

Sex in the Half-Shell: A Review of the Functions and Evolution of Courtship Behavior in Freshwater Turtles

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ABSTRACT. – Freshwater turtle courtship is an exciting and potentially phylogenetically important field of study. Scattered data exist from the past century of research, yet no recent summary is available. Courtship in freshwater turtles includes a number of common behaviors, which usually involve visual, tactile, olfactory, and auditory signals. These signals function in both species and sex recognition and in the seduction of potential mates. Specific behavioral sequences are required to facilitate successful copulation, and these behaviors presumably play a role in mate choice. We performed a series of meta-analyses to investigate the evolution of courtship behavior in freshwater turtles. Biting, an aggressive form of courtship behavior, is plesiomorphic, conserved only in the Chelydridae, Kinosternidae, subfamily Emydinae and South American species in the Pleurodira. Head movement and foreclaw display are apparently apomorphic and evolved independently in the Geoemydinae, Deirochelyinae, and Australian species of the Pleurodira. Display type (pre- or postmounting display) and sexual size dimorphism also show phylogenetic patterns. Therefore, the evolution of courtship behavior in freshwater turtles might accompany the evolution of sexual dimorphism, which is directly subject to natural selection.

KEY WORDS. – Meta-analysis; sexual dimorphism; mating signal; natural selection

The courtship behavior of freshwater turtles (CBFT) has been a topic of research interest for over a century. Anecdotal reports and more detailed observational studies have identified visual, tactile, chemical, and auditory stimuli. Early reviews by Carpenter and Ferguson (1977) and Harless (1979) noted a paucity of data. Over 30 yrs later, an impressive body of literature on CBFT has accumulated, but this literature is scattered, and no recent summary is available. Thus, although observations of courtship behavior exist for many species, our understanding of how CBFT operates remains limited because the functions of most signals used in courtship remain elusive. This is partly attributable to logistical difficulties involved in studying behavior in freshwater turtles and to the difficulty of determining the interpretation of signals by the receiver.

Some more rigorous studies have produced quantifiable models of courtship behavior (e.g., Baker and Gillingham 1983; Liu et al. 2008), and these lend themselves to hypothesis testing. However, analyses and applications of ethograms based on stereotype patterns remain rare, and this precludes combining ethograms for comparative studies. Harless (1979) has identified necessary steps to move forward—hypothesis testing, identification of stimuli that elicit signaling, and identification of signal function—and much of this remains to be accomplished.

Herein, we provide a brief history of the study of CBFT. We review behaviors and signals currently implicated in turtle courtship studies and discuss the methods and statistical analyses commonly used in these studies. This review unifies descriptions of behavioral patterns with phylogenetic data to facilitate an understanding of the function and evolution of each signal. Although data remain limited, where possible we test explicit hypotheses to clarify the evolution of CBFT. Finally, we recommend directions for future study in the hope of stimulating further research.

HIGHLIGHTS IN THE STUDY OF TURTLE COURTSHIP

The literature on CBFT can be roughly divided into 3 categories: 1) anecdotal observations; 2) qualitative study; and 3) quantitative study. Early works contain anecdotal observations only. The first observation of CBFT of which we are aware is Maynard's (1869) description of the display of elongated foreclaws in male *Centrochelys bairdii*. Soon thereafter, Darwin (1871) reported the mounting behavior of *Chrysemys picta*. Natural history texts and literature in the early 20th century contain occasional opportunistic descriptions of courtship behavior in freshwater turtles such as observations of biting and mounting (e.g., Gadow 1901; Camp 1916).

Nowadays, CBFT is a subject unto itself, and anecdotal reports of courtship behavior in different species appear regularly. Observations of in situ turtle courtship (e.g., Pisani 2004, Ashton 2007) are necessarily opportunistic because wild turtles are difficult to observe for long periods of time. Therefore, such observations often contain only one or a few segments of the whole behavioral sequence. However, these observations provide an important basis for comparison because behaviors in captivity, may differ from those exhibited in the wild. As more turtle species are maintained in captivity observations of ex situ courtship have accumulated, especially for species whose behavior is difficult to observe in the wild (e.g., Drajeske 1983, Molina 1996). As a result, most studies dedicated to CBFT have occurred in captivity.

Studies conducted in captivity allow the collection of a greater volume of detailed data in less time and with fewer logistical difficulties (e.g., Lardie 1975; Norris 1996). Most studies of CBFT whether in situ or ex situ consist of qualitative rather than quantitative efforts (e.g., Plummer 1977; Horne 1993; Norris 1996; Jenkins and Babbitt 2003). Taylor (1933) has provided the first study dedicated exclusively to freshwater turtle courtship, focused on *Trachemys scripta elegans*. Next, several researchers have set out to divide turtle courtship into discrete phases. Mahmoud (1967) has characterized 3 phases in the courtship behavior of 4 kinosternid species: 1) tactile, mounting, and intromission; 2) biting; and 3) rubbing. Similarly, Christensen (1975) has divided the courtship of *Rhinoclemmys pulcherrima incisa* into 3 components: 1) male activity; 2) female activity; and 3) copulation. Such studies provide useful starting points for further research, and they often describe previously unknown behaviors. Unfortunately, exclusively qualitative studies preclude statistical hypothesis testing.

New technology facilitated the addition of quantitative analyses of turtle courtship. Photographic (e.g., Lardie 1975; Murphy and Lamoreaux 1978; Duda and Gupta 1981), videographic (e.g., Jackson and Davis 1972), and cinematographic analyses (Baker and Gillingham 1983; Thomas and Altig 2006; Liu et al. 2008) allowed for more detailed observations to be made. Recording allows for the repeated viewing of behaviors and the observation of behaviors in cryptic or shy species who will not exhibit some behaviors while under direct observation. Repeated ex situ observations combined with imaging techniques have facilitated the development of robust courtship ethograms and quantitative analyses.

The extent of quantitative assessment has varied. Some early quantitative studies report the duration and frequency of a few easily recognized behaviors only (Jackson and Davis 1972; Murphy and Lamoreaux 1978). Flow diagrams and sequential photography have been used to qualitatively describe the intrinsic relationships among different courtship behaviors and the order in which they occur (e.g., Jackson and Davis 1972; Lardie

1975; Duda and Gupta 1981; Baker and Gillingham 1983; Bels 1983; Kramer and Fritz 1989; Bels and Crama 1994; Norris 1996; Liu et al. 2008). Some studies have used statistical applications to test for correlations in their order of occurrence. For example, intra-individual dyadic transition matrices have been used to isolate important motor pattern dependencies. Chi-square tests can determine whether or not behavioral sequences are random patterns (Baker and Gillingham 1983; Bels and Crama 1994; Liu et al. 2008). Baker and Gillingham (1983) and Bels and Crama (1994) have used Z-scores (Poole 1978), and Liu et al. (2008) have used kappa analyses (Whitehurst et al. 1986), to find significant correlations between the dyadic pairs and to determine whether certain behaviors are followed predictably by others. A review of statistical analyses of behavior is beyond the scope of this article, but they are an important tool for studying courtship (e.g., Runyon and Haber 1976) and should be incorporated into future research on CBFT.

Hypotheses of the evolution of courtship behavior have sometimes been used for species identification and the construction of phylogenies. For example, Seidel and Fritz (1997) have suggested that foreclaw display provides evidence of monophyly for the genus *Pseudemys*. Although controversial, Berry and Shine (1980) have hypothesized that male courtship and mating strategies are a function of sexual dimorphism in body size.

COURTSHIP SIGNALS IN FRESHWATER TURTLES AND THEIR FUNCTIONS

In the process of communication, a signal is the vehicle by which information passes from the sender to the receiver (Bradbury and Vehrencamp 1998). Therefore, for an honest signal to function it must transmit the intended information to the intended receiver. For example, initiation of successful mating behavior depends first on recognition of conspecifics and then of the opposite sex (Weaver 1970; Murphy and Lamoreaux 1978; Hidalgo 1982; Bels and Crama 1994; Bradbury and Vehrencamp 1998). Deciphering the true function of a signal requires an understanding of both the information coded within it and the effect of that information on the recipient. In this regard, data for CBFT are nearly nonexistent. Nevertheless, when possible, we summarize the current understanding of potential courtship signals in freshwater turtles and discuss their functions to identify future directions for research.

Signals implicated in turtle courtship involve visual, tactile, chemical, or auditory pathways. Some signals may be difficult to observe objectively. For example, olfaction probably plays a key role in finding a mate and in the initiation of courtship in kinosternids (e.g., Lewis et al. 2007). Turtles probably receive and respond to subtle courtship signals (olfactory and subtle visual signals) before they begin to exhibit easily detectable behaviors, which might carry tactile or visual signals.

Table 1. Pathways by which commonly observed turtle courtship signals are potentially assessed by the receiver. See text for definitions of each signal.

	Visual	Tactile	Chemical	Auditory
Body shape	X			
Markings	X			
Head movements (head bobbing and variations)	X	X	X	
Eye blinking	X			
Nudging/rubbing		X	X	
Chinning	X	X	X	
Barbel contact		X	X	
Biting	X	X	X	
Foreclaw displays	X	X	X	
Water propulsion (gulping and nasal squirting)		X	X	
Shell clapping		X	X	X
Chemical (olfactory) signals			X	
Vocalizations				X

Table 1 lists potential courtship signals reported for freshwater turtles and their potential pathways (visual, tactile, chemical, or auditory). In some cases, a signal may involve more than one pathway and/or have more than one function. For example, head bobbing is probably a visual signal but may also dissipate pheromones, thus, functioning as a chemical signal as well (Baker and Gillingham 1983). Below, we review common courtship signals in freshwater turtles. Where sufficient data exist, we also investigate their evolutionary histories by mapping them on an existing phylogeny of freshwater turtles (Seddon et al. 1997; Barley et al. 2010) and test phylogenetic constraints on behaviors using the data listed in Table 2.

BODY SHAPE

Several studies have indicated that body shape is an important visual signal in the initial stages of turtle courtship (e.g., Davis and Jackson 1973; Hidalgo 1982; Baker and Gillingham 1983). Body shape is one of the first things a male turtle can assess when it encounters another turtle. Hidalgo (1982) has reported that male *R. p. incisa* show a positive response to moving objects that resemble turtles. Baker and Gillingham (1983) have observed a male *Emydoidea blandingii* mounting a rock about the size of a conspecific turtle on 3 occasions. There are numerous examples of turtles misidentifying potential mates. Eglis (1962) has described a male *Mauremys rivulata* courting a female *Trachemys scripta*. Davis and Jackson (1973) have reported a *Trachemys scripta taylori* attempting courtship with other turtles regardless of species or sex but not with randomly shaped objects. Arndt (1986) has observed male *Glyptemys muhlenbergii* mounting female *Clemmys guttata* and conspecific males. Kramer and Fritz (1989) have described a captive *Pseudemys nelsoni* with a preference for a female *Pseudemys concinna*. Thus, body shape appears to function as a visual signal in the initial stages of courtship to distinguish turtles from other objects but is not used for the recognition of either species or gender.

MARKINGS AND PIGMENTATION

Most species of turtles have species-specific markings. Although the forces that select for coloration in turtles are not well understood, color pattern may function in species recognition. Mansfield et al. (1998) have reported an experiment using hoop traps, some baited with a turtle-shaped object painted to simulate the markings of *C. guttata*. In the spring mating season, baited traps caught more *C. guttata* than either unbaited traps or traps baited with food. Because the decoys were not providing olfactory, auditory, or movement-related signals, it seems that *C. guttata* likely identifies potential conspecific mates based on their markings. Moll et al. (1981) have reported that males of the closely related and sympatric *Batagur baska* and *Callagur borneoensis* conversely change the color of their head and shell during the breeding season, and Kuchling (1999) considers this shift to function for conspecific recognition only.

