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Precocious Courtship and Play in Emydid Turtles

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Abstract

In many mammal species, precocious sexual behaviour is a component of play. A recent model for the evolution of play fighting behaviour in muroid rodents by PELLIS (1993) proposes that social play in those species has its origin in precocious sexual behaviour. Captive juvenile emydid turtles perform precocious sexual behaviour. After reviewing its occurrence, we focus on detailed observations of *Pseudemys nelsoni.* Precocious sexual behaviour in these turtles is characterized by the striking 'titillation' display, usually observed only when adult males court females. In this display, the digits of the front feet are rapidly vibrated above the eyes of the female. In our observations, both sexes performed the display, which was energetic, spontaneous, and inconclusive (in that sequences of precocious courtship typically ended when either the displayer or recipient stopped and rested, left, or started some other unrelated non-social behaviour). Displaying individuals clearly preferred conspecific recipients and often appeared to seek out specific individuals. We discuss several plausible explanations for precocious courtship in these turtles but find none entirely satisfying. The characteristics of the precocious courtship behaviour we observed most closely match those commonly listed for social play. Thus, we conclude that the most likely explanation for this behaviour is that it is a component of social play.

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Introduction

One facet of ethology involves tracing the evolutionary origins of complex behaviour patterns (MARTINS 1996). Often we discover that major categories of complex behaviour are not the recent evolutionary innovations they seemed to be. For example, tool use was once thought to be restricted to, indeed characteristic of, human beings. Today tools are known to be used by many unrelated animals, all with presumably lesser mental faculties than *Homo sapiens* (BECK 1980). During the 19th century, play behaviour was considered widespread in vertebrates and invertebrates (BURGHARDT, in press). Currently, play behaviour is considered restricted to those groups for which it has been documented: all mammalian and some avian orders (FAGEN 1981). Given the occurrence of play behaviour

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in mammals and birds, it is natural to ask if evidence for play behaviour exists in members of the group ancestral to both, ectothermic reptiles. Turtles are representatives of the oldest extant reptilian radiation (GAUTIER et al. 1989).

Unlike many other behaviour patterns, which can usually be unambiguously identified functionally (feeding, nest building, grooming), play, especially social play, often requires an intimate knowledge of a species' behaviour before it can be recognized as such. For example, there is still controversy on some of the most widely accepted examples of play signals (PELLIS & PELLIS 1996). Evidence for the occurrence of object and locomotor play in ectothermic reptiles (reptiles from here on) has been recently reviewed by BURGHARDT et al. (1996), who presented evidence for such play in an adult Nile soft-shell turtle (*Trionyx triunguis*). The issue of social play in turtles is addressed in this report.

Our intent here is not to develop new criteria for recognizing play, but simply to ask if phenomena that are readily accepted today as playful when seen in mammals and birds are also found in reptiles. Although the latter are biologically similar to the former in many respects, differences in physiology and ontogeny may have precluded the evolution of play as diverse and ubiquitous as that found in birds and mammals. Our examples of putative social play in juvenile turtles are derived from the courtship-like behaviour reported in some aquatic species of North American emydid turtles. PELLIS (1993) has developed a theoretical model for the evolution of 'play fighting' in juvenile muroid rodents. For these and other species, many elements of play, even play fighting, have their origin in sexual rather than agonistic behaviour. He hypothesized that the precocious sexual behaviour patterns already present in immature animals were the bases on which sexual play and play fighting were built. As both juvenile play and adult sexual behaviour became increasingly elaborate, successful sexual behaviour as an adult became contingent on play experience as a juvenile. Eventually, in some species, the sexual acts used in play were modified for use in other social contexts. For juvenile muroid rodents, PELLIS (1993) distinguished the precocious expression of sex (e.g. voles) from play (e.g. rats), both of which incorporate sexual acts. He suggested that one can discriminate between the two based, in part, on the amount of time devoted to each, with play occupying much more time than simple precocious sexual behaviour.

Use of a time criterion may aid in distinguishing play from non-play in other groups of animals where precocious sexual behaviour patterns occur, particularly when it is difficult to recognize play. Evidence for play using a time criterion would exist if the behaviour was performed with a frequency and duration comparable to that of well-accepted examples of play. While this may include many non-play behaviours, it excludes enigmatic behaviours that occur only sporadically.

Precocious courtship has previously been unambiguously documented in juvenile emydid turtles. These include *Chrysemys picta* (RIVES 1978 [both sexes]), *Graptemys flavimaculata* (CAGLE 1955; WAHLQUIST 1970 [both sexes]), *G. kohni* (CAGLE 1955; RIVES 1978), *G. barbouri* (WAHLQUIST 1970 [males]), *Pseudemys concinna* (CAGLE 1955; PETRANKA & PHILLIPPI 1978 [male]; RIVES 1978), *P. floridana* (PETRANKA & PHILLIPPI 1978), and *Trachemys scripta* (MORRIS 1976 [male]; RIVES 1978 [both sexes]). However, the interpretation of these observations has been unclear. During precocious courtship, an individual rapidly vibrates the claws of its front feet near the head of another turtle or, much less commonly, near an object. In all six species, males use a similar display when courting

females (CAGLE 1955; PETRANKA & PHILLIPPI 1978; VOGT 1978; KRAMER & FRITZ 1989). CAGLE (1955) mentions that precocious courtship behaviour was not seen in hatchlings of 32 other species (species not given). In these early observations, unless noted, sex of the displaying individuals was not reported.

