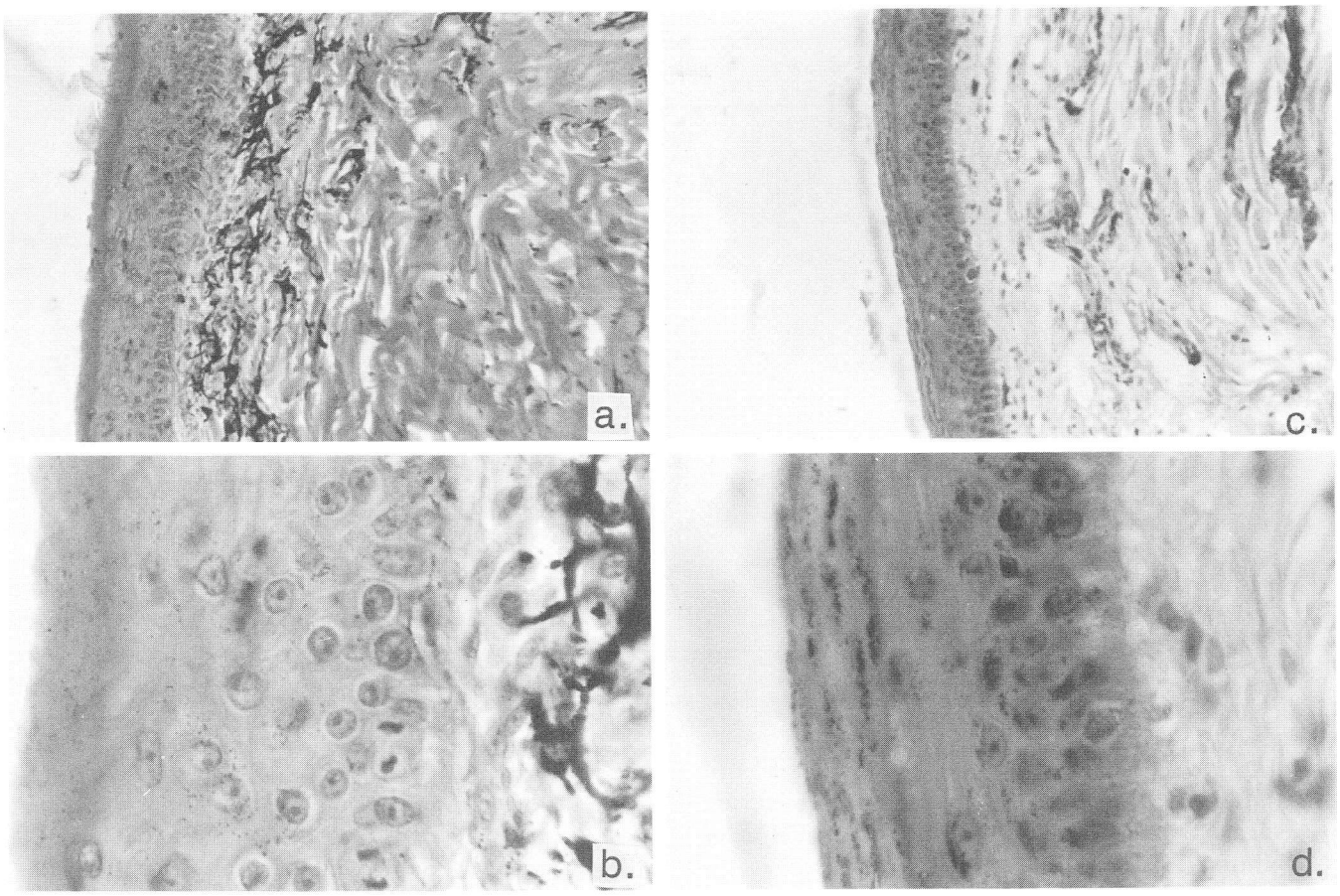

FIGURE 19.3. Histological comparison of melanophore distribution in neck skin of melanistic and nonmelanistic male *Trachemys scripta*. Tissues were fixed in 10% neutral buffered formalin, dehydrated in a graded ethanol series, embedded in paraffin, sectioned at 7 μm, and stained with hematoxylin and eosin. *a*, nonmelanistic male section showing principally dermal distribution of melanophores; *b*, higher-magnification view of the same tissue section as in *a*; *c*, melanistic male section showing principally epidermal distribution of melanophores with cytocrine deposition; *d*, higher-magnification view of the same tissue section as in *c*.

Geographic Variation

The melanization process described for male *T. scripta* appears to vary among subspecies, although there is some disagreement among authors. For example, of the 17 currently recognized races (Iverson, 1986), some, such as *T. s. ornata,* show only slight levels of melanism (Smith and Smith, 1979), and *T. s. venusta* does not normally exhibit melanism (Pritchard, 1979). In contrast, Smith and Smith (1979) report melanism in both male and female *T. s. venusta*. This condition, bisexual melanism, is unusual in the complex and is shared with *T. s. yaquia, T. s. grayi,* and *T. s. taylori* (Legler, 1960b; Smith and Smith, 1979). If any trend exists, it may be that melanism is more characteristic of North Temperate races of *T. scripta* than races in Mesoamerica (see Chapter 7).

Variation within subspecies has also been suggested. Cahn (1937) reported that melanistic *T. scripta elegans* were more common in southern Illinois than in the northern portion of the state. Others have suggested that the size at full attainment of melanism varies geographically in this race (Cagle, 1950; McCoy, 1968). In contrast, the closely related and widely distributed *Chrysemys picta* appears to develop reticulate melanism only at the northern limit of its range (Table 19.2). Latitudinal clines in pigmentation have been reported in the tortoises *Gopherus flavomarginatus* (Morafka and McCoy, 1988) and *G. polyphemus* (Landers et al., 1982).

Seidel (1988) reviewed the occurrence and progress of melanization in West Indian species of *Trachemys*. The phenomenon is poorly developed in *T. terrapen* and nearly absent in *T. decorata*. The pattern of pigment reorganization in *T. stejnegeri* is similar to that of *T. scripta*. In *T. decussata* the process results in a vermiculate or speckled

Table 19.5. Plastron length (mm) statistics for melanistic and nonmelanistic male *Trachemys scripta* from selected South Carolina populations

Pond	Pigmentation	*N*	Mean	SE	Minimum	Maximum	MEL/NON
Cecil's Pond	MEL	17	166	2.9	145	189	0.23
	NON	75	133	2.0	105	178	
Capers Island	MEL	10	200	4.8	177	226	2.50
	NON	4	155	16.4	108	178	
Steel Creek	MEL	30	180	3.6	126	206	0.23
	NON	130	151	2.4	100	209	
McElmurray's Pond	MEL	30	163	2.4	136	194	0.73
	NON	41	154	2.2	113	177	
Par Pond	MEL	167	190	1.3	146	226	0.41
	NON	406	153	1.3	100	243	
Ellenton Bay	MEL	135	168	1.6	104	223	0.27
	NON	493	133	0.9	100	207	
Lost Lake System	MEL	145	164	1.3	116	207	0.34
	NON	429	140	1.0	100	210	
Risher Pond	MEL	16	174	5.5	122	203	0.33
	NON	48	131	3.0	103	191	

Note: Data for animals with multiple captures are based on last capture. Only sexually mature males (plastron length > 100 mm) were used in the analysis. Abbreviations: MEL, melanistic; NON, nonmelanistic.

pattern on the carapace or plastron. These differences in the degree and progression of melanic involvement are perhaps not surprising, given the paraphyletic nature of West Indian *Trachemys* (Seidel, 1988).

Variation in Size, Age, and Relative Abundance

Information presented and reviewed thus far suggests that ontogenetic melanism, typified by *T. scripta*, is associated with large body size or advanced age. This tentative conclusion has not always been supported in the literature. Barbour and Carr (1940) suggested that the onset of melanism in *Trachemys* was not size- or age-dependent but rarely occurred in males smaller than 150 mm, and Hulse (1976) found no correlation between size and ventral melanism in *Kinosternon sonoriense*. In contrast, the development of juvenile plastral melanism in *Chelonia mydas* is entirely dependent on size and not age (Balazs, 1986). Lovich et al. (1985) observed that larger and presumably older *Chinemys reevesii* exhibited increased levels of plastral melanism (also see Table 19.4). Cagle (1948b) reported that all male *T. scripta* greater than 170 mm in an Illinois population were melanistic. Minimum sizes of *T. scripta* at attainment of full melanism were compiled by McCoy (1968) for various populations and ranged from 100 to 152 mm (Table 19.3). These contradictory data illustrate the state of uncertainty regarding the onset of melanism.

Detailed analysis of eight South Carolina populations of *T. scripta* with different growth rates allows insight into the timing and variation of melanic change within a small geographic area (Table 19.5). Sexually mature nonmelanistic males range from 100 to 243 mm in plastron length, and melanistic males from 104 to 226 mm PL. This extensive overlap is a reflection of at least two factors. First, our data do not discriminate between the various levels of melanism. Thus, a turtle showing only very early signs of melanic development is still classified as melanistic. Second, although a substantial portion of the adult male population may be melanistic, some individuals apparently retain the juvenile pattern throughout life or develop melanism much later than others. The mean size of melanistic males from all populations is 175 mm PL. Melanistic males from fast-growth populations on Capers Island (Gibbons et al., 1979) and in Par Pond (Gibbons et al., 1981) have a mean size of 191 mm PL, whereas those in slow-growth populations (Gibbons et al., 1981) have a mean of 167 mm PL. Based on a cumulative frequency distribution of body size, 80% of the melanistic males in the Ellenton Bay population attain their condition by 170 mm PL. In Par Pond a similar percentage attain their condition by 190 mm PL. The mean body size of nonmelanistic males in all populations is less than the values reported above. The mean body sizes of melanistic males are all larger than 100 mm PL; the approximate size at which maturity is reached in all populations (Gibbons et al., 1981; Table 19.3). In northern Alabama all males larger than about 150 mm PL exhibit at least some of the characteristics of melanism. These wide-ranging values among populations suggest that melanic development in *T. scripta* is not strictly size-dependent.

Limited data on the actual age of melanistic males in the slow-growth populations of Lost Lake and Ellenton Bay suggest a mean of 14.8 years (range = 7–24, $N = 12$). In Par Pond, melanistic males have a mean age of 8.8 years (range = 5–18, $N = 20$). Nonmelanistic males in slow-growth populations have a mean age of 5.7 years (range = 4–24, $N = 293$). The dramatic difference in the mean timing of melanic development between slow-growth populations and Par Pond populations suggests that the phenomenon is not age-dependent either. The onset of melanism also appears to be dissociated with the age at which males attain sexual maturity. Males in Ellenton Bay reach sexual maturity in 4 to 5 years, whereas those in Par Pond may mature in only 3 to 4 years (Gibbons et al., 1981). The difference between sexual maturity and the mean age of melanistic males in Ellenton Bay is about 10 years. The difference in Par Pond is about 4 years.