Beyond the initial recognition of potential mates, markings and coloration may play a further role in courtship in some species. Lardie (1975) has noted that male *Kinosternon flavescens* expand their yellow throat while biting and rubbing the head of the female. This may either be incidental or provide a deliberate visual signal to the female. Baker and Gillingham (1983) have suggested that the swaying behavior of *E. blandingii*, in which the male angles his head down in front of the female and sways it from side to side, functions to display his conspicuous yellow throat at a crucial point in the courtship ritual. Rovero et al. (1999) describe a similar chinning behavior in *Emys orbicularis*, in which males also display their yellow throat to females. In both *E. blandingii* and *E. orbicularis*, the action of displaying the chin to the female immediately precedes either successful mating or reticence on the part of the female. Liu et al. (2008) suggest that head bobbing in *Sacalia quadriocellata* functions to display the bright red stripes on the ventral part of the neck. These speculations on the role of bright markings as visual cues in courtship could be tested

Table 2. Some main male courtship behaviors, display type, and mounting position in freshwater turtles. FD, foreclaw display; HM, head-movement; Bite, biting; Nudge, nudging; Rub, rubbing, Gulp, gulping; Disp, display; Pos, position; +, behavior present; -, behavior absent; ?, no data; Pre, premounting display type; Post, postmounting display type; All, 4 limbs clasp female's carapace during copulation; and Two, 2 limbs clasp female's carapace during copulation. See text for definitions and explanations of terminology.

Species	FD	HM	Bite	Nudge	Rub	Gulp	Disp	Pos	Source
Pleurodira									
Australian species									
<i>Chelodina expansa</i>	-	+	-	-	-	-	Pre	?	Legler 1978
<i>Chelodina longicollis</i>	-	+	-	+	-	-	Post	All	Murphy and Lamoreaux 1978
<i>Eseya latisternum</i>	+	+	-	+	-	+	Pre	All	Murphy and Lamoreaux 1978
<i>Emydura macquarii</i>	+	+	-	+	-	+	Pre	All	Murphy and Lamoreaux 1978
<i>Emydura subglobosa</i>	+	+	-	+	-	+	Pre	?	Norris 1996
South American species									
<i>Acanthochelys pallidipectoris</i>	-	-	+	-	+	-	Post	?	Horne 1993
<i>Chelus fimbriatus</i>	+	+	-	?	?	?	Pre	?	Drajeske 1983
<i>Hydromedusa maximiliani</i>	?	?	?	?	?	?	Post	?	Novelli and Souza 2007
<i>Mesoclemmys vanderhaegei</i>	-	+	-	?	+	-	Post	?	Brito et al. 2009
<i>Pelomedusa subrufa</i>	-	+	+	?	?	?	Post	?	Harding 1981; Bels 1983
<i>Phrynops geoffroanus</i>	-	-	+	?	?	?	Post	?	Molina 1996
<i>Phrynops hilarii</i>	-	-	+	?	?	?	Post	?	Richard 1999
<i>Platemys platycephala</i>	+	-	-	+	+	+	Post	All	Harding 1983; Medem 1983
<i>Podocnemis erythrocephala</i>	-	-	+	+	+	-	Post	?	Ferrara et al. 2009
<i>Podocnemis vogli</i>	-	-	+	?	?	?	?	?	Ramo 1982
Emyridae									
Emydinae									
<i>Actinemys marmorata</i>	+	-	-	+	-	-	Post	?	Holland 1988; Ashton 2007; Bettleheim 2009
<i>Clemmys guttata</i>	-	-	+	+	-	-	Post	Two	Ernst 1967, 1970; Chippindale 1989
<i>Emydoidea blandingii</i>	-	+	-	+	+	+	Post	All	Richmond 1970; Baker and Gillingham 1983
<i>Emys orbicularis</i>	-	-	+	-	+	-	Post	Two	Rovero et al. 1999
<i>Glyptemys insculpta</i>	-	+	+	+	-	+	Pre	All?	Evans 1961; Ernst and Lovich 2009
<i>Glyptemys mühlenbergii</i>	-	-	+	?	?	?	?	All	Campbell 1960
Deirochelyinae									
<i>Chrysemys picta</i>	+	-	+	?	?	?	Pre	?	Taylor 1933; Ernst and Lovich 2009; http://www.youtube.com/watch?v=CwHd8eoLLqA
<i>Deirochelys reticularia*</i>	+	-	-	-	-	-	Pre	?	Ewert et al. 2006, Seidel 2010
<i>Graptemys barbouri</i>	+	-	-	-	-	-	Pre	?	Wahlquist 1970
<i>Graptemys ernsti</i>	-	+	-	-	-	-	Pre	?	Ernst and Lovich 2009
<i>Graptemys flavimaculata</i>	+	-	-	-	-	-	Pre	?	Cagle 1955
<i>Graptemys geographica</i>	-	+	-	-	-	-	Pre	?	Ernst and Lovich 2009
<i>Graptemys kohni</i>	-	+	-	-	-	-	Pre	?	Ernst and Lovich 2009
<i>Graptemys nigrinoda</i>	-	+	-	-	-	-	Pre	?	Lahanas 1982
<i>Graptemys ouachitensis</i>	+	+	-	-	-	-	Pre	?	Ernst and Lovich 2009
<i>Graptemys pseudogeographica</i>	+	-	+	-	-	-	Pre	All	Ernst 1974
<i>Graptemys pulchra</i>	+	+	-	-	-	-	Pre	?	Shealy 1976
<i>Graptemys versa</i>	+	-	-	-	-	-	?	?	Ernst and Lovich 2009
<i>Malaclemys terrapin tequesta</i>	+	+	-	+	-	-	Pre	All	Seigel 1980
<i>Pseudemys concinna suwanniensis</i>	+	-	-	+	-	-	Post	All	Marchand 1944; Jackson and Davis 1972
<i>Pseudemys floridana</i>	+	-	-	-	-	-	Pre	?	Cagle 1955
<i>Pseudemys nelsoni</i>	+	-	+	+	-	-	Pre	?	Kramer 1984; Kramer and Fritz 1989
<i>Pseudemys peninsularis</i>	+	-	-	-	-	-	Pre	?	White and Curtsinger 1986
<i>Trachemys gaigeae</i>	-	+	-	-	-	+	Pre	?	Stuart and Miyashiro 1998
<i>Trachemys scripta elegans</i>	+	-	-	-	-	+	Pre	Two	Jackson and Davis 1972
<i>Trachemys scripta taylori</i>	-	-	+	-	-	-	Pre	?	Davis and Jackson 1973
<i>Trachemys scripta troosti</i>	+	-	-	-	-	-	?	?	Conant 1938
Geoemydidae									
<i>Mauremys caspica</i>	-	+	-	?	?	?	Pre	?	Eglis 1962
<i>Rhinoclemmys areolata</i>	-	+	-	+	-	-	Pre	Two	Perez-Higareda and Smith 1988
<i>Rhinoclemmys funerea</i>	+	+	-	-	-	-	Pre	?	Iverson 1975
<i>Rhinoclemmys pulcherrima incisa</i>	-	+	+	+	-	-	Pre	Two	Hidalgo 1982
<i>Sacalia quadriocellata</i>	-	+	-	+	-	+	Pre	Two	Liu et al. 2008
Chelydridae									
<i>Chelydra serpentina</i>	-	+	+	-	-	+	Post	All	Hamilton 1940; Conant 1951
<i>Macrochelys temminckii</i>	-	-	+	+	-	-	Post	Two	Harrel et al. 1996
Kinosternidae									

Table 2. Continued.

Species	FD	HM	Bite	Nudge	Rub	Gulp	Disp	Pos	Source
<i>Kinosternon baurii palmarum</i>	–	+	+	+	+	–	Post	Two	Lardie 1975; Wilson et al. 2006
<i>Kinosternon flavescens</i>	–	–	+	+	+	–	Post	All	Lardie 1975
<i>Kinosternon scorpioides</i>	–	–	+	–	+	–	?	?	Sexton 1960
<i>Kinosternon sonoriense</i>	–	–	+	+	+	–	Post	?	Hulse 1982
<i>Kinosternon subrubrum hippocrepis</i>	–	–	+	+	+	–	Post	All	Mahmoud 1967
<i>Staurotypus salvinii</i>	?	?	?	+	?	?	?	?	Schmidt 1970; Sachsse and Schmidt 1976
<i>Sternotherus carinatus</i>	–	–	+	+	+	–	Post	All	Mahmoud 1967
<i>Sternotherus minor</i>	–	+	+	+	–	–	Pre	All	Bels and Crama 1994
<i>Sternotherus odoratus</i>	–	–	+	+	+	–	Post	All	Lagler 1941; Mahmoud 1967
Trionychidae									
<i>Apalone mutica</i>	–	–	–	+	–	–	Post	All	Plummer 1977
<i>Apalone spinifera</i>	–	–	+	+	–	–	Post	?	Ernst and Lovich 2009
<i>Lissemys punctata</i>	–	+	–	+	–	–	Pre	Two	Duda and Gupta 1981
<i>Pelodiscus sinensis</i>	–	–	+	?	?	–	Post	?	Thieme 1979

^a Foreclaw display of *Deirochelys reticularia* involves the whole arm and is considered to be a primitive version of the foreclaw display used by other emydid turtles (Seidel 2010).

by experimental comparisons of courtship behavior and success in mark-manipulated individuals.

Melanism is common in several species in the family Emydidae (Lovich et al. 1990b), and it correlates with courtship strategy. In *Trachemys scripta scripta*, levels of sex steroids correlate with both the extent of melanism and intensity of courtship behavior (Garstka et al. 1991), although individuals with different extents of melanism employ the same tactic, and the correlation may be, in part, attributable to a problematic system of scoring behavior. Thomas (2002) has reported that small, nonmelanistic males use foreclaw displays in courtship and are unlikely to bite or chase females. In contrast, larger, melanistic males use the converse tactic. This ontogenetic shift in courtship behavior is a conditional strategy under status-dependent selection (Gross 1996; Thomas 2002). These results suggest a causal relationship between melanism (a by-product of hormonal variation) and courtship strategy. Similarly, ontogenetic reticulate melanism occurs in adult *Chrysemys picta bellii* (Gronke et al. 2006), although it does not occur consistently in all individuals (MacCulloch 1981). One hypothesis for reticulate melanism is that these markings serve as visual cues aiding in recognition of inter-specific, intersex, and reproductive condition (Schueler 1983).

Our ability to determine the importance of markings and pigmentation as a stimulus through unaided observations is limited. Turtles have tetrachromatic vision, allowing them to see color in the UV end of the color spectrum (Ventura et al. 2001). This potentially allows them to use or react to color-related displays not visible to humans, including the presence of UV-reflective markings. Responses to color signals are difficult to deduce through observation, and they require experimental testing to confirm. Future work should investigate the effects and interactions of markings, melanism, hormone manipulation, and female response.

NUDGING AND RUBBING

Males of many species first approach a female from the rear, nudging (nosing and gently touching) her cloaca. Nudging is the first observable male–female interaction in CBFT, and it occurs widely (Table 2). In several kinosternid species, males approach females and nudge or nose the female’s plastral bridge (Mahmoud 1967; Seigel 1980). This behavior also plays multiple roles in courtship, yet 2 roles occur most frequently. First, nudging is a tactile signal that stimulates the female and precedes the female turning to facing the male (Murphy and Lamoreaux 1978; Hidalgo 1982; Liu et al. 2008). In species where the male displays other precopulatory behaviors, nudging occurs after securing the female’s attention. Second, nudging facilitates the collection of olfactory signals for mate recognition and female receptivity (Kuchling 1999).

In several species, males rub their head on the female’s carapace and head after mounting (Table 2). In rubbing his chin on the female, the male is presumably giving a tactile signal, but rubbing behaviors may also facilitate transfer of scent from the male’s chin glands to the female, therein providing a chemical signal (Manton 1979).

