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Author(s): Marie E. B. Stone, Troy A. Baird, and Paul A. Stone

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Is Melanism a Consequence of Sexual Selection in Male Red-Eared Sliders, *Trachemys scripta elegans*?

MARIE E. B. STONE,¹ TROY A. BAIRD, AND PAUL A. STONE

Department of Biology, University of Central Oklahoma, Edmond, Oklahoma USA

ABSTRACT.—Male slider turtles change coloration ontogenetically, becoming melanistic as they age and approach the body size of sexually mature females. Several investigators have suggested that melanism is favored by sexual selection, although there is little evidence to support this hypothesis. We conducted experiments in enclosures to test whether melanism in male Red-Eared Sliders is a visual signal favored by sexual selection. In female preference trials, females showed no preference for either nonmelanistic or melanistic males. Melanistic and nonmelanistic males associated together instead of being aggressive toward each other in trials testing male–male competition. Neither result supports the hypothesis that male melanism is a product of sexual selection. Our observations of nonaggressive interactions between melanistic and nonmelanistic males suggest that melanism in male slider turtles may function as sex recognition to avoid mistaken courtship of large males.

In species under strong sexual selection, conspicuous coloration sometimes signals social status (reviewed in Andersson, 1994), and in some species that display alternative social tactics, ontogenetic coloration changes coincide with shifts in mating tactics (Magnhagen, 1992; Mazzoldi and Rasotto, 2002; Baird, 2008). Younger mature males often have coloration similar to that of juveniles or females, whereas coloration of older males is often more conspicuous (Carpenter, 1995; Mazzoldi and Rasotto, 2002; Baird and Curtis, 2010). In addition to changes in coloration, older males often are more aggressive, use conspicuous behaviors to display their bright coloration, and interact with females more frequently than do younger males (Mazzoldi and Rasotto, 2002; Wikelski et al., 2005; Baird, 2013a).

Investigation of the possible role of sexual selection in turtle social systems lags behind that of other taxa (reviewed by Baird, 2013b), but findings on terrestrial and semiaquatic species suggest an important role of both male–male competition and female preference (Berry and Shine, 1980). Social dominance was related to large male size in both Fighting (*Chersina angulata*) and Desert Tortoises (*Gopherus agassizii*), and female Desert Tortoises preferred larger males (Niblick et al., 1994; Mann et al., 2006). Social status was correlated with age in male Wood Turtles (*Clemmys insculpta*; Kaufmann, 1992). Although these examples support the hypothesis that sexual selection plays a role in turtle social structure, none of these species displayed male-biased dimorphic coloration.

Slider turtle (*Trachemys scripta*) males become darker as they age (Lovich et al., 1990). Darker male coloration (hereafter melanistic) is characterized by increased melanin deposition in the integument and shell that obscures the green and yellow stripes on the head, limbs, and shell (Cagle, 1950; McCoy, 1966; Lovich et al., 1990). Females develop limited melanism, becoming slightly darker as they age but not to the extent that males do (McCoy, 1966; Lovich et al., 1990). Male sliders attain sexual maturity on average during their third year, but melanism does not develop until they are 6–11 years old (Lovich et al., 1990). Once the change in coloration occurs, males remain melanistic for their entire lifespan, estimated to be 30 years (Gibbons and Semlitsch, 1982). Melanism might be a nonadaptive byproduct of hormonal changes (Lovich et al., 1990); however, several nonmutually exclusive hypotheses have

been proposed to explain the potential adaptive function of melanism in this species including thermoregulation (but see Gronke et al., 2006), crypsis from predators, sex recognition, and sexual selection (Lovich et al., 1990).

Of these different hypotheses, the possibility that melanism functions as a sexually selected social signal in *T. scripta* has received the most attention. When courting females, non-melanistic males typically vibrate their foreclaws rapidly against the heads of females (titillation; Cagle, 1950; Jackson and Davis, 1972), whereas melanistic males court mainly by chasing and biting females (Thomas, 2002). Nonmelanistic male *T. scripta* attempted to copulate without courtship more frequently than did melanistic males (Thomas, 2002). These differences in courtship behaviors between melanistic and nonmelanistic males are consistent with the hypothesis that two color morphs display alternative reproductive tactics (Thomas, 2002) similar to those displayed by many lizards (Thompson and Moore, 1991; Wikelski et al., 2005; York et al., 2014). Also, numerous researchers have reported anecdotal observations describing melanistic male *T. scripta* as aggressive, socially dominant, or both (Lardie, 1983; Parker, 1990; Tucker et al., 1995). Hites et al. (2013), however, found that propensity to bite was related to size but not melanism in male *T. scripta*.