Sexual maturity in male *Trachemys* of the *scripta* subgroup is evidenced by androgen-dependent foreclaw and tail elongation (Evans, 1946, 1951, 1952; Cagle, 1948a). The elongated foreclaws are used during courtship behavior (Cagle, 1950). In our sample of 131 male *T. scripta* collected in Alabama during the recrudescent period, melanistic males ($N = 45$, claw length/carapace length = 10.1 ± 0.17) differed from nonmelanistic males ($N = 86$, claw length/carapace length = 11.9 ± 0.16; $t = 6.99$, df = 129, $p < .001$). Three of 32 nonmelanistic males under 120 mm PL had foreclaws longer than 16 mm, as did 20 of 51 nonmelanistic males between 121 and 160 mm PL; 30 of 45 melanistic males had foreclaws longer than 16 mm. Furthermore, the largest absolute claw lengths measured in each group were 18.9 mm (175 mm PL) in a melanistic male and 17.7 mm (125 mm PL) in a nonmelanistic male. These results suggest that foreclaws may increase in length very slowly, if at all, after males become melanistic. Plots of claw length versus plastron length for Ellenton Bay and Par Pond *T. scripta* again demonstrate that melanism occurs at different body sizes in populations with different growth rates (Fig. 19.4). Two other associations can be seen. First, the advent of melanism is coincident with population-specific female size at maturity. This unusual relationship is also reflected in the mean plastron lengths of melanistic males given in Table 19.5. In Ellenton Bay and all other slow-growth populations, females mature at about 160 mm, and in Par Pond and Capers Island populations, females mature at about 200 mm (Gibbons et al., 1981). The mean body sizes of melanistic males closely match these respective values. Second, as suggested by data from the Alabama population, melanism is coincident with maximal claw length. The association between androgen-dependent claw length and melanism provides circumstantial support for a hormonal mechanism of melanization of *T. scripta*.

Overall, melanistic males are rarely more abundant

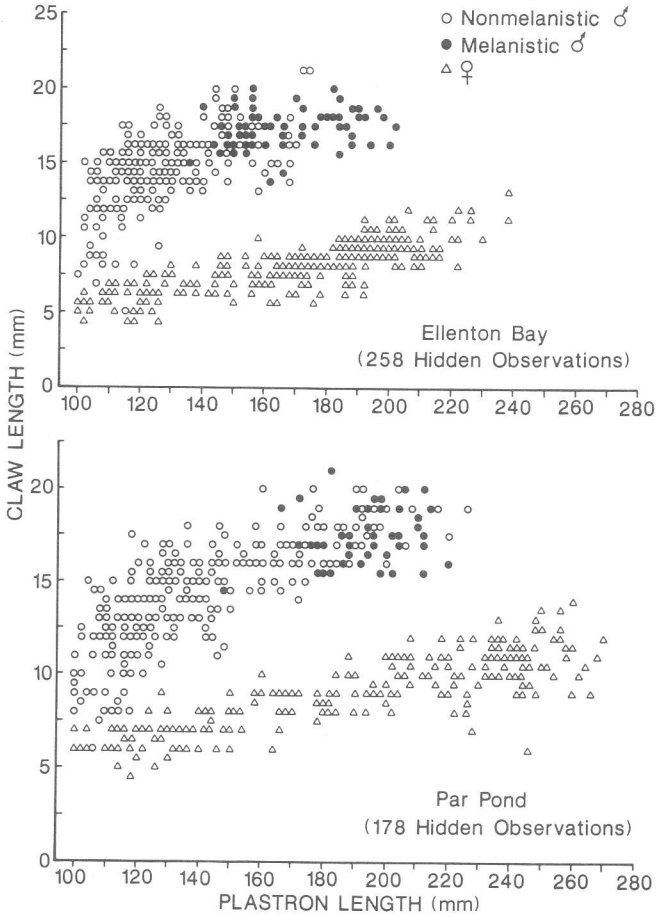

FIGURE 19.4. Relationship between foreclaw length and body size in two South Carolina populations of *Trachemys scripta*. Several outliers (questionable data points) were removed.

than nonmelanistic adult males in a given population (Tables 19.3 and 19.5). However, melanistic males may predominate in larger size classes (Fig. 19.5). Ratios of melanistic to nonmelanistic sexually mature males in Tables 19.3 and 19.5 range from 0.01 to 2.50 with a mean of 0.50. The value reported for Capers Island is unusual and can be explained as a result of size-specific predation. Smaller turtles in this relatively vegetation-free habitat are presumably preyed upon by alligators and eliminated disproportionately (Gibbons et al., 1979). This has resulted in a population composed primarily of very large turtles. In the case of males, this includes mainly large melanistic specimens; hence the inverse ratio observed. Deleting this unusual value gives an overall mean value of 0.30. The proportion of melanistic versus nonmelanistic males varies significantly among the populations shown in Table 19.5 (contingency table analysis: including Capers Island, $\chi^2 = 42.2$, $p < .001$; excluding Capers Island, $\chi^2 = 27.1$; $p < .001$). These differences may be due to sampling error, differential mortality, or differential

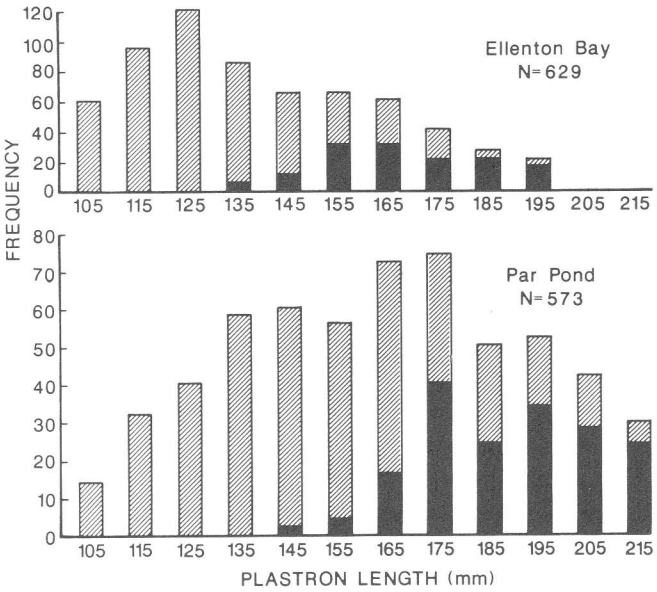

FIGURE 19.5. Size frequency distributions for sexually mature melanistic (dark bars) and nonmelanistic (shaded) male *Trachemys scripta* from two populations in South Carolina. Data are for multiple-capture animals and are based on last capture. Midpoints of each interval are shown.

interpopulation movement patterns in the two male color morphs.

Physiological Basis of Melanization in Male *Trachemys scripta*

There are basically two types of melanization seen in vertebrate animals: (1) physiological color change, an acute phenomenon of rapid darkening (or lightening) typically studied in amphibians or lizards, and (2) morphological color change, a permanent or long-term darkening that occurs with age, season, or some other variable (Bagnara and Hadley, 1974). It is the latter type that concerns us here, specifically the causes and consequences of darkening in older adult, mostly male, emydid turtles.

Hormonal Basis of Melanization in Vertebrates

Previous study of the controlling mechanisms of melanization has concentrated on several hormone systems known to affect the cellular processes involved in darkening. Specifically, these hormone systems may affect the proliferation of melanin-containing pigment cells (melanophores), the dispersal of melanin pigment granules within the melanophores, and the donation of melanin granules by melanophores onto keratinized cells within the skin by cytocrine deposition (Baden et al., 1966; Bagnara et al., 1968; Chavin, 1969; Bagnara and Hadley, 1974). Furthermore, hormonal control of melanization may be complex, with hormones acting separately, synergistically, or antagonistically. In addition, melanization is affected by the distribution and dispersal of pigment cells, processes that are known but are little understood.

Hormonal studies of color change in reptiles have concentrated on the physiological color change seen in *Anolis* lizards (Goldman and Hadley, 1969; Bagnara and Hadley, 1974); there is comparatively little in the literature on the physiology of reptilian morphological color change. Hormones recognized to be involved in the regulation of morphological color change include the following (for general reviews, see Bagnara and Hadley, 1974, and Norris, 1980): (1) pituitary gonadotropins—seasonal breeding colors in birds (Ralph, 1969), melanization in African weaver finches (Segal, 1957), beak demelanization in Lal Munia (Thapliyal and Tewary, 1961); (2) pituitary hormones other than gonadotropins—melanocyte-stimulating hormone, MSH, induces melanocyte dispersion, and hence darkening, as well as coat color deposition in mice (Bagnara and Hadley, 1974), and corticotropin, ACTH, exerts a similar darkening effect (Norris, 1980); (3) pineal melatonin—blanches melanophores in a variety of vertebrates (Bagnara and Hadley, 1974) and reverses the gonadotropic effects on plumage in Lal Munia (Gupta et al., 1987); (4) steroid hormones—estrogens induce the female color in brown leghorn chickens (Trinkhaus, 1948), androgens promote the black portions of male coloration in fence lizards (Kimball and Erpino, 1971), androgens induce the dark bill of the male house sparrow (Witschi and Woods, 1936; Witschi, 1961), and progesterone (or ovarian androgen) induces the characteristic colors in gravid or recently ovulated iguanid lizards (reviewed in Cooper, 1984); (5) thyroid hormones—thyroxine (T4) and triiodothyronine (T3) have been implicated in a variety of skin functions, including developmental processes, especially in salamanders (Bagnara and Hadley, 1974; Norris, 1980), and molting in both birds (Payne, 1972) and squamate reptiles (Chiu et al., 1983; Maderson, 1984); thyroidectomy results in bill lightening in the house sparrow, but testosterone, even at very high doses, is unable to darken the bills of thyroidectomized birds (Lal and Thapliyal, 1982); T4 can inhibit gonadal recrudescence and LH-dependent breeding plumage in Lal Munia (Thapliyal and Gupta, 1984).

Although each of the above hormone systems may act independently, there is evidence of considerable interaction among them. For example, thyroid hormones can affect levels of corticosteroids (Holmes and Phillips, 1976). In chickens, corticosteroids and ACTH deactivate thyroid hormones, depressing plasma levels of T4 and T3 (Decuypere et al., 1982). Both thyroid hormones and corticosteroids may affect food intake as well as nutrient storage and mobilization. In chickens, fasting may result in reduced rhythmicity of plasma thyroid hormones, and

even the sight of food can depress corticosteroid levels in chickens (Sharp and Klandorff, 1985). Furthermore, levels of corticosteroids, androgens, and other hormones of direct importance in regulating coloration can be profoundly affected by social factors (Leshner, 1978; Norris, 1980). Thus, hormone interactions may cause nutritional and metabolic factors, social organization, and sexual and agonistic behaviors to have profound effects on morphological coloration.