FORECLAW DISPLAY

Male turtles of some species use their front limbs and foreclaws during courtship. These courtship displays include gentle stroking of the female’s head, as in *Elseya latisternum* and *Emydura macquarii* (Murphy and Lamoreaux 1978) and the more complex foreclaw displays of some Deirochelyinae, which are also called titillation.

Gentle stroking of the female’s head by the male’s foreclaws is reported in several Australian pleurodire species. During this behavior, the male positions himself

in front and slightly to the side of the female and faces her. He uses the forearm closest to the female to stroke her head slowly; the number and frequency of strokes varies by species (Murphy and Lamoreaux 1978; Norris 1996). A variation of this behavior is recorded in *Chelus fimbriatus* where the male positions himself beside and slightly ahead of the female, turns his head to face her and uses the leg nearest the female to “tickle” her barbells “with a vibrating motion” (Drajeske 1983).

A different use of the male’s forelimbs is noted in many early descriptions of emydid courtship (Table 2, titillation). In the context of courtship, the emydid foreclaw display is also called titillation. Titillation consists of “a complex, stereotyped series of movements in which the adducted forelimbs of the male are brought parallel to the head of the female and the claws of the forelimbs are drummed and vibrated against the eyes and interocular region of the female” (Jackson and Davis 1972). Carpenter and Ferguson (1977) have explicitly identified this as a courtship behavior, and its role in courtship is frequent and well documented. Titillation may or may not involve sexually dimorphic, elongated foreclaws.

Seidel and Fritz (1997) have classified titillation in courting emydid turtles into 2 categories. First, the titillation posture of *Graptemys* and *Trachemys* involves the male facing the female directly, extending his forelimbs, and vibrating his foreclaws near or against her eyes and head. Second, the male *Pseudemys* swims above a female’s carapace, reaches his head and forelimbs down toward her face, and then vibrates his foreclaws. The distinct posture of *Pseudemys* has been used to support the monophyly of the genus (Seidel and Fritz 1997).

Titillation does not only function as courtship display in emydid turtles. In some emydid turtles, males, females, and juveniles use foreclaw displays outside of courtship (Kramer and Burghardt 1998, Thomas and Altig 2006). Foreclaw display in juveniles may function as social play. Kramer and Burghardt (1998) have reported juvenile *P. nelsoni* displaying to each other and have suggested that young turtles learn a behavior that will be used later for courtship. The behavior also occurs in juvenile *P. concinna* and *P. nelsoni*, which display both to each other and to food items (Cagle 1955; Petranka and Phillippi 1978; Kramer and Burghardt 1998). Juvenile *Deirochelys reticularia* exhibit a rudimentary display using the entire arm (Krefft 1955). Thomas and Altig (2006) demonstrated that foreclaw displays of female *T. scripta* are not exclusively courtship related. Foreclaw displays are likely a compound signal with context-dependent functions (including courtship-related male foreclaw displays or titillation), which deserve further attention.

It has been suggested that foreclaw display such as stroking and titillation in courtship function similarly to biting (Murphy and Lamoreaux 1978; Hidalgo 1982; Baker and Gillingham 1983), but the findings of Thomas

(2002) appear to contradict this scenario. In *T. scripta*, young males who are much smaller than the females use titillation. This suggests that, unless it has significantly different functions in different species, foreclaw displays may be more of a fitness signal than an inhibitory or coercive tactic. Foreclaw displays in courtship involve strong visual and tactile signals, and they may serve to immobilize females and facilitate mounting.

From an evolutionary perspective, the complex foreclaw displays known as titillation are considered unique to the Deirochelyinae (Seidel and Fritz 1997) although titillation has been lost by some members of this subfamily. Some Mesoamerican sliders (*Trachemys*), such as *Trachemys gaigeae*, do not use foreclaw displays in their courtship (Seidel and Fritz 1997; Stuart and Miyashiro 1998). Stuart and Miyashiro (1998) suggested that nose squirting may have replaced titillation in *T. gaigeae*. *Deirochelys reticularia* uses the whole arm in a waving display during courtship, which is presumably a plesiomorphic version of this behavior (Seidel 2010). A meta-analysis can determine whether foreclaw display is phylogenetically constrained in freshwater turtles. Figure 1 maps foreclaw display on the phylogeny of freshwater turtles (Seddon et al. 1997; Barley et al. 2010); foreclaw display occurs in a phylogenetically dependent pattern (Pearson’s chi-square test: $\chi^2 = 21.27$, $df = 6$, $p < 0.01$). Further, titillation, or a rudimentary form of it, evolves exclusively in Deirochelyinae (15 of 22 species; 68%) compared with its sister group Emydinae (1 of 6 species; 17%) (Fisher Exact Probability Test [FEPT]: 1-tailed, $p = 0.036$; all of the percentage data can be directly counted and calculated from Table 2).

HEAD MOVEMENTS

Head movements, which are common in chelonid courtship, may be involved with visual, tactile, and chemical signals. Head movements can be placed in 3 general categories: 1) head bobbing (vibrating the head and neck vertically); 2) swaying (swinging the head and neck horizontally without contacting the female); and 3) head movement on the female’s carapace (Fig. 2). Table 3 lists variations on courtship-related head movements.

Although types of head movement vary interspecifically, this behavior is most likely used to identify potential mates (e.g., Murphy and Lamoreaux 1978; Baker and Gillingham 1983; Liu et al. 2008). Head movements can function in mate recognition in several ways. Some head movements may serve as a visual signal, displaying important markings or colorations, for example, as in *E. blandingii* (Baker and Gillingham 1983) and *S. quadriocellata* (Liu et al. 2008). Although evidence is not yet available for freshwater turtles, head bobbing may also play a role in chemical signaling. Auffenberg (1977) suggested that head-bobbing tortoises release chemicals into the air for reception via rostral pores (Winokur and Legler 1974) and mental glands (Winokur

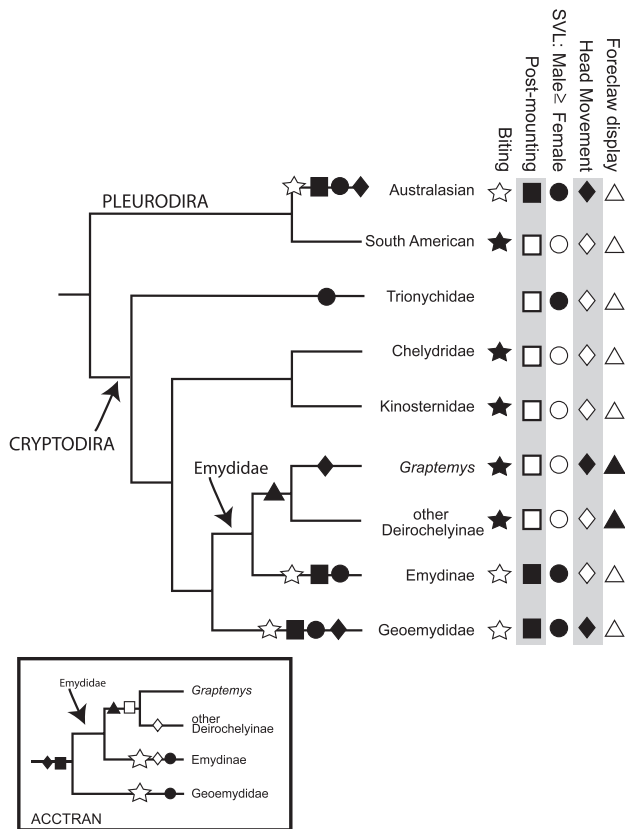


Figure 1. Phylogenetic patterns of male courtship behavior in freshwater turtles. The 5-point star represents biting; square represents premounting; circle represents larger female body size; diamond represents head movement; and triangle represents foreclaw display. Filled shapes indicate that the behavior exists in the lineage, whereas unfilled shapes indicate absence of the behavior from the lineage.

and Legler 1975; Hidalgo 1982). Similar pheromone release may also occur in freshwater turtles. Head movements that involve contact with the female's carapace may also function as a tactile signal (Liu et al. 2008), and such movements may be compound signals that have multiple functions (Bradbury and Vehrencamp 1998). Where a potential mate is successfully recognized, head movements also function as a trigger to subsequent behaviors (Hidalgo 1982).

In addition to head movements, *E. blandingii* releases air bubbles while "frantically head-bobbing" (Graham and Doyle 1979). Harrel et al. (1996) observed a similar behavior in *Macrochelys temminckii*. Both species have been observed mating both with and without bubble-blowing (e.g., Baker and Gillingham 1983), and the function and frequency of bubble blowing requires clarification. It seems unlikely that the bubbles are involved in chemical signaling, because substances confined in the air bubbles will rapidly ascend to the surface.

The 3 types of head movement (head bobbing, swaying, and swaying and head bobbing on the female's carapace or vibrating the head and neck horizontally on

the female's carapace) appear to have evolved independently in freshwater turtles, and each event is phylogenetically constrained (Fig. 1; Pearson's chi-square test: $\chi^2 = 19.45$, $d = 7$, $p < 0.01$). In Pleurodira, the frequency of head movement differs between Australian species (5 of 5 species; 100%) and South American species (3 of 9 species; 33%) (FEPT: 1-tailed, $p = 0.028$). Similarly, the frequency of head movement differs between species of *Graptemys* (6 of 10 species; 60%) and the remaining species in Deirochelyinae (2 of 16 species; 13%) (FEPT: 1-tailed, $p = 0.017$). Finally, geoemydines (all 5 species; 100%) seem to have evolved head movement independently from other clades (7 of 23 species; 30%) (FEPT: 1-tailed, $p = 0.008$). In addition, a strong negative correlation occurs between the occurrence of foreclaw display and head movement based on available data (Phi Coefficient: $\Phi = -0.701$, $p < 0.001$). Because both of these behaviors were suggested to function to calm females and facilitate mounting (Murphy and Lamoreaux 1978; Hidalgo 1982; Baker and Gillingham 1983; Liu et al. 2008), these 2 behaviors may have evolved independently in different taxa for the same function. Further work is required to explore this possibility.

BITING

Biting is common in the social interactions of turtles. It has been reported in most species of freshwater turtles, but it is not involved in courtship in all species (Table 2). Biting in CBFT differs from aggressive male-male biting; it most likely functions to subdue females and get them to contract their head and limbs into the shell (Mahmoud 1967; Hidalgo 1982). Because female quiescence is essential for copulation (Hidalgo 1982; Liu et al. 2008), biting may play an essential role in successful mating where it occurs. When males snap at females, they give both visual and tactile signals. Male bites may be feigned and end with a touch or light hit, or males may also bite with sufficient vigor to leave scars on the females (*pers. obs.*).