Could precocious courtship in turtles be a form of play? Here we review what is known of adult sexual behaviour in *Pseudemys* species and describe the behaviour we observed in juvenile *P. nelsoni*, *P. floridana* and *P. concinna*. In addition, Dale JACKSON (in litt.) graciously made available his unpublished observations on these and additional species. We describe the numerous characteristics that precocious courtship shares with social play behaviour in other species. Some hypotheses concerning the function of this behaviour are presented and discussed. Finally, we consider the general question of reptile social play, and, more specifically, whether this phenomenon is a form of rudimentary play.

In *Pseudemys* species, two external characters are useful in distinguishing males from females: enlargement of the male's tail and hypertrophy (elongation) of the male's foreclaws. The courtship of adult *Pseudemys nelsoni* was described by KRAMER & FRITZ (1989). Courtship appears to start with the male's investigation of the female. This proceeds to active following, interspersed with the aforementioned courtship display termed 'titillation'. During titillation the male swims above and parallel to the female, facing in the same direction, and periodically and repeatedly thrusts his front limbs forward, rotating them inward (pronation) with the palms facing out, while rapidly vibrating the digits of his front feet. The display is clearly orientated toward the head of the female. The male's long front claws appear to emphasize the display. This may continue for many min, possibly hours. At some point the male may attempt to mount and, if the female permits it, to copulate. If unsuccessful, the male may continue to display or may leave the female. Courtship of other species of *Pseudemys* appears to be similar (e.g. *P. concinna*, described in JACKSON & DAVIS 1972a). Courtship of the related *Chrysemys picta* and USA subspecies of *Trachemys scripta* appears to be similar except that males face the females during titillation (ERNST 1971; JACKSON & DAVIS 1972b). On two occasions, a captive female *P. nelsoni* titillated an unresponsive male *P. nelsoni* while facing him (JACKSON 1977). Similar behaviour has been observed in adult female *C. picta* and *T. scripta* (ERNST 1971; LOVICH et al. 1990). That females sometimes, although rarely, perform the titillation display serves to underscore that acts associated with courtship may appear in other contexts.

Methods

Subjects and Housing

Observations of precocious courtship were made on four *Pseudemys nelsoni*, three *P. floridana penninsularis*, and two *P. concinna suwanniensis*. Information concerning the history and size of these individuals is given in Table 1. Although the tail of the male *P. nelsoni* had enlarged prior to these observations, secondary sex characters (e.g. long front claws) were not apparent until the conclusion of the study. During the 4-mo study (Nov. 1984–Apr. 1985), these animals were maintained in one 180 × 39 × 33 cm aquarium containing about 140 l of water. Lighting was on a 12L:12D cycle. Pieces of two cinder blocks provided hiding places and supported a rubber basking platform. Room temperature was maintained at 24–27 °C. A 60 W light bulb suspended about 15 cm above the basking platform provided additional heat 8 h/day. The animals were fed to satiation at least three times per week with live or frozen crickets, dog food and lettuce. A plaster-of-Paris block was placed in the water to provide supplementary calcium. The water was continuously filtered and completely replaced once a week. All

Table 1: Information on *Pseudemys* turtles observed at the University of Tennessee

Subject	Species	Procurement	Measurements (8 Apr. 1985) Plastron length (mm)	Mass (g)	Sex
1	*P. nelsoni*	Captive reared, hatched Aug. 1982	133	491	F
2	*P. nelsoni*	Captive reared, hatched Aug. 1982	131	460	M
3	*P. nelsoni*	Captive reared, hatched Aug. 1982	109	298	F
4	*P. nelsoni*	Captive reared, hatched Aug. 1982	140	532	F
6	*P. concinna*	Captured July 1983, Luraville, Fla.	131	446	?
7	*P. concinna*	Captured July 1983, Luraville, Fla.	198	214	?
8	*P. floridana*	Captured July 1984, Apopka, Fla.	183	141	?
9	*P. floridana*	Captured July 1984, Apopka, Fla.	161	163	?
10	*P. floridana*	Captured July 1984, Apopka, Fla.	102	236	?

individuals were marked for individual identification by drilling a small hole through one of the marginals (CAGLE 1939) and released in Apr. 1985. One of the juvenile female *P. nelsoni*, recaptured some 9 mo later, was in excellent health and had increased in size (30% increase in length, 106% increase in mass; approximately the same growth rate as in our captive animals).

Informal observations by Dale JACKSON (in litt.) on precocious courtship in *Pseudemys nelsoni*, *P. alabamensis*, *P. floridana*, *P. concinna* and *Trachemys scripta* were made from 1977 until 1989. Some of these animals were observed from hatching to age 12. They were maintained in various aquaria and a small plastic wading pool during this time. For most of these observations, individual identities were not recorded. Thus, they are used only to supplement data on the expression of precocious courtship among different age classes and the postures used by different species.

Observation and Analysis Techniques

All interactions among turtles maintained in the laboratory at the University of Tennessee were recorded using paper and pencil during 17 observation periods totalling 810 min (hereafter dataset 1). Observations usually began about 1 h after feeding, in the afternoon, as prior informal observations suggested that social interactions occurred frequently at this time.

Animals generally avoided pointing their heads directly towards another from a distance of less than one body length (see below). Therefore, we considered an interaction to begin when one turtle approached another with its head pointed directly towards it, or when one turtle, already in the proximity of another, orientated to face it. Interactions that included approaches, or approaches and precocious courtship, are presented here.

Additional data using focal animal sampling (ALTMANN 1974) and checksheets (HINDE 1973) were gathered for the four *Pseudemys nelsoni* juveniles under the same conditions described above (hereafter dataset 2). Time periods were divided into 30-s intervals and the order of social and maintenance behaviour patterns within these intervals was recorded. Focal animals for each session (30–60 min) were chosen at random. Observations on these turtles summed to 560 min.