Therefore, in examining possible mechanisms of the morphological color change in male *Trachemys scripta*, we investigated differences between nonmelanistic and melanistic males in (1) the timing and extent of gametogenesis, (2) pineal morphology, and (3) measures of energetics. Any differences in these variables might reflect underlying differences in (1) gonadotropins or sex steroids, (2) melatonin, and (3) thyroid hormones, corticotropin, or corticosteroids.

Comparison of Melanistic and Nonmelanistic Male *Trachemys scripta*

TIMING AND EXTENT OF GAMETOGENESIS

In northern Alabama, *T. scripta* appears to be exclusively a spring breeder (Gross, 1986), but in other areas this species may breed in both spring and fall (Cagle, 1950; Moll and Legler, 1971; Lovich, pers. obs.). In most seasonally breeding vertebrates in temperate regions, gametogenesis in both sexes precedes breeding, so mating occurs when ova and spermatozoa are mature (van-Tienhoven, 1983; Crews, 1984). However, in many reptiles, as well as in an assortment of other vertebrates, gametogenesis in one or both sexes occurs at a time other than the time of breeding (Volsoe, 1944; Crews, 1984; Silva et al., 1984). This dissociated condition (Crews, 1984) occurs in male but not female *T. scripta* in northern Alabama (Gross, 1986). In this population, spermatogenesis occurs in the summer and early fall, and vitellogenesis is not complete until spring. Thus, a study of the gametogenic function in male *T. scripta* requires an analysis of both spermatogenesis and sperm storage.

Spermatogenesis in seasonally breeding vertebrates can be described on the gross anatomic level by changes in testicular size, and at the microscopic level by changes in the size of the seminiferous tubules, in the extent of spermiogenesis (the maturation of spermatozoa from spermatids), and in the movement of spermatozoa from the testes. Testicular mass in monthly samples of male *T. scripta* in northern Alabama differed over the year (melanistic, $F = 8.32$, df $= 9/40$, $p < .001$; nonmelanistic, $F = 5.43$, df $= 10/67$, $p < .001$) and was greatest during summer and fall (Fig. 19.6). Testes of melanistic males were largest during August, whereas testes of nonmelanistic males were largest during September, and melanistic testis mass exceeded nonmelanistic during August and September ($t = 3.08$, df $= 29$, $p < .005$). Seminiferous tubule diameter in the testes differed also in the same monthly samples (melanistic, $F = 7.08$, df $= 8/33$, $p < .001$; nonmelanistic, $F = 5.47$, df $= 9/36$, $p < .001$; Fig. 19.7). Seminiferous tubules of both melanistic and nonmelanistic males were largest in the September sample, but were not significantly different in size ($t = 2.02$, df $= 8$, $.10 > p > .05$). Both nonmelanistic and melanistic males exhibited transforming spermatozoa in the seminiferous tubules beginning in July and lasting, at a much reduced level, through February (Fig. 19.8).

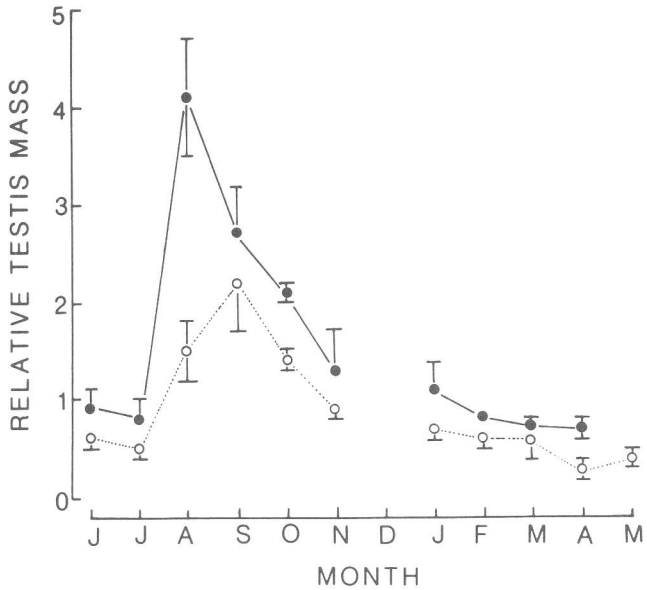

FIGURE 19.6. Monthly variation in relative testis mass of nonmelanistic (open circles, dotted lines) and melanistic (solid circles, solid lines) male *Trachemys scripta* collected in northern Alabama. Relative testis mass was calculated by dividing the wet mass (g) of both freshly dissected testes by the plastron length (mm) and multiplying by 100. The numbers of individuals examined, by month and color phase (nonmelanistic, then melanistic), are as follows: Jan. = 4, 3; Feb. = 9, 1; Mar. = 5, 3; Apr. = 5, 6; May = 4, 0; June = 13, 10; July = 14, 8; Aug. = 11, 7; Sept. = 7, 6; Oct. = 5, 10; Nov. = 8, 2; Dec. = 0, 0. Means ± SE are shown. Data are from Gross (1986) and Garstka et al. (pers. obs.).

To determine if there was an effect of gonadal hormones on scute melanization, we made use of an observation of Gross (1986). He castrated male *T. scripta* in his studies of sperm storage and activation and noted that shell tissue sometimes regenerated to fill the holes in the carapace made during castration. These holes were normally capped with the removed shell piece and sealed with epoxy putty (Lawson and Garstka, 1985; Gross, 1986). In some animals the old shell did not heal but was replaced entirely by new shell from below. Thus, a short-term system was

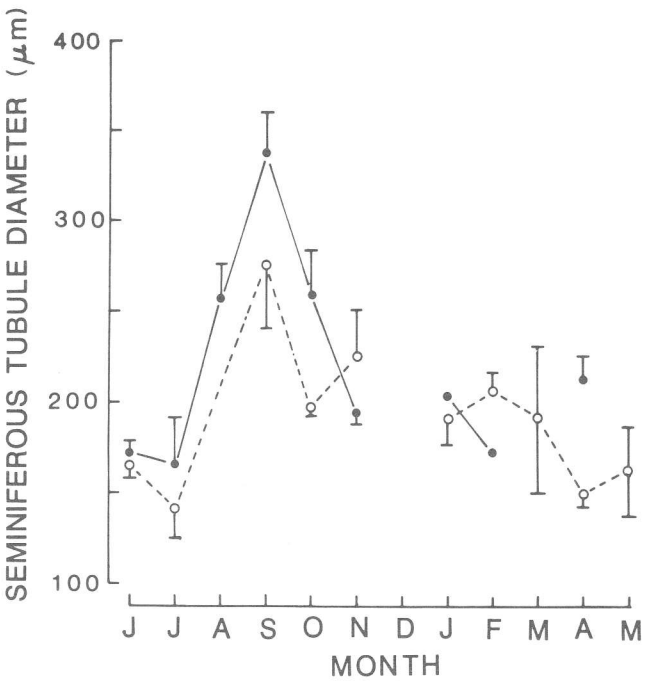

FIGURE 19.7. Monthly variation in seminiferous tubule diameter of nonmelanistic (open circles, dotted lines) and melanistic (solid circles, solid lines) male *Trachemys scripta* in northern Alabama. Tissues were fixed in Zenker's fluid, dehydrated in a graded ethanol series, embedded in paraffin, sectioned at 8 μm, and stained with hematoxylin and eosin. Seminiferous tubule diameter was measured with an ocular micrometer; three tubules per section and two sections per male were measured. Group means were calculated from individual turtle means. Group means ± SE are shown. The numbers of males examined, by month and color phase (nonmelanistic, then melanistic), are as follows: Jan. = 4, 1; Feb. = 8, 1; Mar. = 3, 0; Apr. = 5, 5; May = 2, 0; June = 2, 3; July = 9, 8; Aug. = 0, 7; Sept. = 4, 6; Oct. = 1, 9; Nov. = 8, 2; Dec. = 0, 0. Data are from Gross (1986) and Garstka et al. (pers. obs.).

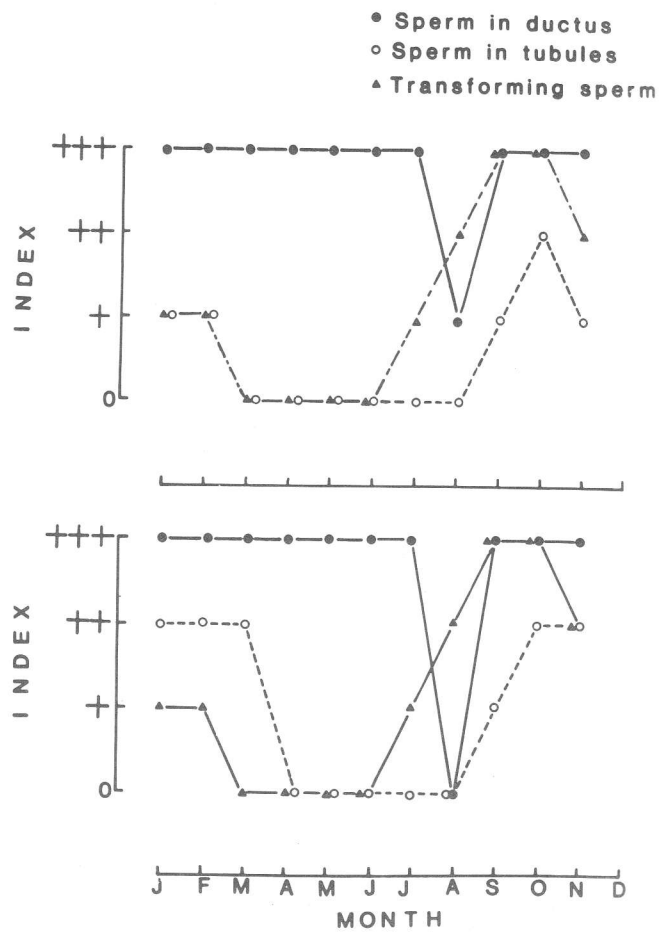

FIGURE 19.8. Monthly pattern of gametogenesis in nonmelanistic (above) and melanistic (below) male *Trachemys scripta* collected in northern Alabama. Tissues were fixed in Zenker's fluid, dehydrated in a graded ethanol series, embedded in paraffin, sectioned at 8 μm, and stained with hematoxylin and eosin. The numbers of spermatozoa free in the seminiferous tubules and in the ductus deferentia were scored in each of three sections for each male as 0 = none observed, + = 1–100, ++ = 101–500, and +++ > 500. A similar numerical scale was used to estimate the number of spermatozoa transforming within the seminiferous tubules. The numbers of testes examined, by month and color phase (nonmelanistic, then melanistic), are as follows: Jan. = 4, 2; Feb. = 9, 1; Mar. = 4, 3; Apr. = 5, 6; May = 2, 2; June = 2, 3; July = 10, 8; Aug. = 6, 7; Sept. = 4, 6; Oct. = 4, 9; Nov. = 8, 2; Dec. = 0, 0. Median scores of each group are shown. Data are from Gross (1986) and Garstka et al. (pers. obs.).

available to examine the effect of castration on carapace coloration. Several such surgeries were performed, but few turtles refilled the holes with shell, and fewer lived long enough to establish a color pattern. However, castrated males seemed to replace the shell with its original pattern: melanistic with black shell, nonmelanistic with striped shell.