Biting in courtship is a conserved behavior (Fig. 1). In contrast to foreclaw display and head movement, its evolution involves degeneration instead of diversification. Biting is phylogenetically constrained (Pearson's chi-square test: $\chi^2 = 25.72$, $df = 6$, $p < 0.001$). In pleurodirids, biting is conserved in South American species (6 of 9 species; 67%) but completely lost in Australian species (0%) (FEPT: 1-tailed, $p = 0.028$). Biting is conserved in the families Chelydridae and Kinosternidae (15 of 19 species; 79%) but usually lost in the subfamily Geoemydinae (1 of 5 species; 20%) (FEPT: 1-tailed, $p = 0.028$). Finally, in the family Emydidae, biting has degraded in the Deirochelyinae (4 of 22 species; 18%) but may be retained in the Emydinae (4 of 6 species; 67%) (FEPT: 1-tailed, $p = 0.038$); this is uncertain because of the low percentage of taxon sampling. Regardless, the statistically significant trend serves as a hypothesis for

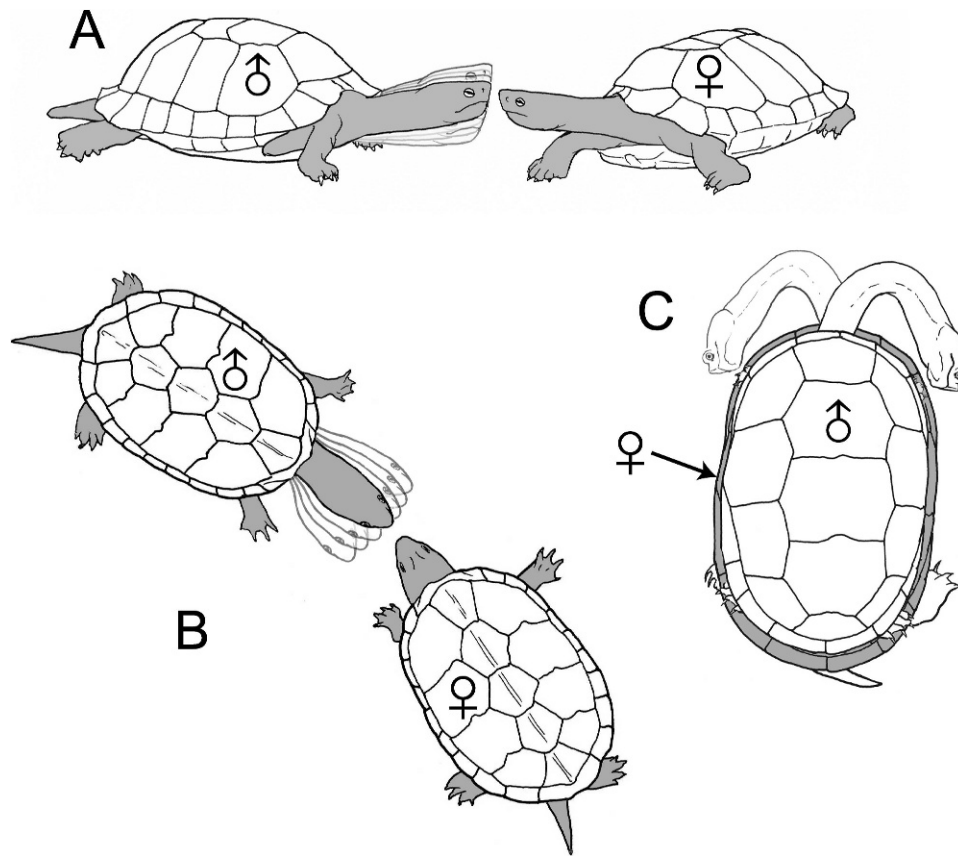


Figure 2. Three types of head movement associated with premounting courtship displays in freshwater turtles. A) Head bobbing: vibrating the head and neck vertically (modified from Hidalgo 1982). B) Swaying: vibrating the head and neck horizontally (modified from Bels and Crama 1994). C) Swaying on the female's carapace: vibrating the head and neck horizontally on the female's carapace (modified from Baker and Gillingham 1983).

future testing. Because we have data from 4 species of Trionychidae only, in which biting behavior occurs in 2, it is not possible to determine the evolution of biting in this taxon. Future work on the courtship behavior in the Trionychidae and other groups is necessary to gain confident insights into the evolution of biting behavior.

WATER PROPULSION: NASAL SQUIRTING AND GULPING

Propulsion of water toward the female or the creation of currents around her eyes and face may function as a tactile signal (Manton 1979). Some species show gulping behaviors, in which water is quickly taken in and pushed out of the mouth (Table 2). Baker and Gillingham (1983) suggested that such behavior might be involved with chemical signaling in conjunction with courtship in several species of freshwater turtles. Turtles can detect conspecific scent secretions dissolved in water (e.g., Muñoz 2004; Poschadel et al. 2006). When taken out of the context of courtship, gular pumping in turtles may function in olfaction (Root 1949; Manton 1979). Therefore, it seems most likely that gular pumping is involved with receipt (and possibly the dissemination) of olfactory signals, as suggested by Baker and Gillingham (1983).

CHEMICAL (OLFACTORY) SIGNALS

Turtles commonly produce scents and musk, which have multiple functions (Mertens 1946; Madison 1977; Manton 1979). Olfactory signals can be energetically costly, and they may provide unintentional information to potential predators (Bradbury and Vehrencamp 1998). Several regions of the body are associated with the production of scent in freshwater turtles, including the mouth, axillary and inguinal regions, cloaca, and chin (e.g., Taylor 1933; Mahmoud 1967; Murphy and Lamoreaux 1978; Graham and Doyle 1979; Harrel et al. 1996; Shi et al. 2002). Because very little is known about the function of scent in CBFT, we have not produced an exhaustive list of species known to produce scent. However, chemical cues likely function in mate recognition, and some works have shed light on this relationship.

Differences in scent production occur between males and females of some species (Worrell 1963; Goode 1967; Schmidt 1970; Sachsse and Schmidt 1976). Mahmoud (1967) has observed that males of four kinosternid species can correctly distinguish females from males and determine whether or not to attempt courtship and mating behavior by sniffing at the cloaca. Hidalgo (1982) found that the cloacal scent produced by female *R. p. incisa* can

Table 3. Variable forms of head movement in male freshwater species. Head movements are classified into 3 types: HB, head-bobbing; S, swaying; and SOFC, swaying on the female's carapace. Details of the classification and descriptions are provided in text and Fig. 2.

Species	Form of head movement	Type	Source
<i>Acanthochelys pallidipectoris</i>	Prodding female's head and neck from top of her back	SOFC	Horne 1993
<i>Chelodina expansa</i>	Dorsoventral movement of fully extended head	HB	Legler 1978
<i>Chelodina longicollis</i>	Swaying on female's carapace	SOFC	Murphy and Lamoreaux 1978
<i>Chelus fimbriatus</i>	Swaying in front of female	S	Drajeske 1983
<i>Chelydra serpentina</i>	Swaying head sided to side in front of female	S	Ernst and Lovich 2009
<i>Mauremys caspica</i>	Vibrating the ventral neck on female's dorsal head	HB	Eglis 1962
<i>Emydoidea blandingii</i>	Swaying while mounted on the female's carapace	SOFC	Baker and Gillingham 1983
	Frantic head bobbing	HB	Graham and Doyle 1979
<i>Elseya latisternum</i>	Dorsoventral head bobbing	HB	Murphy and Lamoreaux 1978
<i>Emydura macquarii</i>	Vigorous head-bobbing in a dorsoventral plane	HB	Murphy and Lamoreaux 1978
<i>Emydura subglobosa</i>	Head bob in dorsa-ventral plane	HB	Norris 1996
<i>Glyptemys insculpta</i>	Face the female bob or sway its head (?)	?	Carr 1952; Ernst and Lovich 2009
<i>Graptemys ernsti</i>	Rapidly vibrates head vertically against the female's snout, alternating sides	HB	Ernst and Lovich 2009
<i>Graptemys geographica</i>	Makes snout-to-snout contact, then rapidly bobs head up and down	HB	Ernst and Lovich 2009
<i>Graptemys kohni</i>	Bobbing head on either side of female's jaws	HB	Murphy and Lamoreaux 1978
<i>Graptemys ouachitensis</i>	Vertical head bobbing followed by nose-to-nose contact	HB	Ernst and Lovich 2009
<i>Graptemys pulchra</i>	Vibrating vertically in a snout-to-snout position	HB	Shealy 1976
<i>Lissemys punctata</i>	Bob head in vertical plane	HB	Duda and Gupta 1981
<i>Platemys platycephala</i>	Brush head across the female while mounted, swinging head rapidly on the top of female's back	SOFC	Harding 1983; Medem 1983
<i>Pelomedusa subrufa</i>	Swinging head on the top of female's back	SOFC	Harding 1981
<i>Rhinoclemmys funerea</i>	Vibrating the head in a sagittal plane	HB	Iverson 1975
<i>Rhinoclemmys pulcherrima</i>	Head and neck vibration	HB	Hidalgo 1982
<i>Sacalia quadriocellata</i>	Vibrating its head and fore-body in a vertical plane	HB	Liu et al. 2008
<i>Kinosternon baurii</i>	Extending neck and bobbing head up and down at about one bob per second	HB	Wilson et al. 2006
<i>Sternotherus minor</i>	Facing female, swinging the head from side to side	S	Bels and Crama 1994
<i>Trachemys gaigeae</i>	Rapid, jerky nodding or bobbing, accompanied with side-to-side wagging head motion	S	Stuart and Miyashiro 1998
<i>Malaclemys terrapin</i>	Head bobbing in front of female	HB	Seigel 1980
<i>Mesoclemmys vanderhaegei</i>	Sliding his head from one side to the other in short and fast movements on the top of female's back	SOFC	Brito et al. 2009

elicit trailing behavior in males. Thus, the current evidence suggests that at least some female turtles produce secretions that can induce sniffing behavior, potentially enabling them to signal receptivity. Many other species also precede courtship with the male trailing the female and sniffing at her cloaca, apparently to detect a chemical releaser (e.g. Marchand 1944; Jackson and Davis 1972; Plummer 1977; Kramer and Fritz 1989; Norris 1996; Liu et al. 2008).

Experimental evidence provides support for olfactory signals functioning in intersexual and interindividual discrimination. Poschadel et al. (2006) demonstrated that, although female *E. orbicularis* show no preference to scents from other turtles, males prefer the scent of females to that of other males or unscented water. Furthermore, these males prefer the scent of larger females to that of smaller females, and males prefer water scented by smaller males to that scented by larger males. Muñoz (2004) has reported similar results for *Mauremys leprosa*. Lewis et al. (2007) found that male *Sternotherus odoratus* prefer water scented by females to water scented by themselves, other males, or no turtles. Thus, these species can use chemical signals, both to seek out mates and to avoid competition. Presumably other species can do the same.

Chemical signals are difficult to detect and quantify, but the assumption that species not displaying a set of pre mounting behaviors (e.g., some kinosternids) have a simpler courtship ritual than species that use many visual or tactile signals (e.g., Miller and Dinkelacker 2008) should be avoided. It is possible that these "simpler" courtship rituals involve very complex but less easily detected olfactory signals. Thus, we recommend that the categorizations "simple" or "complex" be avoided, at least until a greater understanding of signaling is in hand. Likewise, the assumption that turtles smell when touching or approaching objects is justifiable but difficult to test (Manton 1979). Nosing and touching are universally interpreted as a chemical collection functions in CBFT (e.g., Hidalgo 1982; Bels and Crama 1994; Liu et al. 2008). We recommend the use of chemical manipulation experiments to reveal the function of chemical signals in turtle courtship.

AUDITORY SIGNALS

Auditory signals in CBFT are virtually unknown, and turtle vocalizations have only recently become a topic of organized research. Vocalizations have been reported in

Pseudemys concinna suwanniensis (Rose 1950), but at the time of this publication, turtles were generally considered incapable of giving or receiving auditory stimuli (Pope 1955). Weaver and Vernon (1956) confirmed that many turtle species are, in fact, sensitive to airborne sounds, particularly sounds below 1000 Hz. Vocalizations are well-known in male tortoises and can play an important role in mate choice (Auffenberg 1977; Galeotti et al. 2005). However, the first published recordings of underwater turtle vocalizations are from *Chelodina oblonga* (Giles et al. 2009). These include a large repertoire of calls including a potential advertisement call that was recorded only during the breeding season. Other anecdotal evidence for auditory signals in freshwater turtle courtship includes the whistles sometimes produced by *Glyptemys insculpta* (Kaufmann 1992) and vocalizations reported by Liu et al. (2009) in *S. quadriocellata*. Both of these occurrences appear to be infrequent; therefore, the role vocalizations may play in CBFT is unknown. The potential importance of auditory signals in CBFT, and in general communication, is in need of study.

OTHER ACTIVE BEHAVIORS

Three other behaviors are involved in CBFT. Although all of them are distinguishable in courtship, they occur in few species, and their functions remain uncertain.

Barbel Contact. — Murphy and Lamoreaux (1978) have observed barbel contact and barbel stroking during courtship in *E. latisternum* and *E. macquarii*. Males of both species attempt to align their barbels with those of the females and stroke the female's barbels with their forefeet and claws. The barbels are thought to be extremely sensitive, but their exact function(s) remains unknown. Barbel contact and stroking are most likely tactile signals, but what information they might transmit is uncertain.