Temporal data for segments of precocious courtship performed by these turtles were extracted using several min of super-8 film at 18 frames/s. Similar data were collected for a single adult male *Pseudemys nelsoni* maintained with an adult female *P. nelsoni* and three adult *P. floridana* in conditions similar to those described above.

During the observation periods, precocious courtship behaviour occurred in bouts. Because the behaviour did not occur randomly in time and the true variance of the rate is unknown, one cannot use χ^2 or G tests to test if differences exist in the frequency of the behaviour among individuals or species. For behaviours that occur in bouts rather than at random, a true null hypothesis is likely to be rejected more frequently than the stated α value (see KRAMER & SCHMIDHAMMER 1992 for a discussion of this problem). However, some differences

between individuals and species were so great that it seems valuable to present and comment upon them, even without being able to attach specific p-values to the differences. We use a G test to test if breathing frequency following displays differs from breathing frequency at other times. Because, in general, breathing occurs at regular intervals and not at random, this makes the test more conservative, i.e. rejection of a true null hypothesis is less likely than the stated α value (KRAMER & SCHMIDHAMMER 1992; p. 835).

Results

Precocious Courtship

Precocious sexual behaviour occurred when one individual approached another and displayed (titillated) one or more times. Fig. 1 is a scattergram that illustrates, for 25 displays given by five individuals, the variation in both the number of vibrations in displays and display duration. Based on these limited data, we did not demonstrate differences between the vibration rate (number of vibrations/duration in s) of the front claws of juvenile *Pseudemys nelsoni* (4.4–10.8 vibrations/s), an adult male (7.0–16.0 vibrations/s), and three displays of a single *P. floridana* juvenile (5.0–6.7 vibrations/s).

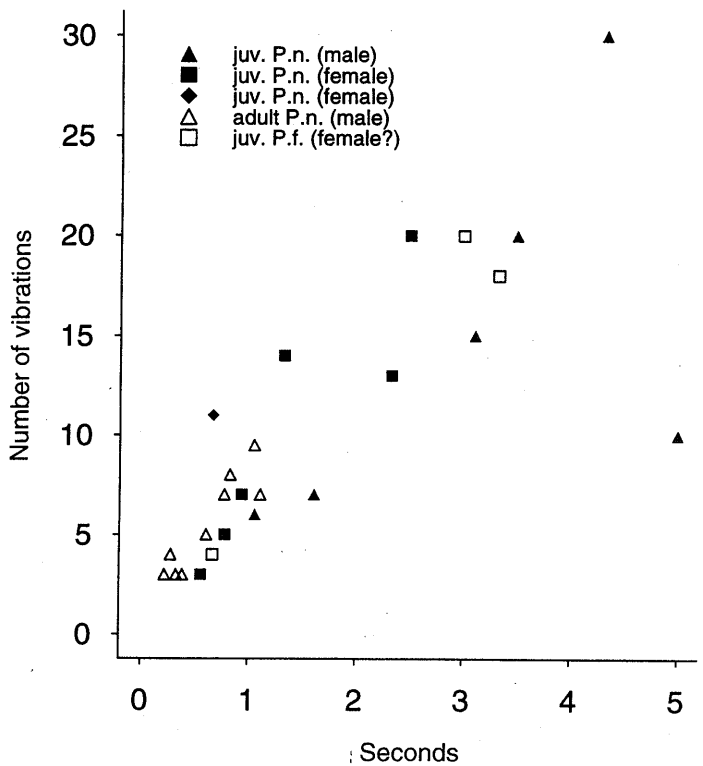

Fig. 1: Frequency of front claw vibrations versus time (s) of *Pseudemys nelsoni* and *P. floridana*, analysed from super-8 film recordings

The response to the displays varied, although not in a systematic way. Often the recipient appeared to ignore the displaying individual, retracted or rubbed its head, or pushed away the displaying animal with a front leg. In these cases, the titillation display terminated when the displaying animal abandoned the recipient (dataset 1, 109 of 213 occasions = 51%). Slightly less often, the recipient appeared to be more disturbed by the display. On 85 occasions (40%), the recipient turned or moved away from the displaying individual. On 18 occasions (8%), the recipient gaped or snapped at an approaching or displaying individual. On one occasion (<1%), a recipient bit the displayer on one of its front feet. Gaping, snapping or biting invariably halted further or incipient displays to the recipient because the displaying animal immediately abandoned the recipient. Furthermore, this recipient would not be approached by the displaying animal again for several min. In general, the individuals reacted similarly regardless of the displayer's identity except for one female *P. nelsoni* juvenile, which usually turned away or left after being displayed to by the male *P. nelsoni* juvenile. Adult female *P. nelsoni* react to a male's display by withdrawing their head, moving it away, or rubbing it with a forefoot. Otherwise, they appear to ignore the male (KRAMER & FRITZ 1989).

Mounts rarely followed displays; only two were seen during the entire period the juveniles were under observation. In both instances, one of the female *P. nelsoni* briefly mounted the male *P. nelsoni* following several bouts of displaying. No attempt at cloacal contact was witnessed. Mounts by adult *P. nelsoni* were also rarely observed (KRAMER & FRITZ 1989).

Part of the energetic appearance of the behaviour was due to the rapid vibration of the forefeet, but most was due to the continuous and, at times, brisk manoeuvring of the displaying animal to maintain its position with respect to the recipient, which was rarely still during displays. The activity of the recipient turtle was possibly a consequence of the displays, which could have exacerbated the manoeuvring requirements of the displaying individual. Overall, the behaviour was at least as vigorous as adult courtship.