We tested the hypothesis that melanism evolved as a sexually selected visual cue by conducting female preference and male–male competition experiments involving melanistic and non-melanistic males. If male melanism evolved by sexual selection, we predicted that females would exhibit a preference for melanistic males, that melanistic males would be socially dominant over nonmelanistic males, or both would be observed.

MATERIALS AND METHODS

Our study population inhabits an impoundment in central Oklahoma (35°39.86'N, 97°41.40'W, NAD27; elev. 363 m; for further description, see Stone et al., 2005). We used a basking trap and hoop nets (Memphis Net and Twine Co., Memphis, TN) baited with sardines to capture subjects that we used in trials. Turtles were marked at initial capture using unique combinations of notches in the marginal scutes (Stone and Babb, 2005). We measured turtle body size as midline plastron length (MPL \pm 1.0 mm) and determined sex based on secondary sexual characteristics (females are larger; males have elongated foreclaws and an enlarged tail; Cagle, 1950; Gibbons and

¹Corresponding Author. E-mail: marieebstone@gmail.com
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Lovich, 1990). We classified three stages of melanization in males following the method of Tucker et al. (1995). Non-melanistic males lacked any indication of melanism, had green and yellow stripes on the integument, and had red bars posterior to the orbit. Partially melanistic males (stage 1 of Tucker et al., 1995) showed some darkening of the integument and shell, but the green and yellow stripes and red postorbital bars were still visible. Fully melanistic males had colored stripes on the shell and integument, and the red postorbital bar was masked by dark brown and black pigment. We used only fully melanistic and nonmelanistic males in experiments.

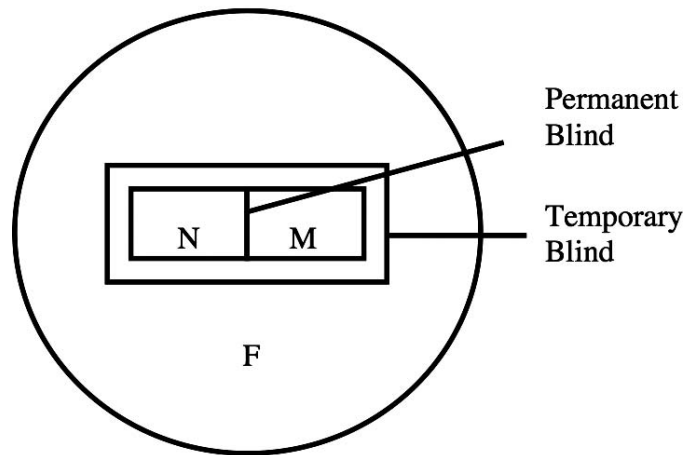
We conducted female preference ($N = 20$) and male–male competition ($N = 20$) experiments between 11 August and 23 September 2003, during the breeding season of *T. scripta* (Thomas et al., 1999). We used round plastic pools (1.8 m \times 38.1 cm, Diam. \times H) for all experiments. Depending on the type of experiment (described below), we placed either two or three 37.9-L aquaria (50.8 cm \times 25.4 cm \times 30.5 cm, L \times W \times H) inside the pools. We drew grids (30.5 cm \times 30.5 cm) on the pool bottom to determine the distance of test subjects from aquaria or from one another. Turtles were held in aquaria inside pools during trials to control for possible effects of odors. Therefore, we tested specifically whether melanism was a functional visual cue. Pools were set on a concrete slab 10 m from the pond where turtles were collected. We filled aquaria and pools to a depth of 20.3 cm using water from a well at this site. All observations of turtle behavior were conducted from behind opaque blinds (plastic sheeting 1.5 m \times 6.4 m, H \times W). Air, pool, and pond temperatures were recorded before and after each trial. Pool temperatures during trials varied with ambient temperature (18.8–23.4°C).

Experimental subjects were captured using hoop nets on the days of each trial. We chose males having MPL ≥ 100 mm and females having MPL ≥ 170 mm to ensure that experimental subjects were sexually mature (Cagle, 1950; Gibbons and Greene, 1990). Individuals were used only once in a female preference trial and only once in a male–male competition trial. Melanistic males in our population tended to be larger than nonmelanistic males. Therefore, we included male size (MPL) as a variable in our analyses to test for effects of body size in both female preference and male–male competition trials, and we minimized possible effects of body size by matching the most similarly sized nonmelanistic and melanistic males in all trials (mean MPL difference ± 1.0 SE = 20.0 mm ± 2.1 ; range 0.7–52.6 mm).