Blinking. — Blinking of the eyes appears to be a courtship signal in female *T. scripta* (Lovich et al. 1990a) and in male *Emydura subglobosa* (Norris 1996). In both cases, blinking occurs during premounting orientation and display. The authors of these two studies consider blinking to be a visual signal, although its function remains unknown.

Shell Clapping. — Shell clapping occurs in *G. insculpta* (Evans 1961; Kaufmann 1992; Tronzo 1993; Mitchell and Mueller 1996). After mounting, the male grasps the female's carapace with all 4 feet. By extending his legs and then quickly pulling himself down toward the female, the male's plastron crashes against the female's carapace making a loud "clapping" noise. This aggressive behavior may exhaust the female and coerce her into accepting intromission. However, biting, shaking, and thumping do not guarantee insemination (Kaufmann 1992). Alternatively, this behavior may provide a signal

of the male's fitness based upon which the female accepts or rejects his intentions.

Shell clapping is potentially a tactile and/or auditory signal. Further, the repeated rapid contact between the male's plastron and the female's carapace may cause the male to produce scent from the glands in his inguinal and axillary areas, providing a possible olfactory signal. Unfortunately, the function of shell clapping has not yet been tested.

The releasing of behavior normally depends on a combination of signals, and CBFT is not an exception. In this section, we reviewed the signals that might be used to communicate between two sexes. However, the signal from external environment, which is almost totally ignored in this field, also plays an important role to trigger courtship. A well-known fact among researchers and turtle breeders alike is that an influx of fresh water, for example from rainfall or snowmelt, can stimulate courtship and mating behaviors. This phenomenon has been observed in a variety of species, including kinosternids (Mahmoud 1967), *Lissemys punctata* (Duda and Gupta 1981), and *Acanthochelys pallidipectoris* (Horne 1993). Environmental stimuli such as rainfall or snowmelt may trigger hormonal changes that elicit courtship behaviors (Woolley et al. 2004). Therefore, future work should also pay attention to the interaction between courtship behavior and environmental signals.

MOUNTING AND COPULATORY POSITIONS

Mounting is a critical stage in courtship because refusal by the female will result in failure. When a female tries to dislodge the male by moving away, he may lose his position on the carapace (Mahmoud 1967; Murphy and Lamoreaux 1978; Hidalgo 1982; Baker and Gillingham 1983; Bels and Crama 1994). Mounting is frequently followed not by copulation but by female refusal (e.g., Murphy and Lamoreaux 1978; Baker and Gillingham 1983; Liu et al. 2008). Males can mount females from any direction, and males typically adjust their position after mounting (Mahmoud 1967; Murphy and Lamoreaux 1978; Hidalgo 1982; Bels and Crama 1994; Liu et al. 2008).

Copulatory positions in turtles involve 2 male postures (Fig. 3). Males grasp a female's carapace either with all 4 limbs or with the forelimbs while placing the hind limbs firmly on the substrate. Generally, species in the Chelidae, Emydidae, and Kinosternidae do the former and the other species the latter (Table 2). Mounting and copulation may involve specialized grasping structures. For example, Mahmoud (1967) reported that smaller males of sexually dimorphic kinosternids use scaly patches on their hind limbs to fix the female's tail in place and has suggested that this makes the female's cloaca accessible for copulation. However, Gibbons and Lovich (1990) pointed out that these structures are more likely to ease the physical difficulty of attaining

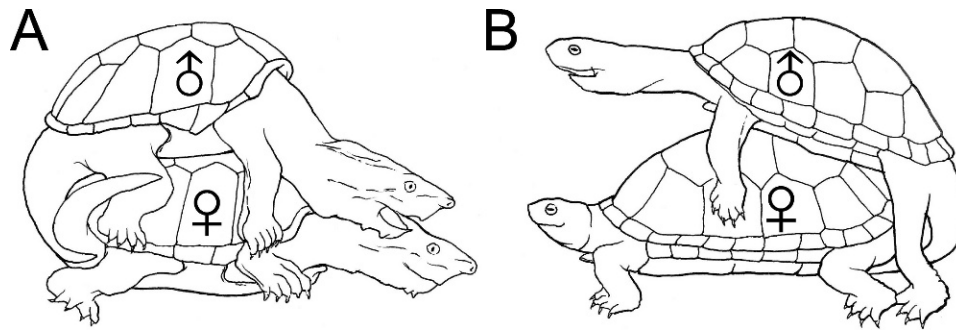


Figure 3. The 2 major copulation postures used by freshwater turtles. A) Male grasps the female's carapace with all 4 feet (modified from Mahmoud 1967). B) Male grasps the female's carapace with his forelimbs and supports his body with his hind limbs planted on the substrate (modified from Hidalgo 1982).

intromission than to forcibly hold the female in any given position. Usually when aquatic turtles copulate, the male's plastron contacts the female's carapace, but this is not always the case. Copulatory postures may differ within species. For example, Kaufmann (1992) reports plastron-to-carapace mating in a population of *G. insculpta*, whereas Tronzo (1993) and Mitchell and Mueller (1996) observed plastron-to-plastron mating. The same variation occurs in *Chelydra serpentina* (Pisani 2004; Ernst and Lovich 2009). Recently, Joyce et al. (2012) published the first observation of mating in a fossil turtle (or in any fossilized vertebrate). Regrettably, the condition of the fossils made it impossible to determine whether the turtles (*Allaechelys crassesculpta*) were mating in the plastron-to-plastron or plastron-to-carapace position.

FEMALE PARTICIPATION IN COURTSHIP

Typically, female courtship behavior in turtles is less obvious to a human observer than that of males, and as a result, details are often wanting. However, several interesting female courtship and mating behaviors have been reported. For example, Murphy and Lamoreaux (1978) observed female *E. latisternum* pivoting 180° such that males and females end up side by side facing in opposite directions, and female head-bobs follow those of males. Hidalgo (1982) reported active nose-to-nose contact and biting by female *R. p. incisa*. Lovich et al. (1990a) have observed female *T. scripta* orienting toward males, performing foreclaw displays, and eye-blinking at approaching males.

Some authors assert that females may play passive roles during courtship (Taylor 1933; Jackson and Davis 1972), whereas others dispute this claim. Harless (1979) stated that the success or failure of an attempted mating ultimately rests on the female because copulation is not possible if the female turtle does not allow it. Several observations support this suggestion. For example, although male *E. blandingii* initiate courtship, ultimately females decide to accept or reject the male's advances (Baker and

Gillingham 1983). Failure to extend her tail after the male's swaying behavior results in unsuccessful mating, despite the sometimes quite agitated persistence by rejected males. Several authors suggested that coercion and forcible insemination may play important roles in some species (Berry and Shine 1980; Lee and Hays 2004; Refsnider 2009), but as discussed below, this is difficult to test.

Males of some species appear to be especially aggressive toward females. When copulation occurs following apparently aggressive signals, such as biting or shell clapping, it can be difficult to objectively identify the specific signal(s) that led to the female's acceptance of the male. Furthermore, it is impossible to determine whether the female is "choosing" to mate or simply "giving in" to coercion. Female turtles disinclined to mate typically flee, bite the suitor, or bite and chase the pursuer (Plummer 1977; Murphy and Lamoreaux 1978; Liu et al. 2008). Murphy and Lamoreaux (1978) reported that female *E. macquarii* often bite courting males; successful copulation does not follow biting. Liu et al. (2008) reported that female *S. quadriocellata* sometimes actively turn to face approaching males and occasionally bite at courting males. Given the absence of mounting or copulation, it is uncertain whether these signals are related to courtship, nonreceptivity, or receptivity followed by termination of courtship in response to some other stimulus.

Berry and Shine (1980) suggested that females may require suitors to coerce or slowly convince them to mate and that this may be a form of selection in which females maximize their reproductive fitness by mating only with extremely persistent males. Refsnider (2009) suggested that female *E. blandingii* exhibit "convenience polyandry", in which they accept a mate simply to avoid further harassment. A similar argument has been made by Lee and Hays (2004) to explain patterns of polyandry in the marine green turtle, *Chelonia mydas*. However, the hypotheses that every female wants to mate but requires the male to prove himself first, or that females are acquiescing to avoid harassment, are untestable because motivation of the female is unknown and untestable. For

example, although fleeing may indicate nonreceptivity, in some cases a fleeing female may move away from the courting male and then return to him and resume walking away (Harless 1979). Therefore, there is potential for an observer to confuse a fleeing female with one attempting to elicit a following response from a male. The argument that coercion is prevalent in the CBFT is common (Berry and Shine 1980; Refsnider 2009), but we suggest that acceptance of this untestable premise may lead to a biased interpretation of observed courtship behavior.

Behavioral evidence for coercion is unconvincing, at least in the case of *E. blandingii*. Males are not particularly aggressive to females, and biting is far less prevalent in their mating ritual than in some other species (e.g., kinosternids). Mating is costly to female turtles because they lose foraging time, run an increased risk of predation during mating, and risk injury from aggressive males; thus, females may not benefit from multiple mating (Uller and Olsson 2008). The frequency with which studies of courtship behavior report repeated courtship attempts but fail to observe that a single copulation suggests that females of at least some species are perfectly capable of being choosy (Ernst 1974; Arndt 1977; Murphy and Lamoreaux 1978, for *E. macquarii*; Kramer and Fritz 1989; Norris 1996). For some chelonians, polyandry and multiple paternities are more common than not (Uller and Olsson 2008; Davy et al. 2011). The benefits seem to outweigh the risks, and this suggests that coercion is not involved.

The question of female choice may be easier to address in groups such as the Trionychidae, where females are significantly larger than males and males of some species apparently are not aggressive toward females (e.g., *Apalone mutica* and *L. punctata*). In this family, coercion of females by males is unlikely. Unreceptive female trionychids bite viciously, and males run a risk of serious injury (Plummer 1977; Ernst and Lovich 2009). In both *A. mutica* and *L. punctata*, males are physically incapable of mounting and attaining intromission if the female does not settle calmly on the substrate (Duda and Gupta 1981, Ernst and Lovich 2009). Thus, biting of males by females appears to signal nonreceptivity in these species, and they may be good models for experimental investigation of factors influencing female mate choice.

Successful courtship requires the participation of both sexes. Thus, the courtship behaviors of female turtles are of great importance. Ultimately, females may determine successful copulation. Ignorance of the female's role in courtship precludes an understanding of male behaviors; a signal must have a receiver to function, and the efficacy of the signal depends largely on its reception (Bradbury and Vehrencamp 1998). Thus, complete models of courtship behavior must involve consideration of both sexes' behaviors and the interactions between them. Such models will allow us to investigate the evolution of different mating behaviors.

EVOLUTION OF MALE COURTSHIP BEHAVIOR IN FRESHWATER TURTLES

Berry and Shine (1980) provided the first study of the evolution of male courtship behavior. They suggested that less courtship and coercion or forceful insemination of females should occur in species where males are the larger, whereas smaller males should display more elaborate courtship behaviors. Gibbons and Lovich (1990) reject this suggestion in part because forcible insemination is not plausible because of difficulties a male turtle would encounter for achieving intromission with an unreceptive female, and we agree. However, if an aggressive behavior such as biting either calms females or functions in mate choice and subsequent mounting behavior, then aggression may be an effective strategy for successful mating. Bels and Crama (1994) also rejected the model on the basis that mate choice cannot be objectively inferred from observed behaviors because they can be interpreted in more than one way. They divided male courtship behavior into 3 categories: premounting courtship, intermediate courtship, and mounting courtship. However, Bels and Crama's (1994) 3 categories and Berry and Shine's (1980) argument are not mutually exclusive. Thus, we performed a set of meta-analyses to better understand the evolution of male CBFT.