The energetic cost of a display was not directly measured. However, using dataset 2, we compared the frequency with which animals surfaced for air within 30 s after displaying with the frequency with which they surfaced for air during other periods (excluding periods with displays) (Table 2). These results indicate that animals surfaced for air more frequently (G test, $p = 0.025$) in the 30-s period following displays than they did during other 30-s periods. Because it is well known for reptiles that increasing sustained activity requires higher oxygen consumption (BENNETT 1982), typically by increasing the ventilation rate, we infer that more energy is required on average for precocious courtship than for the

Table 2: Frequency with which juvenile *Pseudemys nelsoni* surfaced to breathe in 20-s intervals, excluding those in which they displayed

Time interval	Frequency of surfacing: Zero	One or more
Within 30 s after displaying	8	15
Other 30-s intervals	617	442

other activities seen during data collection. Subjectively, precocious courtship appeared to be the most 'energetic' behaviour performed by these animals.

Subjects displayed about once every 10 min in dataset 2. In dataset 1, a display was seen about once every 4 min. This does not adequately summarize precocious courtship frequencies because of the initial choice of observation periods (when interactions were numerous) and the clumped temporal distribution of this behaviour. Generally, displays occurred in bouts lasting 1 min or more and comprised 1–6 individual acts, in each of which the front claws were vibrated several times. Clumping in time is demonstrated statistically by comparing the display frequency from dataset 2 in consecutive 5-min intervals with a Poisson distribution (Table 3).

Ontogeny of Juvenile Courtship Behaviour

The youngest displaying *Pseudemys nelsoni* we observed was wild-caught and about 5 mo old. It displayed briefly to a piece of dried dog food in the water before biting it. CAGLE (1955) observed a much younger (35-d-old) *Pseudemys concinna suwanniensis* displaying to a snail before eating it. One of the laboratory-reared *P. nelsoni* in this study, when about 1 yr old, displayed to a live cricket before eating it. D. JACKSON (in litt.) observed many instances of precocious courtship in *P. nelsoni*, *P. alabamensis*, *P. concinna* and *T. scripta*, starting from 3 wk of age.

Species Differences and Discrimination

Precocious titillation was much more frequent in *Pseudemys nelsoni* juveniles than in the other two species (Table 4). Additionally, *P. nelsoni* juveniles displayed more often to

Table 3: Display frequency. Comparison of display frequency in 5-min periods of juvenile *Pseudemys nelsoni* with expected frequencies from a Poisson distribution, demonstrating that displays occurred in bouts

No. of displays/5 min	Frequency of 5-min periods Observed	Expected
0	93	59.95
1	6	37.47
2	6	11.71
3 or more	7	2.87

Table 4: Total frequency of displays and approaches of each species (*Pseudemys nelsoni*, *P. floridana* and *P. concinna*) from dataset 1

Species	No. individuals	No. approaches	No. displays
P. nelsoni	4	449	213
P. floridana	3	21	1
P. concinna	2	76	2

conspecifics than to heterospecifics (210 vs. 3). This suggests that displaying juvenile *P. nelsoni* can and do recognize and preferentially display to conspecifics.

There were also partner preferences among the four juvenile *Pseudemys nelsoni* (Table 5). Differences were found in the total number of displays given by each animal and the total number of displays received by each animal. Two of the juvenile females directed most of their displays to the juvenile male (Table 5).

The correlation between approaching an individual and displaying to it is 0.83 (an individual may display several times once it approached another) (Table 5). That juveniles selectively approach preferred recipients suggests that they can usually distinguish among potential conspecific recipients from afar before approaching and displaying. However, misidentification may have occasionally occurred, because an individual sometimes approached another, then ignored it and went on to approach a different individual. An alternate interpretation is that some cues are only available at close range. Recognition appeared to be based on sight. This is consistent with results of KRAMER (1989) who trained juvenile *Pseudemys nelsoni* and *P. floridana* to run a T-maze using other caged juveniles as discriminative cues at the choice point.

Comparison of Precocious with Adult Courtship Behaviour

Although clearly identifiable as similar to adult courtship, precocious courtship behaviour of juvenile *Pseudemys nelsoni* differs from adult courtship in several ways. The initiation phase (KRAMER & FRITZ 1989) is cursory or absent, although individuals often sniffed the cloacal or head region briefly prior to, but rarely during, a display. This does not, however, imply that recipients are chosen at random (see above). Adults, depending on species (see below), use only one of two possible displaying orientations towards the partner. In contrast, juveniles of these species appear to use both to varying degrees. The two positions are illustrated in Fig. 2.

The first position (head-to-head) is characteristic of *Chrysemys picta* (TAYLOR 1933), and some species in the genera *Trachemys* (JACKSON & DAVIS 1972b) and *Graptemys* (VOGT 1978); the second position (swim above) is characteristic of all *Pseudemys* species for which courtship has been observed (MARCHAND 1944; JACKSON & DAVIS 1972a; KRAMER & FRITZ 1989). Although positions were not recorded during regular obser-

Table 5: Approaches (A), displays (D), and responses (R) (the recipient turned away or left following a display) for each *Pseudemys nelsoni* to each of the others (read across). See Table 1 for additional information on these animals

	Frequency (approaches, displays, responses)											
	to 1			to 2			to 3			to 4		
Subject	A	D	R	A	D	R	A	D	R	A	D	R
1 (female)				39	16	7	34	17	9	4	1	0
2 (male)	22	5	1	-			72	32	23	38	14	7
3 (female)	22	4	1	59	39	14				34	7	6
4 (female)	21	0	0	61	70	14	14	5	2			