We placed experimental subjects in pools (or aquaria, see below) at approximately 1700 h the day before trials to allow habituation, and turtles were held no longer than 15 h prior to trials. From 0800–1000 h on the following day, we recorded observations continuously when subjects were swimming or interacting with conspecifics and at 5 min intervals when subjects were quiescent. At the conclusion of each trial, turtles were released at the original capture location. Pools, aquaria, and blinds were cleaned with biodegradable soap between trials.

For female preference experiments, we placed two aquaria (described above) in the center of the pool, one aquarium containing a melanistic male and the other containing a nonmelanistic male that were matched for size (see above) and randomly assigned to the two aquaria (Fig. 1). An opaque blind was placed between the aquaria to prevent the males from seeing each other throughout the adjustment period or trials. A female, captured in a different net than either male, was

A.



B.

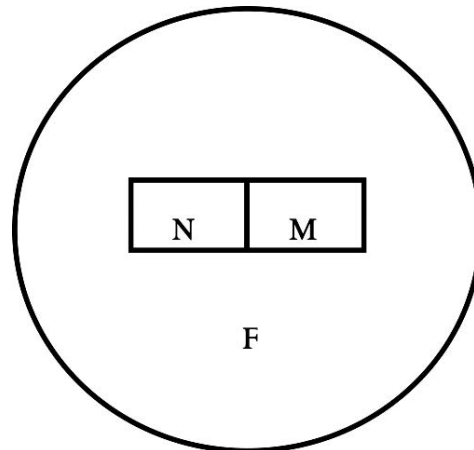


FIG. 1. Female preference experimental setup. N = nonmelanistic male, M = melanistic male, F = female. Males were randomly assigned to aquaria for each trial. (A) Acclimation period; permanent and temporary blinds are in place. (B) Trial period; temporary blind is removed.

introduced into the pool and allowed to swim freely during the adjustment period (approximately 15 h). We surrounded both aquaria with an opaque plastic blind to prevent visual contact between the female and males throughout the adjustment period, and we removed this blind at the beginning of observations. We recorded the amount of time(s) that females spent at the glass looking into the aquaria occupied by each male as a measure of female preference (Martin, 1986; Bisazza and Pilastro, 2000; Witte and Noltemeier, 2002). Also, we recorded the number of trials that any turtle titillated while at the aquarium glass.

For male–male competition experiments, we subdivided pools into three equal sections using a Y-shaped blind (Fig. 2). To induce competition, we placed a female inside an aquarium in one section of the pool. A melanistic male and nonmelanistic