Biting, foreclaw display, and head movement appear to calm females and facilitate mounting (Murphy and Lamoreaux 1978; Hidalgo 1982; Baker and Gillingham 1983; Liu et al. 2008). Foreclaw display and head movement have evolved independently in certain taxa, whereas biting degenerated in some branches of the phylogenetic tree, as discussed above. To determine whether the evolution of foreclaw display and head movement coincides with the degeneration of biting behavior, we tested whether foreclaw display and head movement replace biting from a phylogenetic perspective. Our meta-analysis obtained a very strong, highly significant negative correlation between these two strategies (Phi coefficient: $\Phi = -0.713$, $p < 0.001$), which suggests that foreclaw displays and head movement have evolved to replace biting in certain lineages of freshwater turtles.

We cannot directly test the female-choice model of Berry and Shine (1980), yet we can independently evaluate the three display types described by Bels and Crama (1994) relative to Berry and Shine's (1980) model. To perform this meta-analysis, we collapsed the 3 display types into 2: premounting displays and postmounting displays. We redistribute species into these types based on the timing of the behaviors (Table 2). The meta-analysis resolved highly significant phylogenetically dependent display types (Pearson's chi-square test: $\chi^2 = 36.38$, $df = 6$, $p < 0.001$), suggesting that postmounting might be plesiomorphic (Fig. 1). In pleurodires, postmounting courtship is replaced by premounting courtship in Australian species (1 of 5 species; 20%), and postmount-

ing courtship behaviors are conserved in South American species (8 of 9 species; 89%; FEPT: 1-tailed, $p = 0.023$). Postmounting displays persist in the Trionychidae, Chelydridae, and Kinosternidae (19 of 22 species; 86%) but are replaced by premounting in the subfamily Geoemydinae (0%; FEPT: 1-tailed, $p < 0.001$). In the Emydidae, premounting has evolved in the subfamily Deirochelyinae (postmounting in 1 of 10 species; 10%), whereas postmounting has been retained in the Emydinae (4 of 5 species; 80%; FEPT: 1-tailed, $p = 0.017$). The evolution of display type coincides with the phylogenetic degeneration of biting behavior. Our meta-analysis detects a highly significant negative correlation between biting and premounting (Phi coefficient: $\Phi = -0.507$, $p < 0.001$). In other words, premounting usually accompanies nonbiting courtship. Therefore, Berry and Shine's (1980) theory regarding mating strategy and Bels and Crama's (1994) theory regarding display type involve different aspects of the evolution of CBFT but are not mutually exclusive.

Berry and Shine's (1980) model of male mating strategy is based on a meta-analysis that includes tortoises and sea turtles, which we do not consider. Our meta-analysis only considers freshwater turtles, and it incorporates a larger data set (Table 2). Because we only consider aquatic species, habitat diversity is not a variable in the analysis. Analyses of sexual dimorphism involve binary data with females being larger than males or not. Display type (pre- or postmounting) is indicative of mating strategy because of the intrinsic correlation among display type and other courtship behaviors, such as biting, foreclaw displays, and head movements, as discussed above. Our meta-analysis resolved a highly significant positive correlation between larger female (relative to male body size) and a less aggressive courtship strategy involving foreclaw displays and head movements instead of biting (Phi coefficient: $\Phi = 0.660$, $p < 0.001$). Thus, males tend to adopt a less aggressive mating strategy in the taxa where adult females are larger than males. This result is consistent with Berry and Shine's (1980) models for mating strategy and sexual dimorphism.

To identify the drivers of CBFT, we have analyzed the evolution of sexual dimorphism from a phylogenetic perspective. Sexual dimorphism data are from Berry and Shine (1980) and Ernst and Lovich (2009). Sexual dimorphism appears to be phylogenetically dependent (Pearson's chi-square test: $\chi^2 = 36.34$, $df = 6$, $p < 0.001$). Thus, larger female body size appears to be an apomorphic and homoplastic trait that evolved independently in some taxa (Fig. 1). In Pleurodira, larger female body size evolved in Australian species (100%) but not in South American species (0%; FEPT: 1-tailed, $p = 0.014$). Larger or equal body size in males is conserved in the Chelydridae and Kinosternidae (11 of 14 species; 79%) but replaced by larger females in the Trionychidae (0%; FEPT: 1-tailed, $p = 0.011$) and the Geoemydinae (1 of 5 species; 20%; FEPT: 1-tailed,

$p = 0.038$). Within the Emydidae, larger female body size evolves in the Deirochelyinae rather than the Emydinae (FEPT: 1-tailed, $p < 0.001$). The evolutionary pattern for sexual dimorphism essentially parallels the evolution of display type, mild courtship behaviors, including foreclaw display, head movement, and the loss of biting behavior. Further, display types are highly significantly correlated with sexual dimorphism (Phi coefficient: $\Phi = -0.635$, $p < 0.001$).

Our analyses suggest that the evolution of courtship behavior in male freshwater turtles might accompany the evolution of sexual dimorphism, which is directly subject to natural selection. In the evolutionary history of freshwater turtles, larger female body size has evolved in the more recent taxa, such as some Emydidae and Geoemydidae. Larger female body size can increase fecundity, whereas smaller male body size can benefit male dispersal. Both scenarios appear to promote reproductive efficiency (Ghiselin 1974). Accordingly, males of species where the male is the smaller sex have adjusted their display type from post- to pre-mating courtship and adjusted their mating tactic from aggressive to mild. Because successful copulation requires a female to acquiesce (Gibbons and Lovich 1990; Liu et al. 2008), relatively smaller males may increase mating success by adopting the less aggressive strategy (Berry and Shine 1980).

RECOMMENDED FUTURE DIRECTIONS FOR RESEARCH

Publish Natural History Data. — Although progress has been made in understanding the courtship behavior of freshwater turtles, we are left with pleas made more than 30 yrs ago. Carpenter and Ferguson (1977) and Harless (1979) discussed the need to report behavioral observations to build a knowledge base. This need remains. Courtship data are available for a few species only, and most of these observations are incomplete, because many consist of one or two courtship episodes in one pair only. Isolated observations of CBFT do not allow for statistical analysis of the significance of the observation in terms of specific hypothesis testing. However, they have great value as the first records of either new behaviors or previously described behaviors in species for which no data exist. Such reports continue to suggest new directions for study. We strongly encourage future work on species either with no observation of courtship behavior or only anecdotal descriptions. Observations of courtship in cryptic species are difficult at best, and we encourage researchers who are fortunate enough to witness such events to publish their observations. Combined, these observations can guide hypothesis testing into a species' behavior.

Focus on Hypothesis Testing. — Although the literature on turtle courtship has grown significantly and continues to do so, almost nothing is known about the

functions of courtship signals, their interactions, or the ways in which courtship behavior influences mate choice or reproductive success in turtles. Even among studies with large sample sizes and statistical strength, most do not test hypotheses about courtship, communication, or mate choice, with notable exceptions, such as Garstka et al. (1991), Thomas (2002), and Thomas and Altig (2006). Future studies should aim to elucidate the function of courtship signals through experiments that evaluate the response of turtles receiving signals of different strengths and quality.

Description and Statistical Methods. — Disorder in applying techniques hinders progress in certain research fields, especially in behavioral studies (Liu et al. 2009). Often the same behavior is described differently in two papers, and this tendency leads to confusion. We have scanned the literature, gleaned data, and applied universal terms to identify courtship signals. Thus, we encourage the use of these terms rather than the creation of new terms to describe behavior. Because robust statistical methods are available for sequential analyses, quantified courtship studies have yielded useful behavioral models and hypotheses (Baker and Gillingham 1983; Bels and Crama 1994; Liu et al. 2008). We recommend improving the quality and standardization of data by quantifying the duration and frequency of each behavioral pattern in the courtship sequence. These new data will be useful not only to investigate the importance and function of certain behaviors in courtship but also to provide data for more robust comparison between studies.

SUMMARY

Research into the courtship behavior of freshwater turtles has succeeded in identifying a number of courtship signals used by many species of turtles. Many behaviors appear to be phylogenetically constrained; they have evolved in the common ancestor of lineages and persist in the descendants. However, the database is far from complete, and hypotheses require further testing with data from additional species. The priority in the coming years should be to start testing hypotheses regarding the reception and function of these signals. Three areas require particular attention. First, hypothesis testing requires a comparative biology perspective. A phylogenetic approach can lead to predictions of behavioral patterns in species whose courtship behavior is completely unknown. Second, an experimental approach is required to clarify further the functions of specific male behaviors. Finally, the role played by female turtles in courtship and mate choice requires investigation to identify the ways in which females receive male courtship signals and the signals they may send to the male. No doubt, the age of genomics will open many new opportunities (Haussler et al. 2009). Future studies may be able to identify the genes involved in controlling specific behaviors.

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LITERATURE CITED

- ARNDT, R.G. 1977. Notes on the natural history of the bog turtle, *Clemmys muhlenbergii*, in Delaware. *Chesapeake Science* 18: 67–76.
- ARNDT, R.G. 1986. Notes on the bog turtle, *Clemmys muhlenbergii* in Warren County, New Jersey. *Bulletin of the Maryland Herpetological Society* 22:56–61.
- ASHTON, D.T. 2007. *Actinemys* (= *Clemmys*) *marmorata* (north-western pond turtle): courtship behavior. *Herpetological Review* 38:327–328.
- AUFFENBERG, W. 1977. Display behavior in tortoises. *American Zoologist* 17:241–250.
- BAKER, R.E. AND GILLINGHAM, J.C. 1983. An analysis of courtship behavior in Blanding's turtle, *Emydoidea blandingii*. *Herpetologica* 39:166–173.
- BARLEY, A.J., SPINKS, P.Q., THOMSON, R.C., AND SHAFFER, H.B. 2010. Fourteen nuclear genes provide phylogenetic resolution for difficult nodes in the turtle tree of life. *Molecular Phylogenetics and Evolution* 55:1189–1194.
- BELS, V.L. 1983. Analyse de la parade de *Pelomedusa subrufa subrufa* (Lacépède). *Amphibia-Reptilia* 4:297–309.
- BELS, V.L. AND CRAMA, Y.J.M. 1994. Quantitative analysis of the courtship and mating behavior in the loggerhead musk turtle *Sternotherus minor* (Reptilia: Kinosternidae) with comments on courtship behavior in turtle. *Copeia* 1994:676–684.
- BERRY, J.F. AND SHINE, R. 1980. Sexual size dimorphism and sexual selection in turtles (Order: Testudines). *Oecologia* 44: 185–191.
- BETTLEHEIM, M.P. 2009. *Actinemys* (= *Clemmys*) *marmorata* (western pond turtle). Courtship behavior. *Herpetological Review* 40:212.
- BRADBURY, J.W. AND VEHCAMP, S.L. 1998. Principles of Animal Communication. Sunderland, MA: Sinauer Associates, Inc., 882 pp.
- BRITO, E.S., STRUSSMANN, C., AND BAICERE-SILVA, C.M. 2009. Courtship behavior of *Mesoclemmys vanderhaegei* (Bour, 1973) (Testudines: Chelidae) under natural conditions in the Brazilian Cerrado. *Herpetology Notes* 2:67–72.