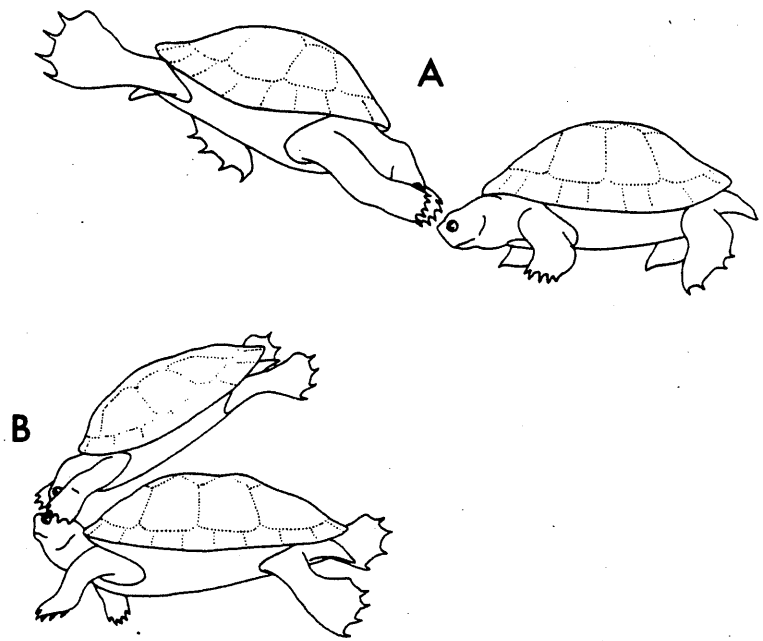

Fig. 2: Positions of displaying juvenile *Pseudemys nelsoni:* A. head-to-head (also characteristic of adult *Trachemys scripta elegans*; B. swim above (characteristic of adult *Pseudemys*)

vations, of the 30 juvenile *P. nelsoni* displays filmed from this period all but two were head-to-head. Data collected by D. JACKSON (in litt.) on *P. nelsoni* corroborate the use of both positions; each position was used about half the time by his juveniles. The second position was used in the four filmed displays of one of the *P. floridana* juveniles.

In contrast to adult females, juvenile *P. nelsoni* females displayed frequently in our observations. For dataset 1, the total number of displays (to all individuals in the aquarium) given by the four *P. nelsoni* juveniles were 34, 52 and 76 (female), and 51 (male).

There were other differences from adult courtship. Juveniles displayed only to turtles on the substrate, whether moving or stationary. Adult males in the field and laboratory displayed only to swimming females (KRAMER & FRITZ 1989; pers. obs.). On occasion, the interaction between two juveniles attracted a third, which started displaying to one of the other two. On one occasion, all four juveniles were clustered together, with at least three displaying. In contrast, adults were not seen to join courting pairs in the field.

Discussion

While differing from the courtship behaviour of adult male *Pseudemys nelsoni* (KRAMER & FRITZ 1989), precocious sexual behaviour shares most of its components with adult courtship and not with other adult or juvenile behaviour patterns. The courtship display of male *Trachemys scripta elegans* appears to involve considerable time and energy (JACKSON

& DAVIS 1972b). Indirect evidence, presented above for *Pseudemys nelsoni*, indicates that precocious courtship behaviour is also energetically costly. In particular, precocious sexual behaviour resembles the swim-above phase (KRAMER & FRITZ 1989) of adult courtship. If the titillation display is used by males to induce female receptivity, the energy expenditure by adult males can be justified by tying it directly to reproductive success. However, if this was the sole function of the display, its presence in both genders of juveniles is paradoxical. The two recorded instances of an adult female *P. nelsoni* displaying (JACKSON 1977) were more similar to the juveniles' displays than those of adult males because this female also displayed from the head-to-head position.

Although the presence of precocious courtship may be enigmatic, the high frequency of these apparently costly displays suggests that this behaviour may have a function. In any event, it seems too complex, ritualized, and frequent to be merely a developing (incipient), precocious behaviour as found, for example, in voles (PELLIS 1993). We first discuss four possible explanations: information gathering, social dominance, artefact of captivity, and consequence of environmental sex determination. We next discuss practice and motor training; both have been proposed as possible functions of play (FAGEN 1981; BYERS & WALKER 1995). There are difficulties with all the above explanations and we conclude by proposing that precocious courtship is a component of rudimentary social play.

Information Gathering

CAGLE (1955) speculated that titillation is a social signal or provides information about novel objects. Results from this study found no evidence in support of CAGLE's second hypothesis. JACKSON & DAVIS (1972b) suggested that in adult courtship the titillation display serves a species recognition function. However, because animals in this study demonstrated selectivity of partner choice prior to displaying and individuals of both sexes displayed, this explanation appears inadequate.

Social Dominance

Based on experimental work and informal observations of juvenile *Chrysemys picta* and *Trachemys scripta*, RIVES (1978) suggested that titillation was aversive to recipients and might serve to establish and maintain social dominance. The goal of his experimental work was to identify factors influencing the expression of precocious courtship when two unfamiliar, wild-caught juveniles first encountered each other. Thus, he did not test his hypothesis. However, observations he made during his experiments agree with ours on two important points: 1. males and females displayed at about the same rates; and 2. conspecifics were the preferred recipients. He adds that, in informal observations of long-term captives, when long mutual titillation episodes (where two animals were simultaneously titillating each other) were observed for a pair of turtles, the smaller of the two almost always quit first. Under this interpretation, mutual titillation episodes are contests and the larger turtle usually wins. We did not observe any mutual titillation episodes by our turtles. On three occasions, two female juvenile *P. nelsoni* simultaneously titillated the juvenile male *P. nelsoni*. These turtles are usually attentive and perhaps attracted to active movements by others. Juveniles often approached other active juveniles, whether they were eating or titillating.