PINEAL MORPHOLOGY

To determine if the pineal glands of nonmelanistic and melanistic male *T. scripta* differed, pineal glands were dissected from 29 males collected during the period of gonadal recrudescence between August and November (Lawson and Garstka, unpubl. data). Measurements of pineal mass were normalized to body size by dividing pineal mass (mg) by plastron length (cm). Relative pineal mass did not differ between nonmelanistic (0.212 ± 0.027, N = 15) and melanistic (0.178 ± 0.025, N = 14) males (t = 0.90, df = 29, $p > .35$). Histological analysis of 7 μm paraffin sections stained with hematoxylin and eosin revealed no obvious morphological difference between the two groups of males.

To determine if there was an effect of the pineal on carapace color pattern, a pilot experiment in which 18 males were surgically manipulated was performed (Law-

Table 19.6. Monthly variation in energy use and availability in male *Trachemys scripta* collected from Limestone County, Alabama, as measured by circulating levels of nutrients

Month	Total serum protein (g/100 ml)		Total serum lipid (mg/100 ml)		Serum glucose (mg/100 ml)	
	NON	MEL	NON	MEL	NON	MEL
Jan.	--	--	232 ± 91 (5)	--	--	169 ± 42 (2)
Feb.	2.5 ± 0.3 (9)	2.4 (1)	206 ± 72 (9)	--	135 ± 141 (8)	44 (1)
Mar.	2.4 ± 0.5 (5)	2.1 ± 0.4 (3)	153 ± 88 (5)	--	119 ± 72 (5)	247 ± 200 (3)
Apr.	2.8 ± 1.3 (5)	2.7 ± 0.3 (6)	139 ± 92 (5)	--	252 ± 42 (5)	175 ± 49 (6)
May	2.4 ± 0.2 (4)	--	83 ± 49 (4)	--	56 ± 70 (4)	--
June	4.9 ± 0.4 (10)	4.3 ± 0.3 (10)	448 ± 275 (10)	524 ± 298 (4)	200 ± 74 (9)	259 ± 17 (5)
July	3.3 ± 0.2 (12)	4.2 ± 0.2 (8)	237 ± 228 (12)	344 ± 212 (8)	112 ± 17 (12)	200 ± 20 (8)
Aug.	3.6 ± 0.3 (10)	4.0 ± 0.3 (7)	155 ± 80 (10)	416 ± 105 (7)	71 ± 21 (10)	48 ± 27 (7)
Sept.	3.6 ± 0.5 (4)	3.2 ± 0.3 (5)	300 ± 46 (4)	297 ± 69 (6)	35 ± 25 (4)	73 ± 29 (6)
Oct.	3.0 ± 0.6 (5)	3.8 ± 0.2 (9)	275 ± 62 (5)	324 ± 41 (9)	107 ± 50 (5)	169 ± 59 (9)
Nov.	3.5 ± 0.3 (8)	2.9 ± 0.3 (2)	294 ± 30 (8)	184 ± 7 (2)	138 ± 80 (8)	169 ± 42 (2)

Sources: Terrell and Garstka, 1984; Gross, 1986; Garstka et al., pers. obs.

Note: Serum protein was measured by the biuret reaction, serum glucose by the *o*-toluidine reaction, and total serum lipid by the sulfuric acid-vanillin reaction (all methods in Tietz, 1982). Turtles were killed by decapitation immediately after capture. Blood was collected, allowed to clot on ice and at 5° C overnight, and centrifuged, and the serum was stored at -20° C until tested. Means ± SE are shown, with sample size in parentheses. No turtles were collected in December. Abbreviations: MEL, melanistic; NON, nonmelanistic.

son and Garstka, unpubl. data). Seven males were pinealectomized and castrated, two were pinealectomized and sham-castrated, five were castrated and sham-pinealectomized, and four were simply castrated. Biopsies were removed from the healing wounds in the shell of the animals, which died between 9 and 67 days following surgery. However, only three animals survived more than 30 days, and of them only one was pinealectomized. It was a melanistic male (169 mm PL) that died 67 days after surgery, and it showed definite linear arrays of melanophores in the regenerating shell. Details of the role that the pineal complex plays in vertebrate color change are reviewed by Ralph et al. (1979).

ENERGETICS

Seasonal cycling of nutritionally important molecules and of the size of metabolically important organs has been reported in many reptile species (Dessauer, 1955; Hutton and Goodnight, 1957; Masat and Musacchia, 1965; Emerson, 1967; Telford, 1970; Aleksiuk and Stewart, 1971; Brisbin, 1972; Goldberg, 1972; Derickson, 1976; Garstka et al., 1983; Silva et al., 1984; and others). We sought first to make comparisons of the cycling of serum protein, serum lipid, and serum glucose, especially during critical breeding and recrudescent periods. Because we had already seen differences in gametogenic function between melanistic and nonmelanistic males, we hypothesized that energetics might be more pronounced during reproductively important periods. Monthly samples of nonmelanistic and melanistic males were analyzed (Table 19.6). Although serum protein of both nonmelanistic ($F = 3.11$, df = 9/62, $p < .005$) and melanistic ($F = 6.17$, df = 8/42, $p < .001$) males varied over the year, there was no difference between the color phases during either the April breeding period or the July–September period of testicular recrudescence. Serum lipid of nonmelanistics ($F = 3.44$, df = 10/64, $p < .005$) varied over the year, but comparisons with melanistics were complicated by the lack of spring samples for melanistics. Serum glucose of both nonmelanistics ($F = 4.12$, df = 9/50, $p < .001$) and melanistics ($F = 7.13$, df = 8/31, $p < .001$) varied over the year, and April breeding samples differed significantly between melanistic and nonmelanistic males ($t = 2.56$, df = 8, $p < .005$).

Turtles do not have the gonad-associated fat bodies of lepidosaurian reptiles. Fat bodies of lepidosaurians have been shown to vary in size inversely with the gonads and to provide an important nutrient store for gonadal recrudescence (Derickson, 1976; Crews, 1979; but see Congdon and Tinkle, 1982b; Long, 1985). However, because the liver is so important in nutrient cycling, and because its size and function have been shown to vary seasonally in reptiles (Dessauer, 1955; Emerson, 1967; Aleksiuk and Stewart, 1971; Goldberg, 1972), we examined monthly liver samples of male *T. scripta* for evidence of seasonal fluctuations. Relative liver mass (Fig. 19.9) varied among the sampled months in both nonmelanistic ($F = 5.20$, df = 9/70, $p < .001$) and melanistic ($F = 3.62$, df = 9/40, $p < .005$) males. Although no difference was detected between nonmelanistic and melanistic males during recrudescence, relative liver mass did differ between male groups during the April breeding season ($t = 2.85$, df = 9, $p < .02$).

Total liver protein, lipid, and glycogen were measured in monthly samples of nonmelanistic and melanistic males (Table 19.7). Neither significant variation among monthly samples nor male group differences were detected in liver protein results. Total liver lipid of non-

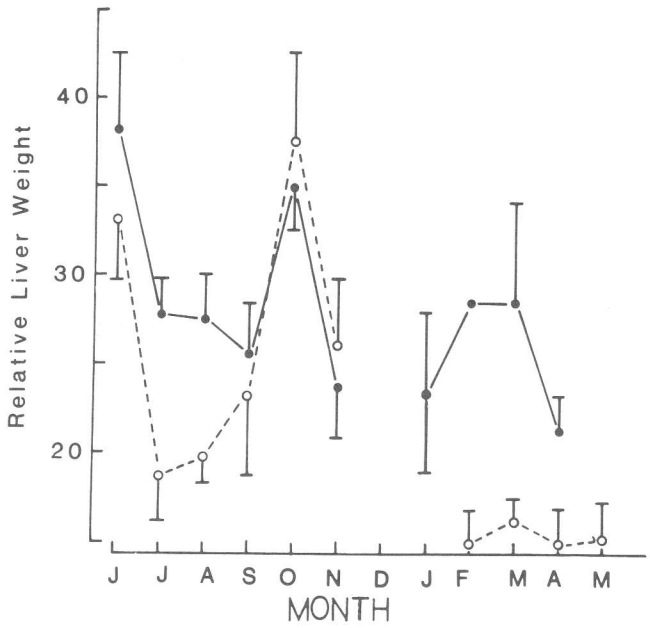

FIGURE 19.9. Monthly variation in relative liver mass in nonmelanistic (open circles, dotted lines) and melanistic (solid circles, solid lines) male *Trachemys scripta* collected in northern Alabama. Relative liver mass was calculated by dividing the wet mass (g) of freshly dissected liver by the plastron length (mm). Monthly means ± SE are shown. The numbers of males examined, by month and color phase (nonmelanistic, then melanistic), are as follows: Jan. = 0, 3; Feb. = 5, 1; Mar. = 9, 3; Apr. = 5, 6; May = 5, 0; June = 14, 5; July = 11, 8; Aug. = 1, 7; Sept. = 7, 6; Oct. = 5, 10; Nov. = 8, 2; Dec. = 0, 0.

melanistic males did not differ among monthly samples, but in monthly samples of melanistic males it did (F = 6.24, df = 8/38, $p < .001$). No differences in liver lipid between nonmelanistic and melanistic males were detected during either recrudescence or breeding. Liver glycogen varied among monthly samples of nonmelanistic (F = 3.18, df = 10/62, $p < .005$) but not melanistic males. Liver glycogen further differed between male groups during the April breeding season (t = 3.83, df = 9, $p < .005$).