- CAGLE, F.R. 1955. Courtship behavior of juvenile turtles. *Copeia* 1955:307.
- CAMP, C.L. 1916. Note on the local distribution and habits of the amphibians and reptiles of southeastern California in the vicinity of the Turtle Mountains. University of California Publications in Zoology 12:503–544.
- CAMPBELL, H.W. 1960. The bog turtle in Maryland. *Maryland Naturalist* 30:15–16.
- CARR, A.F. 1952. *Handbook of Turtles*. Ithaca, NY: Cornell University Press, 542 pp.
- CARPENTER, C.C. AND FERGUSON, G.W. 1977. Variation and evolution of stereotyped behaviour in reptiles. In: Gans, C. and Tinkle, D.W. (Eds.). *Biology of the Reptilia*. Volume 7. London: Academic Press, pp. 335–554.
- CHIPPINDALE, P.T. 1989. Courtship and nesting records for spotted turtles, *Clemmys guttata*, in Mer Bleue Bog, southeastern Ontario. *Canadian Field Naturalist* 103:289–291.
- CHRISTENSEN, R.M. 1975. Breeding Central American wood turtles. *Chelonia* 2:8–81.
- CONANT, R. 1938. The reptiles of Ohio. *American Midland Naturalist* 20:1–200.
- CONANT, R. 1951. *The reptiles of Ohio*. Second edition. South Bend, IN: University of Notre Dame Press.
- DARWIN, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- DAVIS, J.D. AND JACKSON, C.G., JR. 1973. Notes on the courtship of a captive male *Chrysemys scripta taylori*. *Herpetologica* 29:62–64.
- DAVY, C.M., EDWARDS, T., LATHROP, A., BRATTON, M., HAGAN, M., NAGY, K.A., STONE, J., HILLARD, L.S., AND MURPHY, R.W. 2011. Polyandry and multiple paternities in the threatened desert tortoise, *Gopherus agassizii*. *Conservation Genetics* 12:1313–1322.
- DRAJESKE, P.W. 1983. Husbandry and captive reproduction of the mata mata, *Chelus fimbriatus* (Schneider). *Bulletin of the Chicago Herpetological Society* 18:73–81.
- DUDA, P.L. AND GUPTA, V.K. 1981. Courtship and mating behaviour of the Indian soft shell turtle, *Lissemys punctata punctata*. *Proceedings of the Indian Academy of Science (Animal Science)* 90:453–461.
- EGLIS, A. 1962. Tortoise behavior: a taxonomic adjunct. *Herpetologica* 18:1–8.
- ERNST, C.H. 1967. A mating aggregation of the turtle *Clemmys guttata*. *Copeia* 1967:473–474.
- ERNST, C.H. 1970. Reproduction in *Clemmys guttata*. *Herpetologica* 26:228–232.
- ERNST, C.H. 1974. Observations on the courtship of male *Graptemys pseudogeographica*. *Journal of Herpetology* 8: 377–378.
- ERNST, C.H. AND LOVICH, J.E. 2009. *Turtles of the United States and Canada*. Second edition. Baltimore, MD: Johns Hopkins Univ. Press, 827 pp.
- EVANS, L.T. 1961. Aquatic courtship of the wood turtle, *Clemmys insculpta*. *American Zoologist* 1:353.
- EWERT, M.A., JACKSON, D.R., AND BUHLMANN, K.A. 2006. *Deirochelys reticularia*—chicken turtle. *Chelonian Research Monographs* 3:249–259.
- FERRARA, C.R., SCHNEIDER, L., VOGT, R.C., AND BURGER, J. 2009. The role of receptivity in the courtship behavior of *Podocnemis erythrocephala* in captivity. *Acta Ethologica* 12:121–125.
- GADOW, H. 1901. *Amphibia and Reptiles*. San Francisco: Macmillan and Co., 668 pp.
- GALEOTTI, P., SACCHI, R., PELLITTERI ROSA, D., AND FASOLA, M. 2005. Female preference for fast-rate, high-pitched calls in Hermann's tortoises *Testudo hermanni*. *Behavioural Ecology* 16:301–308.
- GARSTKA, W.R., COOPER, W.E., JR., WASMUND, K.W., AND LOVICH, J.E. 1991. Male sex steroids and hormonal control of male courtship behavior in the yellow-bellied slider turtle, *Trachemys scripta*. *Comparative Biochemistry and Physiology* 98A:271–280.
- GHESELIN, M.T. 1974. *The Economy of Nature and the Evolution of Sex*. Berkeley: Univ. of California Press, 346 pp.
- GIBBONS, J.W. AND LOVICH, J.E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs* 4:1–29.
- GILES, J.C., DAVIS, J.A., MCCAULEY, R.D., AND KUCHLING, G. 2009. Voice of the turtle: the underwater acoustic repertoire of the long-necked freshwater turtle, *Chelodina oblonga*. *Journal of the Acoustical Society of America* 126:434–443.
- GOODE, J. 1967. *Freshwater tortoises of Australia and New Guinea (in the family Chelidae)*. Melbourne: Lansdowne Press, 154 pp.
- GRAHAM, T.E. AND DOYLE, T.S. 1979. Dimorphism, courtship, eggs and hatchlings of the Blanding's turtle, *Emydoidea blandingii* (Reptilia, Testudines, Emydidae), in Massachusetts. *Journal of Herpetology* 13:125–127.
- GRONKE, W.K., CHIPPS, S.R., BANDAS, S.J., AND HIGGINS, K.F. 2006. Reticulate melanism in western painted turtles (*Chrysemys picta bellii*): exploring linkages with habitat and heating rates. *American Midland Naturalist* 156:289–298.
- GROSS, M. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* 11: 92–98.
- HAMILTON, W.J., JR. 1940. Observations on the reproductive behavior of the snapping turtle. *Copeia* 1940:124–126.
- HARDING, J.H. 1981. Observations on the African helmeted turtle, *Pelomedusa subrufa*, in captivity, with comments on breeding behavior. *Bulletin of the Chicago Herpetological Society* 16:86–94.
- HARDING, J.H. 1983. Life history notes. Testudines. *Platemys platycephala* (twistneck turtle). *Reproduction. Herpetological Review* 14:22.
- HARLESS, M. 1979. Social behavior. In: Harless, M. and Morlock, H. (Eds.). *Turtles: Perspectives and Research*. New York: John Wiley and Sons, pp. 475–492.
- HARREL, J.B., DOUGLAS, N.H., HARAWAY, M.M., AND THOMAS, R. 1996. Mating behavior in captive alligator snapping turtles (*Macrochelys temminckii*). *Chelonian Conservation and Biology* 2:101–105.
- HAUSSLER, D., O'BRIEN, S.J., RYDER, O.A., BARKER, F.K., CLAMP, M., CRAWFORD, A.J., HANNER, R., HANOTTE, O., JOHNSON, W.E., MCGUIRE, J.A., MILLER, W., MURPHY, R.W., MURPHY, W.J., SHELDON, F.H., SINERVO, B., VENKATESH, B., WILEY, E.O., ALLENDORF, F.W., BAKER, C.S., BAUER, A., BEJA-PEREIRA, A., BERMINGHAM, E., BERNARD, G., BONVICINO, C.R., BRENNER, S., BURKE, T., CRACRAFT, J., DIEKHANS, M., EDWARDS, S., ERICSON, P., ESTES, J., FJELSA, J., FLESNESS, N., GAMBLE, T., GAUBERT, P., GRAPHODATSKY, A.S., GRAVES, J.A.M., GREEN, E.D., GREEN, R.E., HACKETT, S., HEBERT, P., HELGEN, K.M., JOSEPH, L., KESSING, B., KINGSLEY, D.M., LEWIN, H.A., LUIKART, G., MARTELLI, P., MOREIRA, M.A.M., NGUYEN, N., ORTÍ, G., PIKE, B.L., RAWSON, D.M., SCHUSTER, S.T. C., SEUÁNEZ, H.N., SHAFFER, H.B., SPRINGER, M.S., STUART, J.M., SUMNER, J., TEELING, E., VRIJENHOEK, R.C., WARD, R.D., WAYNE, R., WILLIAMS, T.M., WOLFE, N.D., AND ZHANG, Y.-P. 2009. Genome 10K: a proposal to obtain whole-genome sequence for 10,000 vertebrate species. *Journal of Heredity* 100:659–674.

- HIDALGO, H. 1982. Courtship and mating behavior in *Rhinoclemmys pulcherrima incisa* (Testudines: Emydidae: Batagurinae). *Transaction of the Kansas Academy of Science* 85:82–95.
- HOLLAND, D.C. 1988. *Clemmys marmorata* (western pond turtle): behavior. *Herpetological Review* 19:87–88.
- HORNE, B.D. 1993. Courtship behavior and oviposition of captive *Acanthochelys pallidipectoris* Freiberg. *Herpetological Review* 24:25.
- HULSE, A.C. 1982. Reproduction and population structure in the turtle, *Kinosternon sonoriense*. *Southwestern Naturalist* 27:447–456.
- IVERSON, J.B. 1975. Notes on courtship in *Rhinoclemmys funerea*. *Journal of Herpetology* 9:249–250.
- JACKSON, C.G., JR. AND DAVIS, J.D. 1972. A quantitative study of the courtship display of the red-eared turtle, *Chrysemys scripta elegans*. *Herpetologica* 28:58–64.
- JENKINS, R.J. AND BABBITT, K.J. 2003. *Emydoidea blandingii* (Blanding's turtle): mating behavior. *Herpetological Review* 34:361–362.
- JOYCE, W.G., MICKLICH, N., SCHAAL, S.F.K., AND SCHEYER, T.M. 2012. Caught in the act: the first record of copulating fossil vertebrates. *Biology Letters* doi:10.1098/rsbl.2012.0361.
- KAUFMANN, J. 1992. The social behavior of wood turtles, *Clemmys insculpta*, in central Pennsylvania. *Herpetological Monographs* 6:1–25.
- KRAMER, M. 1984. *Pseudemys nelsoni* (Florida red-bellied turtle): behavior. *Herpetological Review* 15:113–114.
- KRAMER, M. AND BURGHARDT, G.M. 1998. Precocious courtship and play in emydid turtles. *Ethology* 104:38–56.
- KRAMER, M. AND FRITZ, U. 1989. Courtship of the turtle, *Pseudemys nelsoni*. *Journal of Herpetology* 23:84–86.
- KREFFT, G. 1955. *Deirochelys reticularia* (Latreille), eine wenig bekannte Schmuckschildkröte der USA. *Aquarium und Terrarium Zeitschrift* (Stuttgart) 4:157–160.
- KUCHLING, G. 1999. *The Reproductive Biology of the Chelonian*. Berlin: Springer Press, 223 pp.
- LAGLER, K.F. 1941. Fall mating and courtship of the musk turtle *Sternotherus odoratus*. *Copeia* 1941:268.
- LAHANAS, P.N. 1982. Aspects of the life history of the southern black-knobbed sawback, *Graptemys nigrinoda elticola*, Folkerts and Mount. Master's Thesis, Auburn University, Auburn, AL.
- LARDIE, R.L. 1975. Courtship and mating behavior in the yellow mud turtle, *Kinosternon flavescens flavescens*. *Journal of Herpetology* 9:223–227.
- LEE, P.L.M. AND HAYS, G.C. 2004. Polyandry in a marine turtle: females make the best of a bad job. *Proceedings of the National Academy of Sciences* 101:6530–6535.
- LEGLER, J.M. 1978. Observation on behavior and ecology in an Australian turtle, *Chelodina expansa* (Gray) (Testudines: Chelidae). *Canadian Journal of Zoology* 56:2449–2453.
- LEWIS, C.H., MOLLOY, S.F., AND CHAMBERS, R.M. 2007. Response of common musk turtles (*Sternotherus odoratus*) to intraspecific chemical cues. *Journal of Herpetology* 41:349–353.
- LIU, Y., HE, B., SHI, H., MURPHY, R.W., FONG, J.J., WANG, J., FU, L., AND MA, Y. 2008. An analysis of courtship behaviour in the four-eyed spotted turtle, *Sacalia quadriocellata* (Reptilia: Testudines: Geoemydidae). *Amphibia-Reptilia* 29:185–195.
- LIU, Y., WANG, J., SHI, H., MURPHY, R.W., HONG, M., HE, B., FONG, J.J., WANG, J., AND FU, L. 2009. Ethogram of *Sacalia quadriocellata* (Reptilia: Testudines: Geoemydidae) in captivity. *Journal of Herpetology* 43:318–325.
- LOVICH, J.E., GARSTKA, W.R., AND COOPER, W.E., JR. 1990a. Female participation in courtship behavior of the turtle *Trachemys s. scripta*. *Journal of Herpetology* 24:422–424.
- LOVICH, J.E., MCCOY, C.J., AND GARSTKA, W.R. 1990b. The development and significance of melanism in the slider turtle. In: Gibbons, J.W. (Ed.). *Life History and Ecology of the Slider Turtle*. Washington, DC: Smithsonian Institution Press, pp. 233–254.
- MACCULLOCH, R.D. 1981. Variation in the shell of *Chrysemys picta belli* from southern Saskatchewan. *Journal of Herpetology* 15:181–185.
- MADISON, D.M. 1977. Chemical communication in reptiles and amphibians. In: Muller-Schwartz, D. and Mozell, M.M. (Eds.). *Chemical Signals in Vertebrates*. New York: Plenum Press, pp. 135–168.
- MAHMOUD, I.Y. 1967. Courtship behavior and sexual maturity in four species of kinosternid turtles. *Copeia* 1967:314–319.
- MANSFIELD, P., STRAUSS, E.G., AND AUGER, P.J. 1998. Using decoys to capture spotted turtles (*Clemmys guttata*) in water funnel traps. *Herpetological Review* 29:157–158.
- MANTON, M.L. 1979. Olfaction and behavior. In: Harless, M. and Morlock, H. (Eds.). *Turtles: Perspectives and Research*. New York: John Wiley and Sons, pp. 289–301.
- MARCHAND, L.J. 1944. Notes on the courtship of a Florida terrapin. *Copeia* 1944:191–192.
- MAYNARD, C.J. 1869. The capture of the *Centronyx bairdii* at Ipswich. *American Naturalist* 3:554–555.
- MEDEM, F. 1983. Reproductive data on *Platemys platycephala* (Testudines: Chelidae) in Colombia. In: Rhodin, A. and Miyata, K. (Eds.). *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams*. Cambridge, MA: Harvard University: Museum of Comparative Zoology, pp. 429–434.
- MERTENS, R. 1946. Die warn- und Droh-Reaktion der reptilien. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 471:1–108.
- MILLER, J.D. AND DINKELACKER, S.A. 2008. Reproductive structures and strategies of turtles. In: Wyneken, J., Godfrey, M.H., and Bels, V. (Eds.). *Biology of Turtles*. Boca Raton, FL: Taylor and Francis Group, pp. 225–278.
- MITCHELL, J.C. AND MUELLER, R.F. 1996. *Clemmys insculpta* (wood turtle): reproductive behavior. *Herpetological Review* 27:197.
- MOLINA, F.B. 1996. Mating behavior of captive Geoffroy's side-necked turtles, *Phrynops geoffroanus* (Testudines: Chelidae). *Herpetological Natural History* 4:155–160.
- MOLL, E.O., MATSON, E.K., AND KREHBIEL, E.B. 1981. Sexual and seasonal dichromatism in the Asian river turtle *Callagur borneoensis*. *Herpetologica* 37:181–194.
- MUÑOZ, A. 2004. Chemo-orientation using conspecific chemical cues in the stripe-necked terrapin (*Mauremys leprosa*). *Journal of Chemical Ecology* 30:519–530.
- MURPHY, J.B. AND LAMOREAUX, W.E. 1978. Mating behavior in three Australian chelid turtles. *Herpetologica* 4:398–405.
- NORRIS, J.L. 1996. Male courtship in the New Guinea turtle, *Emydura subglobosa* (Pleurodira, Chelidae). *Journal of Herpetology* 30:78–80.
- NOVELLI, I.A. AND SOUZA, B.M. 2007. Análise descritiva do comportamento de corte e cópula de *Hydromedusa maximiliani* (Mikan, 1820) (Testudines, Chelidae) em laboratório. *Revista Brasileira de Zootecias* 9:49–56.
- PÉREZ-HIGAREDA, G. AND SMITH, H.M. 1988. Courtship behavior in *Rhinoclemmys areolata* from western Tabasco, Mexico (Testudines: Emydidae). *Great Basin Naturalist* 48:263–266.
- PETRANKA, J.W. AND PHILLIPPI, A. 1978. Observations on the courtship behavior of juvenile *Chrysemys concinna concinna* and *Chrysemys floridana hoyi* (Reptilia, Testudines, Emydidae). *Journal of Herpetology* 12:417–419.