There are three other reasons we believe titillation is unlikely to establish or maintain dominance. Firstly, despite its frequent occurrence and energetic appearance, recipients often appeared to ignore it. Furthermore, a gape or snap by the recipient was sufficient to halt displays. Secondly, while the establishment of dominance may be costly, its maintenance typically involves less costly testing or probing rather than outright challenging. Titillation does not appear to be a good candidate for testing because the recipient's behaviour appeared largely unpredictable from previous interactions and the interactions themselves terminated inconclusively. Thirdly, there were several other behaviour patterns clearly used in aggressive interactions (e.g. snapping, biting, gaping) and aggressors never combined titillation with these. Thus, we found no evidence to support the hypothesis that precocious courtship behaviour is used to establish or maintain dominance.

Artefact of Captivity

Bizarre behaviour patterns, often self-injurious, that may be artefacts of long-term captivity are exhibited by many animals (HEDIGER 1964), although this has not been well documented for reptiles (but see BURGHARDT et al. 1996). If the behaviour is not aberrant, it may be abnormal in other respects, e.g. occurring more or less frequently than in nature. Juvenile *Pseudemys nelsoni* are rarely observed in the field (other than basking) and no underwater field observations are available. Thus, the frequency and nature of naturally occurring interactions, including precocious courtship, are unknown. The juveniles used in this study did not have to forage or travel appreciable distances to bask. Density (i.e. crowding) in the water probably exceeded natural levels by several orders of magnitude. Animals may have had difficulty escaping the attention of others because they could not leave the aquarium. However, although the possibility that precocious courtship is an artefact of captive conditions cannot be eliminated, we think that it is an unlikely explanation for reasons given below.

Firstly, individuals did not appear troubled by their inability to distance themselves from other turtles. To avoid a displaying turtle, an animal usually did not swim away, crawl into a hiding place or retract into its shell. Instead the turtle would turn, or crawl several cm, then resume the behaviour that had been interrupted by the displayer. Further aggressive behaviour (gapes, snaps and bites) was infrequent and invariably halted displays and approaches. Secondly, wild-caught *P. nelsoni*, *P. floridana* and *P. concinna*, as well as captive-reared *P. nelsoni*, were also recorded making precocious courtship displays. RIVES (1978) presented similar results for *Chrysemys picta* and *Trachemys scripta*. Thirdly, 9 mo following the release of laboratory-hatched and reared *P. nelsoni*, one of the female juveniles was recaptured. She was in excellent health and had increased in size. This last point suggests that conditions in captivity were similar enough to conditions in the wild that long-term captivity did not unduly disturb normal development.

Sex Determination

The existence of precocious courtship displays in juvenile females and the occasional adult is interesting from an additional perspective. Many turtles investigated to date, including all genera where precocious courtship has been observed, are now known to have temperature-dependent, not chromosomal-dependent, sex determination (BULL 1980; EWERT et al. 1994). In the absence of detailed knowledge of the physiological, hormonal and behavioural development of turtles, the contribution of environmental sex determination to the behaviour reported here is unresolvable. However, precocious courtship has not been reported for most species of turtles with environmental sex determination. Thus, we believe it unlikely that precocious courtship is merely an artefact of environmentally determined gender. Hormonal assays of turtles at different ages correlated with behaviour might clarify what relationship, if any, exists between gender-specific behaviour patterns and environmental sex determination.

Practice of Social Skills

There may be important social skills that must be learned for males to become reproductively successful. Successful courtship by males may require a delicate adjustment of the courtship display to particular individuals, situations or seasons. This is true in agonistic and sexual behaviour of male rats (PELLIS 1993). In this scenario, those turtles that have been unable to participate in precocious courtship with other animals may be less able to predict their partner's movements, may give inappropriate responses or displays, or may not learn the optimal orientation from which to give the display. It may be advantageous for them to start when young so as to be better prepared when sexual maturity is attained. Practice of social skills has also been suggested as a function of play behaviour (FAGEN 1981).

There is evidence that the stimulus control for precocious courtship shifts with age. The youngest animals display to many small objects while older juveniles and adults display mostly to conspecifics (RIVES 1978). The high frequency of this behaviour among juvenile *P. nelsoni* allows each individual to have many interactions with others, providing substantial opportunities for learning to occur. This explanation, however, fails to account for display behaviour in juvenile females, nor does it explain partner preferences. Although observations of adults are clearly deficient, there is little evidence to suggest that this display is used in contexts other than courtship in nature. The function of the two displays by the adult female in JACKSON's (1977) study remains unclear.

Motor Training

The motor-training hypothesis is highly favoured in discussions of locomotor play, both social and non-social (BYERS & WALKER 1995). Because play is most prominent early in ontogeny and exercise effects are generally transient, these effects of play should not extend into adulthood. Recently, however, BYERS & WALKER (1995) presented evidence suggesting that play behaviour in some juvenile mammals may permanently modify muscle fibre differentiation and cerebellar synapse distribution. We know of no data that might address similar phenomena for precocious courtship in turtles. However, exercise seems to have little effect on endurance in reptiles at any age (BURGHARDT 1984), which discounts this line of reasoning. The changes posited by BYERS & WALKER (1995) for mammals are permanent and unlikely to be induced by behavioural routes other than play. Could the precocious courtship behaviour of juvenile turtles be a means of consolidating, not specific behavioural routines, but the neural (cerebellar) and muscular

substrates necessary for complex negotiation in a three-dimensional world? If so, then this explanation might account for display behaviour in both juvenile male and female turtles.