Cholesterol was also measured. Cholesterol may provide additional insight into lipid cycling because of its connection with circulating lipoprotein and because it serves as the precursor for the biosynthesis of steroid hormones. Serum cholesterol was expressed as a fraction of total serum lipid (mg cholesterol per 100 ml divided by mg total lipid per 100 ml; Fig. 19.10). The fraction of total lipid as cholesterol differed between nonmelanistic and melanistic males during the recrudescence period (t = 3.61, df = 55, $p < .001$). Testicular cholesterol (Fig. 19.11) also differed between the male groups during recrudescence (t = 12.39, df = 68, $p < .001$), but it was the melanistics that had significantly higher testicular cholesterol, although the nonmelanistics had significantly higher serum cholesterol. Melanistic males also exhibited testicular cholesterol levels higher than nonmelanistics during the April breeding period (t = 2.36, df = 8, $p < .05$).

Hypothesis of the Control of Melanism in Male *Trachemys scripta*

There are consistent differences relating seasonal energetics and reproduction in melanistic and nonmelanistic male *T. scripta* sampled from northern Alabama. During

Table 19.7. Monthly variation in metabolic stores and turnover as measured by total protein, total lipid, and glycogen concentrations in the liver of male *Trachemys scripta* collected in northern Alabama

Month	Total protein (g/100 g)		Total lipid (mg/100 g)		Glycogen (μmole/g)	
	NON	MEL	NON	MEL	NON	MEL
Jan.	0.06 ± 0.03 (5)	0.60 ± 0.08 (3)	244 ± 194 (5)	314 ± 90 (3)	1.02 ± 0.22 (5)	0.11 ± 0.17 (3)
Feb.	0.90 ± 0.11 (9)	--	405 ± 290 (9)	--	1.20 ± 0.50 (9)	--
Mar.	--	0.90 ± 0.12 (3)	334 ± 406 (5)	218 ± 40 (3)	0.80 ± 0.30 (5)	0.06 ± 0.04 (2)
Apr.	--	0.70 (1)	633 ± 717 (5)	151 ± 59 (5)	0.38 ± 0.20 (5)	0.03 ± 0.01 (6)
May	--	--	271 ± 225 (2)	--	0.93 ± 0.40 (3)	--
June	0.90 ± 0.11 (9)	0.90 ± 0.13 (5)	533 ± 412 (9)	600 ± 216 (4)	0.59 ± 0.25 (9)	0.20 ± 0.07 (5)
July	0.60 ± 0.11 (10)	0.40 ± 0.03 (8)	238 ± 82 (10)	188 ± 94 (8)	0.86 ± 0.48 (10)	0.44 ± 0.32 (8)
Aug.	0.50 ± 0.07 (10)	0.40 ± 0.06 (7)	357 ± 351 (10)	244 ± 140 (7)	0.66 ± 0.23 (10)	0.30 ± 0.07 (7)
Sept.	0.50 ± 0.02 (4)	0.40 ± 0.04 (6)	171 ± 119 (3)	435 ± 168 (6)	1.18 ± 0.57 (4)	0.06 ± 0.12 (6)
Oct.	0.30 ± 0.09 (5)	0.60 ± 0.10 (9)	592 ± 297 (5)	442 ± 209 (9)	1.08 ± 0.41 (4)	0.04 ± 0.07 (9)
Nov.	0.80 ± 0.14 (8)	0.70 (1)	521 ± 359 (8)	686 ± 182 (2)	1.18 ± 0.06 (8)	0.05 ± 0.07 (2)

Sources: Gross, 1986; Garstka et al., pers. obs.

Note: Turtles were killed by decapitation and exsanguinated, and the liver and other organs were removed. Liver mass was recorded; 3 g of liver tissue was homogenized with 12 ml reptilian Ringer's saline and centrifuged; and 5 ml of the supernatant was reserved for analysis at -20° C. Supernatant total protein was measured by the biuret reaction, and total lipid by the sulfuric acid-vanillin reaction (Tietz, 1982). Glycogen was ethanol-precipitated from a KOH digest and then hydrolyzed to glucose, which was measured colorimetrically with phenol-sulfuric acid (Montgomery, 1957). Means ± SE are shown, with sample size in parentheses. No turtles were collected in December. Abbreviations: MEL, melanistic; NON, nonmelanistic.

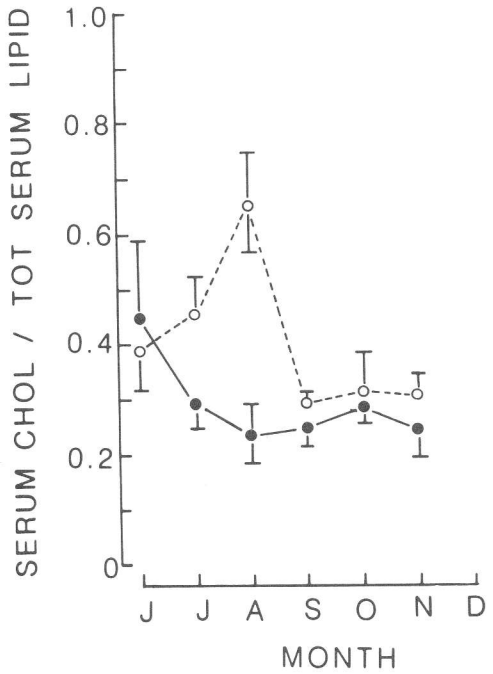

FIGURE 19.10. Monthly variation in serum cholesterol as a fraction of total serum lipid in nonmelanistic (open circles, dotted line) and melanistic (solid circles, solid line) male *Trachemys scripta* collected in northern Alabama. Serum cholesterol was measured by the ferric chloride reaction after isopropanol extraction, and total serum lipid by the sulfuric acid–vanillin reaction (methods in Tietz, 1982). Means ± SE are shown. The numbers of males examined, by month and color phase (nonmelanistic, then melanistic), are as follows: Jan. = 4, 0; Feb. = 9, 0; Mar. = 5, 3; Apr. = 5, 6; May = 4, 3; June = 11, 11; July = 12, 8; Aug. = 10, 7; Sept. = 4, 6; Oct. = 5, 9; Nov. = 8, 2; Dec. = 0, 0. Abbreviations: CHOL, cholesterol; TOT, total.

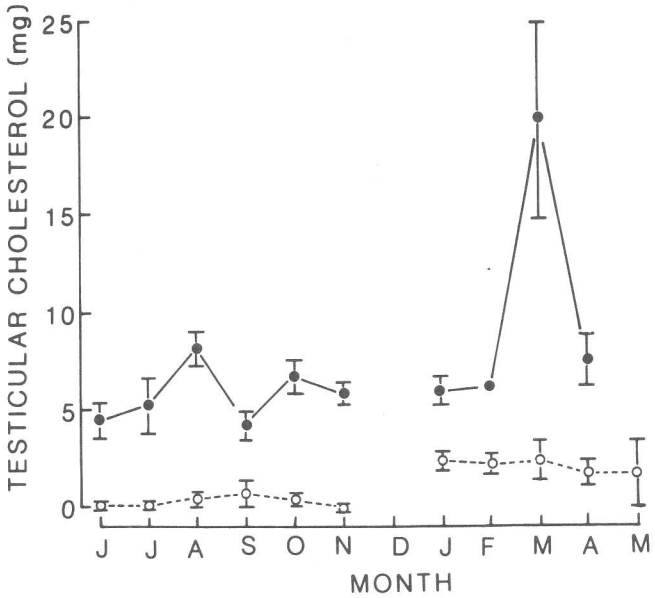

FIGURE 19.11. Monthly variation in testicular cholesterol in nonmelanistic (open circles, dotted lines) and melanistic (solid circles, solid lines) male *Trachemys scripta* collected in northern Alabama. Cholesterol was measured by the ferric chloride reaction (Tietz, 1982) in 1:5 wt./vol. testes homogenates in reptilian Ringer's saline and is expressed as mg/testes. Means ± SE are shown. The numbers of testes examined, by month and by color phase (nonmelanistic, then melanistic), are as follows: Jan. = 5, 3; Feb. = 9, 1; Mar. = 5, 3; Apr. = 5, 6; May = 4, 0; June = 13, 11; July = 12, 8; Aug. = 10, 7; Sept. = 4, 6; Oct. = 5, 9; Nov. = 8, 2; Dec. = 0, 0.

the breeding period melanistic males exhibited significantly lower levels of serum glucose, liver lipid, and liver glycogen than nonmelanistic males. However, melanistic males had significantly greater liver mass during that period. These findings suggest that melanistic males may have higher energy-use rates than nonmelanistic males during the breeding period. Melanistic males further exhibited higher (albeit not significantly) cloacal body temperature than nonmelanistic males during the breeding period.

It is tempting to connect higher rates of energy devoted to reproduction with the fact that testicular size during recrudescence is greater in melanistic than nonmelanistic males. However, measured parameters of energy storage and mobilization do not differ between melanistic and nonmelanistic males during the recrudescent period. It is only in measures of cholesterol that melanistic and nonmelanistic males differ during testicular recrudescence; melanistic males have lower circulating and higher testicular cholesterol than nonmelanistics.

Because of the importance of cholesterol as a biosynthetic precursor for steroid hormones, and because of the differences found between melanistic and nonmelanistic males in both serum and testicular cholesterol, we investigated aspects of steroid hormone metabolism in both male groups. We expected to find differences in the metabolism of androgens, perhaps with increased conversion to estrogens (Callard et al., 1977; vanTienhoven, 1983) in melanistic males. Conversion of the androgen testosterone to the estrogen estradiol occurs in neural and other tissue, and the estradiol is thought to be the behaviorally active hormone, inducing male sexual behavior (Callard et al., 1977; Leshner, 1978).

We approached the problem of androgen determinations in melanistic and nonmelanistic *T. scripta* with some hesitation. Like male *T. scripta*, garter snakes (*Thamnophis*) also exhibit dissociated gametogenesis, and previous extensive study of hormones and behavior in *Thamnophis sirtalis* showed no evidence that testosterone could induce male courtship behavior, no correlation of circulating testosterone and sexual behavior, and indeed no necessity for the presence of the gonads (Crews, 1984; Crews et al., 1984). Our interest here with male *T. scripta* was in hormone metabolism, however.

Little is known directly about steroid metabolism in reptiles (Eik-Nes, 1969; Sandor, 1969; vanTienhoven, 1983). However, we do know that (1) turtles possess aromatase enzymes to convert androgens to estrogens (Callard et al., 1977), (2) androgen levels in the blood are generally highest when testis size is greatest (Hews and Kime, 1978; Courty and Dufaure, 1980; Crews et al., 1984; Silva et al., 1984; and others), (3) androgen levels may be elevated during the breeding season even though the breeding season may be dissociated from testicular recrudescence (Kuchling et al., 1981), and (4) although the basic pattern of steroid biosynthetic pathways seems to be consistent throughout the vertebrates, there is variation among reptilian taxa in the importance of certain paths, and the paths may vary seasonally (Bourne and Seamark, 1978; Bourne, 1981; Bourne and Licht, 1985; Bourne et al., 1985).