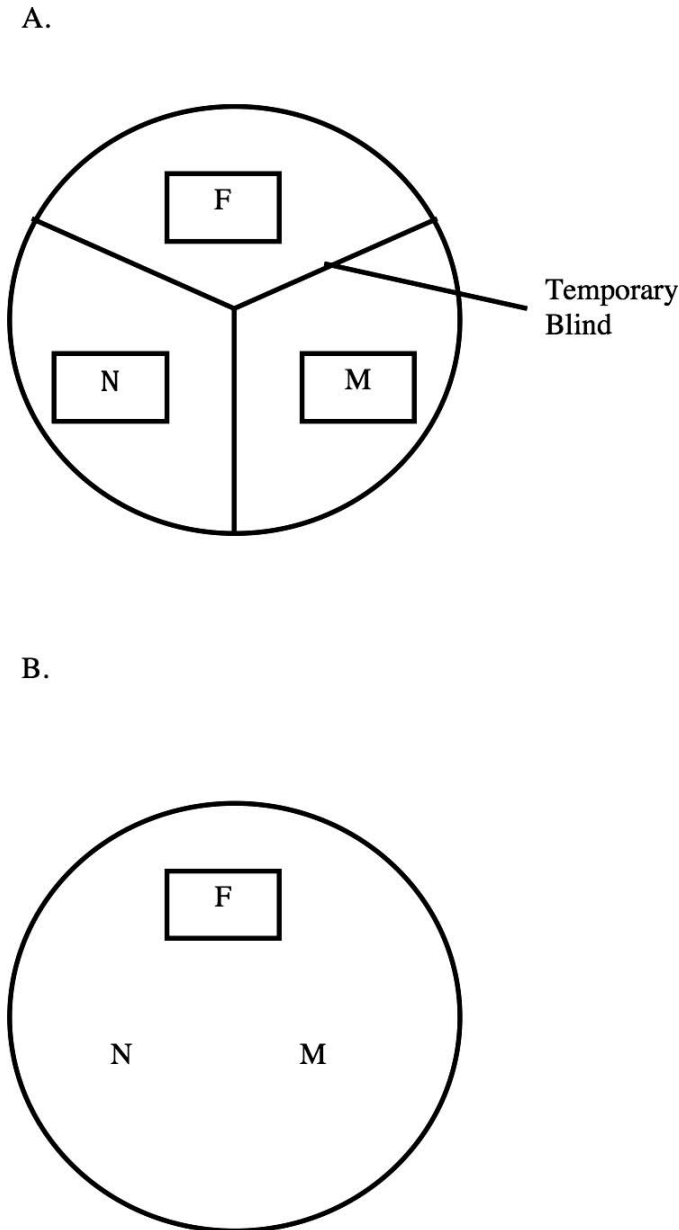


FIG. 2. Male–male competition experimental setup. N = nonmelanistic male, M = melanistic male, F = female. Males were randomly assigned to aquaria for each trial. (A) Acclimation period; temporary blind is in place, and all turtles are contained in aquaria. (B) Trial period; blind is removed, and males are released from aquaria.

male were placed in aquaria in the other two sections to limit their movements prior to beginning trials. We used size-matched males captured in different nets to reduce possible effects of familiarity. Subjects were allowed to habituate for approximately 15 h prior to the onset of trials. Prior to recording observations, we released males into their sections of the pool, removed their aquaria, and removed the blind. We recorded these dependent variables: number of titillations; length of time(s) that either male spent at the glass looking into the aquarium containing the female; and the number of times that either male bit, followed, approached, and perched on the carapace of the other male. We defined “following” as one turtle swimming in the same direction 60 cm or less behind the leading turtle, and we defined “approaching” as one male moving toward and touching another male that was stationary.

TABLE 1. Summary of analyses comparing slider behavior during female preference trials. For amount of time at glass, data are means \pm SE. Asterisks indicate statistically significant differences between melanistic and nonmelanistic males as determined through GLM analysis.

| Variable | Melanistic | Nonmelanistic |
|--|--------------|---------------|
| Number of seconds at aquarium glass | 207 \pm 50 | 146 \pm 30 |
| Number of trials when females titillated males | 1 | 4 |
| Number of trials when males titillated females | 4* | 0 |

Statistical Analyses.—Data were analyzed using the Program R version 3.01 (R Development Core Team, 2013). For female preference experiments, we used generalized linear models (GLM) to compare the influence of melanistic status and male MPL (mm) on the number of seconds females spent at the glass of aquaria containing the males, the number of trials when females titillated males, and the number of trials that males titillated females. Because the amount of time at the glass is a continuous variable, we used Gaussian error structure and identity link function, whereas we used Poisson error structure and log link function for the two discrete variables. For male–male competition experiments, we used GLM to examine male melanistic status and MPL on the length of time males spent looking at females through the aquarium glass and the number of times that males followed, approached, titillated, or perched on the other male. As with female-choice experiments, we used Gaussian or Poisson error structure for continuous or discrete variables, respectively.

RESULTS

Air temperature ranged from 17–31°C during trials, but none of the behavioral variables varied significantly with air temperature over this range (r^2 values = 0.005–0.085). Therefore, air temperature was not used as a covariate.

In all female preference trials, females spent less than 10% of total trial time with either male (Table 1). There was no effect of male MPL on the amount of time that females spent at the aquarium glass ($t_{19} = 0.70$, $P = 0.49$) or the number of trials when females titillated males ($t_{19} = 0.30$, $P = 0.77$). Melanistic status of males did not influence either variable (time at glass, $t_{19} = 0.47$, $P = 0.64$; trials with female titillation, $t_{19} = 1.13$, $P = 0.27$; Table 1). By contrast, both melanistic status ($t_{19} = 2.85$, $P = 0.007$) and male MPL ($t_{19} = 2.13$, $P = 0.04$) had positive effects on the number of trials when males titillated females.