Precocious Courtship and Play

Precocious courtship in *Pseudemys nelsoni* can be compared with play behaviour, for which demonstrable functions have also proved elusive (FAGEN 1981; MARTIN & CARO 1985; BYERS & WALKER 1995). An adult softshell turtle's interactions with objects appeared to meet all criteria used in labelling similar behaviour as object play in birds and mammals (BURGHARDT et al. 1996). Social behaviour in reptiles has been even less frequently described as playful (BURGHARDT 1984), but it has been advanced as a possible interpretation of the rather indiscriminate headbob displays performed by hatchling fence lizards, *Sceloporus undulatus* (ROGGENBUCK & JENSSEN 1986). Could precocious courtship in turtles be the basis for a type of social play? This has been advocated by PELLIS (1993) for muroid rodents.

Play has been a difficult category of behaviour to define. The structural definition given by BEKOFF & BYERS (1981) is clear and consistent with most others: "Play is all motor activity performed postnatally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and altered temporal sequencing" (p. 300). FAGEN (1981) described five main characteristics of play behaviour and we compare them with precocious courtship in *P. nelsoni* below. In addition, he listed features of the structure and causation of play. Some items on these latter two lists, as FAGEN states, are controversial. Nonetheless, they give an additional basis by which to judge the plausibility of play as a possible explanation for precocious courtship behaviour in *Pseudemys* turtles. Table 6 compares the structures and causes of play from FAGEN (1981) with precocious courtship in turtles. Features of precocious courtship in turtles match all but one item of those lists. The main characteristics of play are compared with precocious courtship in *P. nelsoni* below.

The first main characteristic of play, that behaviour patterns occurring in play are similar, but not identical, to those occurring in a well-defined functional context of adults (or juveniles), clearly applies to precocious courtship in these turtles. For example, the orientation, manoeuvring and titillating behaviour patterns observed during precocious courtship of juvenile *Pseudemys nelsoni* are similar, but not identical, to adult male courtship. The second, that behaviour patterns in play are exaggerated, is difficult to assess with the data collected. The individual motor patterns do not appear to differ from those of adults in the way that the motor patterns of young mammals playing are exaggerated when compared with those motor patterns in 'serious' contexts. There may be differences between adult and precocious courtship in the duration or timing of the various behavioural acts; for the most part, these were not measured. The duration of a bout of titillation does appear, on average, somewhat longer (exaggerated?) in juveniles than in the single adult male measured (Fig. 1). The third characteristic, that "... individual acts are repeated more often in play sequences" (p. 44) is also difficult to assess because the data needed to make detailed comparisons between precocious and adult courtship are not available. The remaining two characteristics, that play sequences tend to be variable and that they lack the normal consummatory behaviour and biological consequences of non-play behaviour,

Table 6: List of structural and causal play behaviour characteristics in Fagen (1981, pp. 45–46). As well as could be determined, all characteristics but one (preceded by *) are features of precocious courtship in *Pseudemys nelsoni*

Structure
1. Play acts having temporal structure may be relatively incomplete, e.g. a movement may be started, but not finished (incomplete execution, serial incompleteness).
2. Acts that involve several parts of the body may lack some components found in non-play (instantaneous incompleteness).
3. Play sequences are relatively brief.
4. Play sequences may be relatively reordered or disrupted.
5. Play sequences show relatively rapid alternation of acts.
6. Play sequences are relatively incomplete.

Causation
1. Play sequences may be interrupted by higher-priority behaviour and fragmented by inclusion of motivationally irrelevant activities.
*2. Play appears to be pleasurable to the performers.
3. Play occurs in a relaxed motivational field.
4. Play patterns are relatively inhibited.
5. Non-specific items, including objects and living or dead organisms, may substitute for a conspecific partner in play.
6. There is a specific motivation to play.
7. Transitions from play to non-play, or mixed forms of play, may occur.
8. Play occurs characteristically in immature animals.
9. Play sequences occur in different situations from non-play sequences that include the same acts, or they occur as a result of different stimuli, including stimuli normally inadequate to elicit these acts.
10. In a given play sequence, the same behaviour may be directed in turn at different stimuli.
11. The patterns of behaviour in play are relatively less dependent on normal stimulus–response relationships.
12. In play, animals return repeatedly to the same stimulus source.

apply to precocious courtship behaviour of these turtles. It should be noted that even many 'good' examples of play do not possess all five characteristics.

PETRANKA & PHILLIPPI (1978) also remarked that the context and stereotypy of precocious courtship in turtles they observed (*Pseudemys concinna* and *P. floridana*) differed greatly from adult courtship. Their juveniles exhibited prolonged interspecific and intra-sexual exchanges and displayed towards inanimate objects. Displays they observed occurred sporadically and were less intense than those of adults. In our study, juvenile displays were as intense as those of adults and occurred frequently.

Precocious courtship and play have been well studied in rodents and comparing this work with our turtle observations is instructive. PELLIS (1993) contrasts precocious sexual behaviour in various small rodents including voles and rats. In voles, juvenile courtship behaviour differs from the courtship of adults only because copulation at the conclusion of the interaction was absent. Rats, employing acts used by adults in sexual interactions,

are clearly playing (e.g. some behavioural elements are added or exaggerated). PELLIS finds no justification for labelling the vole's behaviour as play, preferring to label it immature sexual behaviour or the precocious expression of sex. He also discusses the steps by which play behaviour proper might have arisen from rudimentary play and immature sexual behaviour before that. A characteristic distinguishing the latter two categories is the amount of time juveniles devote to each, with far more time spent by animals in play behaviour. In most mammals, 1–10% of the total time budget is spent in play. This is time and energy that could conceivably be put to other uses, e.g. growth or foraging (FAGEN 1981). In dataset 2, an individual *Pseudemys nelsoni* initiated an act of precocious sexual behaviour on average once every 10 min. This suggests that the amount of time occupied by this behaviour is within the range of mammalian play.