We used gas-liquid chromatography to fractionate androgen and estrogen extracts of blood serum, liver, and testes collected from nonmelanistic and melanistic male *T. scripta* during early spring emergence from hibernation, April breeding, and fall testicular recrudescence (Garstka et al., unpubl; Table 19.8). This is the first report of such a comprehensive examination of steroid metabolism in any reptile. Several results are striking: (1) Testosterone was detected in only a few samples of testis

Table 19.8. Steroid hormones identified in blood sera, testes homogenates, and liver homogenates of male *Trachemys scripta* collected in northern Alabama

	Emergence		Breeding		Recrudescence	
Hormone	NON	MEL	NON	MEL	NON	MEL
Androgen precursors in testes						
Pregnenolone	--	--	--	--	DET	DET
Progesterone	DET	DET	DET	DET	DET	DET
17-OH-pregnenolone	--	--	--	--	--	DET
17-OH-progesterone	DET	DET	DET	DET	DET	DET
20-OH-progesterone	--	--	--	DET	--	--
Androgens in testes						
Dehydroepiandrosterone	DET	DET	DET	DET	DET	DET
Androstenedione	DET	DET	DET	DET	DET	DET
Testosterone	DET	--	--	--	DET	--
Epitestosterone	--	--	--	--	--	--
Dihydrotestosterone	DET	--	DET	--	--	--
Androgens in blood serum						
Dehydroepiandrosterone	DET	DET	DET	DET	DET	DET
Androstenedione	DET	--	DET	DET	DET	--
Testosterone	DET	--	--	--	--	--
Epitestosterone	--	DET	--	DET	--	--
Dihydrotestosterone	--	--	--	--	--	--
Androgen metabolites in testes						
Androsterone	DET	--	DET	--	DET	--
Etiocholanolone	DET	DET	DET	DET	DET	DET
Epiandrosterone	--	--	--	--	DET	--
Estrone	DET	DET	DET	DET	DET	DET
17-β-Estradiol	--	--	--	--	--	--
Estriol	--	--	DET	--	--	--
Androgen metabolites in liver						
Etiocholanolone	DET	DET	DET	DET	DET	DET
Androsterone	DET	--	DET	--	DET	--
Epiandrosterone	DET	--	--	--	DET	--
Dihydrotestosterone	--	--	--	--	DET	DET

Note: Samples were pooled to obtain sufficient data for analysis; "emergence" refers to pooled samples collected from January through March during emergence from hibernation, "breeding" refers to pooled samples collected during the April breeding period, and "recrudescence" refers to pooled samples collected from August through October during annual testicular recrudescence. Replicate pools were made: 4 nonmelanistic emergence pools, 2 nonmelanistic breeding pools, 5 nonmelanistic recrudescence pools, 1 melanistic emergence pool, 2 melanistic breeding pools, and 5 melanistic recrudescence pools. Each pool was of the corresponding samples from the same three males. For example, pool SM3 (melanistic breeding) was of the sera of males 20686, 20688, and 20689, their liver homogenate pool was LM3, and their testes homogenate pool was GM3. Tabulated results indicate that the hormone in question was detected in at least one pool (DET) or was not detected in any pool (--). Steroids were analyzed by gas-liquid chromatography as their trimethylsilyl ether derivatives on a 30-meter fused silica capillary column using a 160°-240° C temperature profile elution. Steroids were identified based on their retention time relative to the retention time of cholestane, a nonbiological steroid used as an internal standard. Although quantification is possible with this method, quantitative data are not reported because the specimens were pooled. Abbreviations: MEL, melanistic; NON, nonmelanistic.

and blood serum, (2) 20-OH-progesterone, an important progesterone metabolite in the lizard *Tiliqua rugosa* (Bourne and Seamark, 1978; Bourne, 1981), was rare in male *T. scripta,* (3) dehydroepiandrosterone (DHEA) and androstenedione, which are androgenic precursors of testosterone, were identified in almost all serum and testis samples, unlike findings for lacertid lizards (Hews and Kime, 1978; Courty and Dufaure, 1980), (4) androsterone, a metabolite (inactive?) of testosterone, was present in all nonmelanistic testis and liver samples but was not detected in any melanistic samples, (5) epitestosterone, an alpha stereoisomer of testosterone reported in the lizard *Tiliqua rugosa* (Bourne et al., 1985), was detected in melanistic but not nonmelanistic serum samples, and (6) although estradiol was not detected in any sample, the estrogen estrone, which is the aromatization product of androstenedione (Sandor, 1969; vanTienhoven, 1983), was detected in all groups of testis samples.

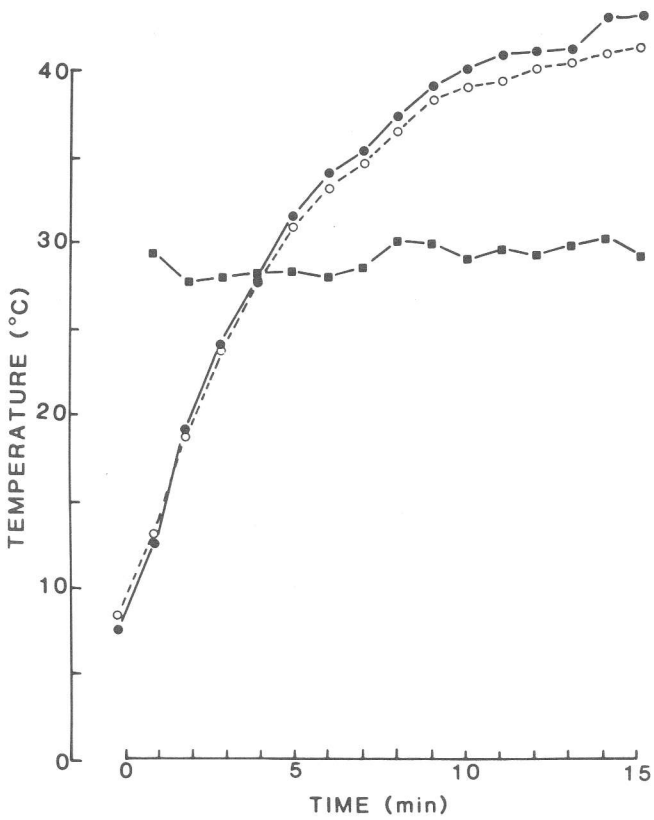

FIGURE 19.12. Rate of warming of size-matched nonmelanistic (open circles with dotted line) and melanistic (solid circles with solid line) male *Trachemys scripta*. Size-matched pairs of *T. scripta* males were placed in crushed ice and monitored by means of a cloacal Yellow Springs Instruments thermistor probe until equilibration at between 5° and 10° C. Both were set in adjacent small arenas and the cloacal temperatures were recorded. Environmental temperatures during the experiments were recorded (squares). In this typical example, no difference between the melanistic and nonmelanistic size-matched males is seen in rate of warming. Data are from Terrell and Garstka (1984).

These results clearly indicate differences in steroid metabolism between nonmelanistic and melanistic male *T. scripta*. Furthermore, they suggest that in male *T. scripta* the biosynthetic conversion of androstenedione to testosterone to estradiol, found to be the most important pathway in other vertebrates (vanTienhoven, 1983), may be supplanted by one of the following alternate pathways: (1) androstenedione to epitestosterone, (2) androstenedione to androsterone via androstanedione intermediate, or (3) aromatization of androstenedione to estrone. This situation could result from suppressing the activity of 17-β-hydroxysteroid dehydrogenase, which catalyzes the conversions of androstenedione to testosterone and estrone to estradiol, and from regulating other enzymes differently between nonmelanistic and melanistic males.

Ultimately, the question is whether these differences in steroid metabolism account for the differences in color pattern between nonmelanistic and melanistic male *T. scripta*. Because the change from nonmelanistic to melanistic apparently involves a suppression of dermal melanocytes and enhancement of epidermal melanocytes (Fig. 19.3), and because steroid hormones characteristically interact with epidermal rather than dermal melanophores, we suggest that steroid differences might indeed account for the color pattern differences between melanistic and nonmelanistic male *T. scripta*. However, castrated males regenerate their shell color pattern without change, and shell regeneration in a pinealectomized melanistic male exhibited linear arrays of melanophores. Clearly, more experiments studying the effects of various treatments on shell color-pattern regeneration as well as more study of steroid biosynthesis must be done. In addition, the behavioral and energetic effects of the steroids identified in male *T. scripta* need clarification.

Adaptive Significance of Male Melanism in *Trachemys scripta*

Thus far we have discussed the occurrence and ontogeny of melanization in male *T. scripta* and have suggested a possible hormonal mechanism for the phenomenon. Yet this question remains: What are the possible adaptive functions of this dramatic color change?

Boyer (1965) tested the hypothesis that melanistic male *T. scripta,* being black, would thermoregulate more efficiently than nonmelanistic males. He found no difference in the rates of heating in his experiments. In another experiment, Terrell and Garstka (1984) obtained similar results with 11 size-matched pairs of males (Fig. 19.12). In each case, nonmelanistic-melanistic pairs reached ambient air temperature within one minute of each other. In contrast, Bustard (1970) suggested that the black carapacial coloration of hatchling *Chelonia mydas* plays an impor-

tant role in elevating body temperature while the turtle floats at the surface. However, his results were based on experiments using whitewashed turtles as a treatment group, a most unlikely extreme in nature. Boyer (1965) interpreted his findings as being consistent with the idea that visible (to humans) wavelengths have little to do with overall light absorption. As a further test, we measured cloacal temperatures of a sample of 7 melanistic and 17 nonmelanistic males during the April breeding period (females collected on the same date showed sperm in cloacal lavages). No difference was observed (water temperature = 16.7°–17.8° C by depth, melanistic temperature = 17.2° C ± 0.15°, nonmelanistic temperature = 16.8° C ± 0.11°, $t = 1.61$, df = 22, $0.2 > p > .1$).

Thermoregulatory efficiency might also be affected by the shape of the absorbing surface. The ratio of carapace height to carapace width was calculated for a sample of 12 nonmelanistic (82–159 mm PL) and 8 melanistic (141–197 mm PL) male *T. scripta*. No difference was found (nonmelanistic = 0.34 ± 0.009, melanistic = 0.36 ± 0.007, $t = 1.59$, df = 18, $0.2 > p > .1$).