Male MPL did not influence any of the behavioral variables that we recorded during male–male competition trials ($t = 0.15$ – 1.25 , $P = 0.88$ – 0.10). By contrast, nonmelanistic males exhibited higher frequencies of approaching ($t_{19} = 3.21$, $P = 0.003$), following ($t_{19} = 2.70$, $P = 0.01$), and perching on ($t_{19} = 2.37$, $P = 0.023$) melanistic males (Table 2). Melanistic males titillated nonmelanistic males more frequently than nonmelanistic males titillated melanistic males, but the difference was not significant. In three of 20 (15%) trials, melanistic males bit nonmelanistic males, but the opposite also occurred in one trial. Biting did not appear to be aggressive but seemed more like nipping (Comuzzie and Owens, 1990).

TABLE 2. Summary of analyses comparing slider behavior during male–male competition trials. Data are mean frequencies of behaviors directed at other males \pm SE. Asterisks indicate statistically significant differences between melanistic and nonmelanistic males as determined through GLM analyses.

| Acts/Trial | Melanistic | Nonmelanistic |
|-------------|-----------------|-------------------|
| Approach | 8.35 \pm 1.18 | 13.85 \pm 1.67* |
| Follow | 3.65 \pm 0.57 | 6.95 \pm 1.21* |
| Perching | 0.9 \pm 0.33 | 3.55 \pm 0.88* |
| Titillation | 1.90 \pm 1.02 | 0.0 |

DISCUSSION

Our observations do not support the hypothesis that melanism functions as a sexually selected visual cue. Females associated with males independent of melanistic status, indicating no preference by females for the visual cue of melanism. Instead of avoiding melanistic males, nonmelanistic males approached, followed, and interacted with them. In several trials, one male perched on the carapace of the other male while he was stationary or swimming. Melanistic male nipping of nonmelanistic males did not appear to be aggression because nonmelanistic males did not swim away.

Contrary to Thomas's (2002) observations, nonmelanistic males did not titillate females or melanistic males in any of our experiments. Instead, we observed melanistic males titillating females in both female preference and male–male competition trials, as well as nonmelanistic males in male–male competition trials. Titillation in freshwater turtles has been described in variable contexts, including play among juveniles (Cagle, 1955; Morris, 1976; Kramer and Burghardt, 1998), courtship between the sexes (Jackson and Davis, 1972; Thomas, 2002), aggression between males (Seidel and Fritz, 1997), and during interactions between females (Thomas and Altig, 2006). In our experiments, titillation of females by melanistic males might have been courtship behavior, whereas the function of their titillating nonmelanistic males was not obvious. Titillation of males by females might function in courtship to relay female receptivity.

We designed our experiments to test specifically for melanism as a visual signal while controlling for tactile and olfactory cues and eliminating the potential effects of male–male competition on female preference. Although we found no evidence supporting the hypothesis that the visual component of melanism is favored by sexual selection, alternative mating tactics have been described in male Slider Turtles (Thomas, 2002), and melanism might be favored by sexual selection in other populations. Alternatively, our results might have differed from Thomas's (2002) because of differences in experimental design. Thomas (2002) used six turtles (two melanistic males, two nonmelanistic males, and two females) in his experiments, and turtles were able to swim and interact freely in their enclosure. These experiments provided valuable baseline data on behavior in seminatural conditions but were not designed to control specifically for the visual cue of melanism. In particular, other species of semiaquatic turtles use chemical cues to detect conspecifics (Lewis et al., 2007), and odors in water might be important for interactions in sliders. Moreover, the experimental design of Thomas (2002) did not separate the potential confounding effects of male–male competition on female preference (Niblick et al., 1994; reviewed in Berglund et al., 1996).

Instead of sexual selection, our results are more consistent with the hypothesis that melanism in male sliders functions for sex recognition (Lovich et al., 1990). Sex recognition based on coloration has been documented in a variety of animal taxa (reviewed in Cooper and Greenberg, 1992; Andersson, 1994). That male *T. scripta* develop melanism when they approach the size at which females mature sexually is consistent with the possibility that becoming melanistic may prevent large males from being mistaken as females. If melanism functions to prevent inappropriate courtship by male conspecifics, males would not be expected to display intrasexual aggression based on melanistic status, and females would not exhibit preference for either male morph. Close interactions between males (following and contact) also might be adaptive for avoiding inappropriate courtship of conspecific males especially in turbid, dark aquatic habitats where visual cues do not transmit well (Berry and Shine, 1980; Baird and Olla, 1991). We suggest that future experiments on slider turtles should seek to identify the role of olfactory and tactile cues during interactions between conspecifics to examine the potential effects on male–male competition and female preference.

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