- PISANI, G.R. 2004. *Chelydra serpentina* (common snapping turtle): mating behavior. *Journal of Kansas Herpetology* 11: 15.
- PLUMMER, M.V. 1977. Notes on the courtship and mating behavior of the softshell turtle, *Trionyx muticus*. *Journal of Herpetology* 11:87–90.
- POOLE, T.B. 1978. An analysis of social play in polecats (Mustelidae) with comments on the form and evolutionary history of the open mouth play face. *Animal Behavior* 26:36–49.
- POPE, C.H. 1955. *The Reptile World*. New York: A. Knopf, 325 pp.
- POSCHADEL, J., MEYER-LUCHT, Y., AND PLATH, M. 2006. Response to chemical cues from conspecifics reflects male mating preference for large females and avoidance of large competitors in the European pond turtle. *Behaviour* 143: 569–587.
- RAMO, C. 1982. Biología de Galápago (*Podocnemis vogli* Müller, 1935) en el Hato El Frio, llanos de Apure, Venezuela. *Doñana Acta Vertebratica* (Sevilla) 9(3):1–161.
- REFSNIDER, J.M. 2009. High frequency of multiple paternity in Blanding's turtle (*Emys blandingii*). *Journal of Herpetology* 43:74–81.
- RICHARD, E. 1999. Tortugas de las regiones áridas de Argentina: Contribución al conocimiento de las tortugas de las regiones áridas de Argentina (Chelidae y Testudinidae) con especial referencia a los aspectos eto-ecológicos, comerciales y antropológicos de las especies del complejo chilensis (*Chelonoidis chilensis* y *Ch. donosobarrosi*) en la provincia de Mendoza. Buenos Aires: Argentina Monografía Especial L.O.L.A. 10:1–24.
- RICHMOND, G. 1970. The marsh awakens. *International Turtle and Tortoise Society Journal* 4:28–29.
- ROOT, R.W. 1949. Aquatic respiration in the musk turtle. *Physiological Zoology* 22:172–178.
- ROSE, W. 1950. *The Reptiles and Amphibians of Southern Africa*. Capetown, South Africa: M. Miller.
- ROVERO, F., LEBBORONI, M., AND CHELAZZI, G. 1999. Aggressive interactions and mating in wild populations of the European pond turtle *Emys orbicularis*. *Journal of Herpetology* 33:258–263.
- RUNYON, R. AND HABER, A. 1976. *Fundamentals of Behavioral Statistics*. Boston, MA: Addison Wesley, 446 pp.
- SACHSSE, W. AND SCHMIDT, A.A. 1976. Nachzucht in der zweiten Generation von *Staurotypus salvinii* mit weiteren Beobachtungen zum Fortpflanzungsverhalten (Testudines, Kinosternidae). *Salamandra* 12:5–16.
- SCHMIDT, A.A. 1970. Zur Fortpflanzung der Kreuzbrustschildkröte (*Staurotypus salvinii*) in Gefangenschaft. *Salamandra* 6: 3–10.
- SCHUELER, F.W. 1983. Reticulate melanism in Canadian western painted turtles. *Blue Jay* 41:83–91.
- SEDDON, J.M., GEORGES, A., BAVERSTOCK, P.R., AND MCCORD, W. 1997. Phylogenetic relationships of chelid turtles (Pleurodira: Chelidae) based on mitochondrial 12S rRNA gene sequence variation. *Molecular Phylogenetics Evolution* 7:55–61.
- SEIDEL, M.E. 2010. *Deirochelys reticularia* (chicken turtle). Courtship behavior. *Herpetological Review* 41(3):345–346.
- SEIDEL, M.E. AND FRITZ, U. 1997. Courtship behavior provides additional evidence for a monophyletic *Pseudemys*, and comments on Mesoamerican *Trachemys* (Testudines: Emydidae). *Herpetological Review* 28:70–72.
- SEIGEL, R.A. 1980. Courtship and mating behavior of the diamondback terrapin *Malaclemys terrapin tequesta*. *Journal of Herpetology* 14:420–421.
- SEXTON, O.J. 1960. Notas sobre la reproducción de una tortuga Venezolana, la *Kinosternon scorpioides*. *Memoria de la Sociedad de Ciencias Naturales La Salle* 20:189–197.
- SHEALY, R.M. 1976. The natural history of the Alabama map turtle, *Graptemys pulchra* Baur, in Alabama. *Bulletin of the Florida State Museum, Biological Sciences* 21:47–111.
- SHI, H., FU, Y., AND WANG, J. 2002. The riddle of *Sacalia quadriocellata*. *Man and Biosphere* 6:33–39 (in Chinese).
- STUART, J.N. AND MIYASHIRO, J.B.M. 1998. *Trachemys gaigeae* (Big Bend slider): courtship behavior. *Herpetological Review* 29:235–236.
- TAYLOR, E.H. 1933. Observations on the courtship of turtles. *University of Kansas Science Bulletin* 21:269–271.
- THIEME, U. 1979. Erfahrungen mit Weichschildkröten 12: Erste Nachzucht der chinesischen Weichschildkröten *Trionyx sinensis*. *Das Aquarium und Terrarium Zeitschrift* 26:26–29.
- THOMAS, R.B. 2002. Conditional mating strategy in a long-lived vertebrate: ontogenetic shifts in the mating tactics of male slider turtles (*Trachemys scripta*). *Copeia* 2002:456–461.
- THOMAS, R.B. AND ALTIG, R. 2006. Characteristics of the foreclaw display behaviors of female *Trachemys scripta* (slider turtles). *Southeastern Naturalist* 5:227–234.
- TRONZO, R.D. 1993. *Clemmys insculpta* (wood turtle): reproduction. *Herpetological Review* 24:149.
- ULLER, T. AND OLSSON, M. 2008. Multiple paternity in reptiles: patterns and processes. *Molecular Ecology* 17:2566–2580.
- VENTURA, D.F., ZANA, Y., DESOUZA, J.M., AND DEVOE, R.D. 2001. Ultraviolet colour opponency in the turtle retina. *Journal of Experimental Biology* 204:2527–2534.
- WAHLQUIST, H. 1970. Sawbacks of the Gulf Coast. *International Turtle and Tortoise Society Journal* 4:10–13.
- WEAVER, E.G. AND VERNON, J.A. 1956. The sensitivity of the turtle ear as shown by its electrical potential. *Proceedings of the National Academy of Sciences* 42:213–220.
- WEAVER, W.G. 1970. Courtship and combat behavior in *Gopherus berlandieri*. *Bulletin of the Florida State Museum, Biological Sciences* 15:1–43.
- WHITE, C.P. AND CURTSINGER, W.R. 1986. Freshwater turtles: design for survival. *National Geographic* 169:40–59.
- WHITEHURST, G.J., FISCHER, J.E., DEBARYSHE, B., CAULFIELD, M.B., AND FALCO, F.L. 1986. Analyzing sequential relations in observational data: a practical guide. *Journal of Psychopathology and Behavioral Assessment* 8:129–148.
- WILSON, D.S., MUSHINSKY, H.R., AND MCCOY, E.D. 2006. *Kinosternon barui*—striped mud turtle. *Integrative Biology Faculty Publications* 145.
- WINOKUR, R.M. AND LEGLER, J.M. 1974. Rostral pores in turtles. *Journal of Morphology* 143:107–120.
- WINOKUR, R.M. AND LEGLER, J.M. 1975. Chelonian mental glands. *Journal of Morphology* 147:275–292.
- WOOLLEY, S.C., SAKATAB, J.T., AND CREWS, D. 2004. Evolutionary insights into the regulation of courtship behavior in male amphibians and reptiles. *Physiology and Behavior* 83:347–360.
- WORRELL, E. 1963. *Reptiles of Australia*. Sydney: Angus and Robertson, 207 pp.

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