The possible role of color in reptilian thermoregulation has been suggested many times (Parker, 1935; Cole, 1943; Hutchison and Larimer, 1960; Norris, 1967; Bustard, 1970; Hamilton, 1973). Whether or not a dark-colored turtle will heat faster or stay warmer than a lighter-colored turtle depends on the complex interaction of the absorption of solar radiation, metabolic heat gain, reradiation of heat in the thermal portion of the electromagnetic spectrum, convective cooling, evaporative cooling, and conduction. In the case of *T. scripta,* we would not expect a melanistic individual to heat more rapidly than a normally pigmented turtle of the same size, because there is little difference in their solar absorptivities. Normal *T. scripta* vary in absorptivity from .86 to .90 (see Chapter 22), whereas a melanistic individual would probably have an absorptivity of about .95 to .97. Thus, there would be only a slight difference in their rate of heat gain from basking in the sun, and their rate of heat loss would be the same. This would result in at most a very small difference in body temperature. Even on a cold, clear day with little wind the effect of this color difference on body temperature would be minimal.

Boyer (1965) effectively laid to rest hypothetical functions related to thermoregulation in turtles, at least insofar as melanism's increasing the rates of warming. Ernst (1982) and Cloudsley-Thompson et al. (1985) noted the prevalence of melanism among tropical turtles and suggested that the opposite might be true: Black shells might aid radiant heat loss. Ernst (1982) further suggested that cloacal temperatures might be an inappropriate measure of any energetic significance of melanism and that increased activity during the cooler periods of the year and decreased basking time might be alternative effects to measure. Landers et al. (1982) noted a reverse latitudinal cline in coloration of *Gopherus polyphemus* (darker in the north) and suggested thermal adaptation as an explanation. A thermoregulatory function has also been suggested for the reticulate melanism observed in *Chrysemys picta* (Schueler, 1983). We have shown energetic differences between melanistic and nonmelanistic male *T. scripta,* but from our data it is impossible to determine if one is cause and the other consequence or if both are effects of an underlying, possibly steroidal cause.

A second possible function of melanism is protection from radiation (McGinness and Proctor, 1973). Melanin dissipates as heat the energy absorbed from light over a wide spectral range from far ultraviolet through infrared, as well as energy absorbed from free radicals. It seems unlikely that light would penetrate a turtle shell, yet by holding a turtle carapace to a light as if candling an egg it is easy to demonstrate that it does. In addition, more light is visible in areas lacking melanin pigmentation. Bodenheimer et al. (1953) found that even ultraviolet radiation below 300 nm passed through some animal tissue. In an extensive study of light transmission through reptile skin (mostly of desert lizards), Porter (1967) clearly showed that although ultraviolet radiation could penetrate lizard tissue, the black peritoneum of most desert species blocked those wavelengths. In *Cnemidophorus* and *Eumeces,* which lack the black peritoneum, skin melanophores functioned similarly. Cloudsley-Thompson et al. (1985) attributed darker coloration of equatorial tortoises to protection from shortwave radiation.

If protection is the function of melanism in larger male *T. scripta,* why not in small males and females? What is being protected? Male *T. scripta* exhibit dissociated gametogenesis, with sperm being stored within the body cavity from fall through the following April. Dissociated gametogenesis and sperm storage have also been reported in the closely related, and possibly conspecific (Pritchard, 1979; Iverson, 1986), *Pseudemys dorbigni* (Silva et al., 1984). Fall and early spring are the times of the year in which increased basking by *T. scripta* is observed (Boyer, 1965; Garstka and Terrell, pers. obs.). Therefore, melanism might be a gamete protection device. This hypothesis is further substantiated by the fact that the organ of sperm storage, the ductus deferens, is heavily melanized (Fig. 19.13). Porter (1967) reported that diurnal snakes possess the black peritoneum only posteriorly, and Neill (1974) reported the highest incidence of black body linings in snakes that are diurnal and arboreal. Snake gonads and snake sperm storage areas are posterior (Camazine et al., 1981). If gamete protection under conditions of long-term storage in the male is a function of melanism, what about the smaller yet sexually mature males?

Another possible function of melanism is communica-

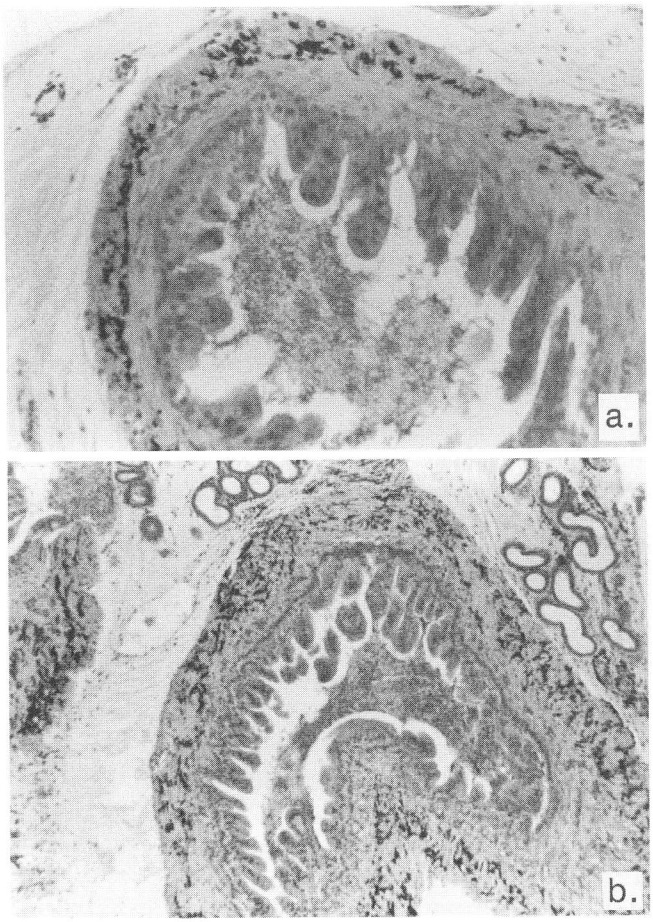

FIGURE 19.13. Photomicrographs showing the ductus deferens of *Trachemys scripta* from Alabama. *a*, nonmelanistic individual; *b*, melanistic individual.

tion. Although Madison (1977) has suggested that chemical cues are probably the primary mode of communication in turtles, he admits that visual cues cannot be excluded. The importance of color and pattern in turtles during behavioral interactions has already been suggested (Bury and Wolfheim, 1973; Schueler, 1983; Lovich, 1988). If visual communication is important, then perhaps it is the dark forelimbs and the distinctive pattern of wavy lines and dots on the head and neck that are important, because those features would be visible to a female during the foreclaw titillation phase of courtship (Cagle, 1950). But what would be communicated? Perhaps male mating ability, an effect of steroid hormones? Sexual selection by females could possibly be expected under this scenario and may ultimately be responsible for the origin, maintenance, and enhancement of the polymorphism. Alternatively, the development of melanism may facilitate species recognition by prospective mates (Moll et al., 1981). This would be particularly important in areas where *T. scripta* is sympatric with other similarly patterned emydids (those with head and forelimb stripes) such as *Pseudemys floridana, P. nelsoni, P. rubriventris, Chrysemys picta,* and *Deirochelys reticularia*. It is of interest to note that melanism is apparently infrequent in tropical populations of *T. scripta* where similarly patterned emydids are rare or absent (Moll and Legler, 1971; also see Chapter 7). Sexual dichromatism may also allow males to recognize the sex of conspecifics. This has been demonstrated for the lizard *Sceloporus undulatus* by Cooper and Burns (1987).

The idea that melanism might form an important social cue indicating maturity or social status is not without precedent. The ornithological literature in particular is replete with examples. For instance, Harris's sparrows show tremendous variability in winter plumage related to social status (Rohwer, 1975). In this case, blacker birds are "studlier" (sensu Rohwer, 1975); that is, they are socially dominant, presumably physiologically different, and possibly endowed with greater sexual prowess. Other examples of the importance of plumage polymorphisms in avian social systems are discussed by Rohwer (1975), Lawton and Guindon (1981), Rohwer and Ewald (1981), Lawton and Lawton (1985, 1986), and Whitfield (1987). Whether melanism functions as a "badge signaling" device (Rohwer and Ewald, 1981) in possible *T. scripta* dominance hierarchies (Lardie, 1983) remains to be demonstrated.

Not surprisingly, behavioral differences have been observed between melanistic and nonmelanistic turtles. The first report of unusual behavior in melanistic male *T. scripta* was given by Cahn (1937), who noted, "The nonmelanistic 'elegans' is a rather quiet, inoffensive, peaceful species, not given especially to snapping or pugnacious qualities in either sex; the melanistic 'troosti', on the other hand, frequently exhibits decided pugnacity." Aggressive interactions among melanistic male *T. scripta* were also reported by Lardie (1983). He observed that groups of turtles occupying pools in a stream habitat usually had one melanistic male that exhibited territorial behavior toward other males whenever they were present. Under laboratory conditions, melanistic males were predictably aggressive to conspecific and heterospecific turtles of about the same size and color. A possible dominance hierarchy existed, and melanistic males dominated over other males during courtship behavior. This latter observation requires further investigation. Kramer (1986) reported that aggressive interactions between *Pseudemys nelsoni* were initiated primarily by large melanistic males.

Differences in the behavior of melanistic and nonmelanistic male mosquitofish (*Gambusia affinis*) have also been reported (Martin, 1977, 1986). Martin (1977) observed that at high laboratory densities, melanistic males were highly aggressive to nonmelanistic males and ex-

hibited a clear dominance advantage during behavioral interactions. Sexual activity was also elevated in melanistic males at these high densities. However, in 120 separate trials, females responded equally to both morphs when given a choice (Martin, 1986).

A possible explanation for why melanism is primarily a male-only phenomenon in *T. scripta* may be associated with differential terrestrial activity between the sexes. Adult males may make extensive overland movements between aquatic habitats, presumably in search of mating opportunities (Morreale et al., 1984; Parker, 1984). It is likely that the bright pattern of stripes characteristic of young males is overly conspicuous to potential terrestrial predators. Thus, melanistic males may be more cryptic. Given that melanism generally occurs in larger males, we would expect them to move more frequently than smaller males, if this hypothesis is correct. Data reported in Chapter 16 appear to support this contention.

Conclusions

Although the phenomenon of ontogenetic melanism in *T. scripta* is complex, certain trends and mechanisms are now apparent. First, although the onset of this condition was previously thought to be size-specific, data from populations with different growth rates clearly indicate that the beginnings of melanic change vary concordantly. In Par Pond, for example, males characteristically exhibit signs of melanism at a plastron length of 190 mm, whereas males in Ellenton Bay and all other slow-growth populations achieve the same condition at approximately 160 mm PL. In addition, melanism appears to become evident in Par Pond males at an earlier age and sooner after sexual maturity than in Ellenton Bay males. Collectively, these data on body size and age suggest that the onset of melanism in *T. scripta* is related to population-specific growth rates. Populations in environments favoring rapid growth appear to become melanistic at an earlier age and larger body size than populations in slow-growth conditions. However, because size and age are confounded, these results do not necessarily rule out the possibility of an age-specific mechanism. Of particular interest is that for all populations we examined, the onset of melanism is coincident with population-specific female size at maturity. Whether this association is an artifact of age-related melanism or of some complex feedback mechanism associated with dominance hierarchies (Lardie, 1983) or reproductive behavior is a question that should be asked in future investigations. It is also of interest that the advent of melanism is coincident with maximum claw length development. Because claw elongation has been demonstrated to be androgen-dependent, it is possible that the two processes are interlinked, thus strengthening the argument for a hormonal basis of melanization, as indicated in our analyses. Alternatively, melanism may simply be a nonadaptive by-product of the hormonal processes responsible for claw elongation.

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In memory of Donald Tinkle

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ample, although a large proportion of adult males in a given population may become melanistic, others do not. In addition, various studies have reported a tendency toward the melanic condition in female *T. scripta* (Viosca, 1933; Conant, 1951; Legler, 1960b; Webb, 1961; McCoy, 1968; Moll and Legler, 1971; Lardie, 1983). Thus, from available data it is not clear if the phenomenon is related to size, age, or even sex. To confuse the issue further, several closely related species do not appear to exhibit melanism, for reasons that are as yet unknown. Although there are many unanswered questions with regard to melanism in turtles, our objectives in this chapter are (1) to review what is known about the occurrence and development of melanism in turtles, (2) to suggest and test possible mechanisms of sexually dichromatic melanization in *T. scripta* that might be applicable to other turtles, and (3) to provide an understanding of the adaptive significance of melanism in *T. scripta*.

In this review we compare melanistic with nonmelanistic, but sexually mature, males and report the results of experiments performed to test hypotheses generated by our comparisons. All of these hypotheses have concerned possible hormonal mechanisms that could explain the melanization process. In the case of *T. scripta*, a hypothesis of hormonal control would have to explain the permanence, the sexual dichromatism, and the timing (not coincident with gonadal maturation) of melanic change.

Table 19.1. References to melanism in selected populations of *Trachemys scripta*

Location	Subspecies	Reference	Comment
Alabama	*scripta*	16	--
Illinois	*elegans*	2,4	--
		9	Both sexes
Indiana	*elegans*	15	--
Louisiana	*elegans*	1	--
North America	--	5,7,14,17	--
		21	Both sexes
Mexico	*taylori*	8	Both sexes
	Refer to text	18	Refer to text
Ohio	*elegans*	6	Both sexes
Oklahoma	*elegans*	10,12	--
		20	Both sexes
Panama	"Panamanian"	13	Both sexes
South Carolina	*scripta*	22	--
Texas	*gaigeae*	3	--
	elegans	20	Both sexes
Virginia, North Carolina, South Carolina	--	19	--
West Virginia	*elegans*	11	--

References: 1, Viosca, 1933; 2, Cahn, 1937; 3, Hartweg, 1939; 4, Cagle, 1948b; 5, Cagle, 1950; 6, Conant, 1951; 7, Carr, 1952; 8, Legler, 1960b; 9, Smith, 1961; 10, Webb, 1961; 11, Adler, 1968a; 12, McCoy, 1968; 13, Moll and Legler, 1971; 14, Ernst and Barbour, 1972; 15, Minton, 1972; 16, Mount, 1975; 17, Pritchard, 1979; 18, Smith and Smith, 1979; 19, Martof et al., 1980; 20, Lardie, 1983; 21, Ward, 1984; 22, this study.

Melanism and Turtle Taxonomy

The existence of melanistic forms of some species has been responsible for numerous errors of classification. For example, although melanism is well known in adult male *Chinemys reevesii* (Sachsse, 1975; Lovich et al., 1985), such individuals were previously considered to be separate species: *Damonia* (= *Chinemys*) *unicolor* (Gray, 1873). Similar problems, exacerbated by dramatic sexual size dimorphism, plagued taxonomists working with turtles of the genus *Trachemys* for more than 100 years. Early naturalists recognized melanistic and nonmelanistic forms of West Indian *Trachemys* as different species, even though each "species" was represented in collections as mostly males or mostly females (DeSola and Greenhall, 1932; Conant and DeSola, 1934). Recognition of melanistic males as *Pseudemys* (= *Trachemys*) *rugosa* persisted from the original description of Shaw (1802) until Barbour and Carr (1940) revealed the true condition. According to Carr (1952), Cuban provincials also recognized male and female *T. decussata* as different turtles. Danforth (1925) reported that Puerto Rican natives considered the green (nonmelanistic) and black (melanistic) individuals of *Pseudemys palustris* (= *T. stejnegeri stejnegeri*) to be distinct species, although he found "intergrades" between the two.

A similar situation existed with *T. scripta*, whereby a melanistic obviously male-only form was described by Holbrook (1836) as *Emys troostii* and the nonmelanistic form was described as *P. elegans* (Wied, 1839). Viosca (1933) concluded that the *troostii* form was based on melanistic males, but herpetologists were slow to accept the new proposal (Carr, 1952). The situation was further complicated by temporary retention of the name *P. troostii* (as a senior synonym) for turtles currently recognized as *T. scripta*. Moreover, subsequent revisions at the subspecies level resulted in use of the trinomen *Trachemys scripta troostii* for one of the geographic races of *T. scripta* (see Chapter 4). Far more detailed accounts of the taxonomic turmoil resulting from the failure of early herpetologists to recognize the true nature of ontogenetic melanization in *T. scripta* are found in Viosca (1933), Cahn (1937), Barbour and Carr (1940), and Carr (1952).

More recently described variants such as *Chelonia mydas carrinegra* (Caldwell, 1962b) and *Platemys platycephala melanonota* (Ernst, 1983) are subspecies of otherwise nonmelanistic species and are characterized by unusual development of dark pigmentation. In *P. p. melanonota* the melanic condition is well established even in juveniles (Carl Ernst, pers. com.). The Mexican trionychid *Trionyx ater* (Webb and Legler, 1960) is a derivative of *T. spiniferus* distinguished mainly by the early onset and complete development of melanic coloration in both sexes. A thorough understanding of the incidence and development of melanism is crucial in assessing the validity of taxa based on this character.

Table 19.3. Size and proportion of melanistic individuals in selected populations of *Trachemys scripta*

Location	Plastron length (mm)			N		MEL/NON	Sex	Reference
	At maturity	At attainment of melanism						
		Minimum	Mean	MEL	NON			
Illinois	--	152	177	7	--	--	M	2
	90-100	126	--	10	55	0.18	M	3
Louisiana	--	140[a]	165[a]	35	88	0.28	M	1
Oklahoma	≈ 100	145	--	--	--	--	M	6
	≈ 166	147	--	--	--	--	F	6
	≈ 100	150	--	--	--	--	M	5
Tennessee, Illinois	90-100[b]	130[b]	--	--	--	--	M	4
Texas	90-100[b]	100[b]	--	--	--	--	M	4
Texas, Oklahoma	--	--	--	1	81	0.01	M	7

Note: Numbers are based on best estimates from figures, tables, or text. Abbreviations: MEL, melanistic; NON, nonmelanistic.

References: 1, Viosca, 1933; 2, Cahn, 1937; 3, Cagle, 1948b; 4, Cagle, 1950; 5, Webb, 1961; 6, McCoy, 1968; 7, Lardie, 1983.

[a]Carapace length (mm), rather than plastron length.

[b]Size variable not specified.

turtles" and normally pigmented forms are sympatric in parts of Polynesia as well as Guatemala (Pritchard, 1971).

The second level of melanic expression, seasonal melanism, has been most thoroughly studied in *Batagur baska*. In this species, males develop black head and shell pigmentation during the breeding season (Moll, 1980; Moll et al., 1981). A reversal of this phenomenon has been reported in the closely related *Callagur borneoensis*, whereby some males become lighter during the breeding season because of a loss of epidermal melanosomes (Moll et al., 1981). Although seasonal dichromatism has been reported in other turtle species, such as *Kachuga kachuga* (E. Moll, 1986b), *Geochelone travancorica* (Auffenberg, 1964), and *Heosemys silvatica* (Groombridge et al., 1983; but also see Moll et al., 1986), these are the only examples of seasonal melanism that we are aware of in turtles. The complex mechanics and histology of these transmutations are discussed in detail by Moll et al. (1981).

Reticulate melanism results from dendritic deposition of melanin in epidermal scutes that is usually superimposed on a relatively unchanged underlying pattern. This phenomenon has been reported in several northern populations of *Chrysemys picta* (Table 19.2) and is illustrated in Agassiz (1857: plate 27) and Babcock (1919: plate 24) for male *Pseudemys rubriventris*. Other possible examples of this phenomenon have been discussed by Schueler (1983). The process is not progressive and may affect only the oldest individuals in *C. picta* (MacCulloch, 1981); hence the term "senile reticulate melanism." Once the pattern is established, it presumably remains essentially unchanged for the life of the turtle. Whether this type of melanism affects males and females alike is unclear.

The fourth and perhaps most familiar type of melanism is the one we refer to as ontogenetic melanism. In this case the development of the melanic condition is progressive, generally occurs in males, and is associated with age or body size. This type of melanization is best known in some populations of *T. scripta* and its allies (Tables 19.1–19.3) and is discussed below.

Other patterns of melanic change, not included in the four primary types noted above, have been reported in turtles. Species such as *Rheodytes leukops* (Legler and Cann, 1980) and *Gopherus berlandieri* (Auffenberg and Weaver, 1969) appear to become lighter with age, a reversal of the usual trend. This change is dramatic in male *R. leukops* and appears to result from a progressive loss of melanin accompanied by subsequent replacement with brighter pigments (Legler and Cann, 1980). Some large male *Trachemys terrapen* are reported to "assume an overall white color," and the plastral pigmentation of large female *Trachemys scripta cataspila* may fade out completely (Pritchard, 1979). Ontogenetic patterns of melanic plastral pigment reorganization have been reported in juvenile Hawaiian *Chelonia mydas* (Balazs, 1986). In this case, hatchlings possess a white plastron that becomes diffused with black pigment at a length of about 6 to 8 cm. From this point on the pigment fades, usually disappearing completely by 13 cm; formation and deposition of pigment are dependent entirely on size and not age. Another example of pattern reorganization apparently occurs in *Trionyx spiniferus*. In this species the carapace pattern of adult females may be obscured by blotches of dark pigment (Webb, 1962).

Finally, no discussion of melanism would be complete without reference to such classic examples as "industrial melanism" in moths (Kettlewell, 1965; Wickler, 1968; Askew et al., 1971), other forms of reptilian melanic proliferation or reduction associated with background