If the turtles were rodents, where would the precocious courtship behaviour by *Pseudemys* turtles fit in the PELLIS (1993) scheme? Because precocious courtship behaviour was rarely observed in two of the species on which we made observations, it might be best characterized as immature sexual behaviour for them. However, precocious courtship behaviour occurred frequently in *P. nelsoni* and differed in obvious ways from adult courtship behaviour, as reported above. This suggests that it might be characterized as part of rudimentary or true play in the PELLIS model.

Similar arguments have been made by BURGHARDT et al. (1996) for an adult soft-shell turtle's (*Trionyx triunguis*) interactions with various objects as object play. As with the juvenile *Pseudemys nelsoni* of this study, had comparable behaviours been observed for mammals, play behaviour would have been an obvious interpretation.

One puzzling aspect of precocious courtship in *Pseudemys nelsoni* is the passive role of the recipient. In many reported accounts of social play, all or most individuals actively participate. The passive role of the participant suggests a connection between object and social play. It is not always easy or even useful to distinguish between the two. For example, a young kitten playing with its mother's tail might be labelled object play unless the mother purposely twitched her tail to retain the kitten's attention. If one observed the mother twitching her tail, one might erroneously conclude that the mother was irritated and simply moving her tail away. Precocious courtship in *P. nelsoni* may be in a rudimentary stage where juveniles may prefer displaying to others rather than inanimate objects, but where more complex interaction involving active participation of both individuals has not evolved. It is worth noting that in mammals with well-developed social play (e.g. humans), social play is typically the last form of play to be expressed ontogenetically. Solitary object play is often the first, and there are several stages (e.g. parallel play) passed through to get from one to another (RUBIN et al. 1983; PELLEGRINI & BOYD 1993).

Reptile Play

In recent years, play has been thought to be virtually non-existent in reptiles (BURGHARDT 1984). Physiological, developmental and life history factors have been advanced to explain this apparent discontinuity (BURGHARDT 1984, 1988). One of these factors is that reptiles, lacking endothermy, do not appear to possess the physiological scope to engage in sustained vigorous play activity. A second factor is that most reptiles, and all turtles, lack parental care; thus neonates need to engage in the full panoply of life-sustaining

activities on their own without a protected juvenile period. In addition, perhaps as a consequence of the lack of extensive parent–offspring communication, reptiles are not capable of changing their facial expression, at least not in a way that is apparent to people. Thus indicators of play (to humans), such as the 'play face' typical of canid or primate play, are not evident. This last point has also made it difficult to distinguish play in birds from other behaviour (FICKEN 1977).

That play may be too energetically costly to turtles is contradicted by the data presented above, in that apparently functionless and vigorous behaviour is engaged in with great frequency. Although most reptiles may not be capable of large increases in basal metabolic rate, *Trachemys scripta*, a related species, is capable of aerobically supporting a 24-fold increase in basal metabolic rate at 30 °C, a rate comparable to that of active lizard species (GATTEN 1974). Furthermore, the aquatic medium allows locomotion and manoeuvring at a far lower energetic cost than similar behaviour patterns on land (SCHMIDT-NIELSEN 1972), and it has been predicted that any ectothermic reptile play would be most likely to occur in aqueous environments (BURGHARDT 1984, 1988). This prediction has also been supported in observations on object play in an aquatic turtle (BURGHARDT et al. 1996).

There are several reasons that turtles (and perhaps crocodilians) might be expected to be the most likely reptile to have evolved play or play-like behaviour. Many turtles are aquatic, thus costs of locomotion are low. Most are tolerant of conspecifics and are often found in aggregations (BURY 1979), allowing ample opportunity for interactions to occur. The social system of *P. nelsoni* (and perhaps other species) appears complex (KRAMER 1986) and may be mediated through individual recognition (KRAMER 1989). Turtles are considered to be 'intelligent', suggested by, among other things, the consistent bias of comparative psychologists to use them rather than other reptiles. About 50% of the studies cited by BURGHARDT (1977) in a review of the reptilian learning literature used Chelonians (less than 5% of all reptiles). One may argue that reptiles, despite their other achievements, do not possess a sufficiently complex brain to support a behaviour as complex as play. Of all extant reptiles, the turtle brain is arguably the 'closest' to that of mammals (BUTLER & HODOS 1996) and the turtle brain has homologues of all major mammalian brain structures. Finally, turtles are both long-lived and take many years to reach sexual maturity, which would give any of the proposed long-range benefits of play sufficient time to accrue (FAGEN 1981). Some of these arguments may also apply to crocodilians, for which anecdotal reports of object or locomotor play are rare but available (LAZELL & SPITZER 1977). BURGHARDT (1984, 1988) has developed the surplus resource theory as a framework for understanding the evolution of play. This model is considered in some detail by BURGHARDT et al. (1996) when interpreting the behaviour of a Nile soft-shelled turtle's interactions with objects. Of relevance to this discussion are two salient predictions from the model: 1. captive conditions may be insufficiently stimulating for optimal arousal, thus animals may increase time spent in play or other activities aimed at increasing arousal levels; and 2. captive animals are liberated from expending energy for food procurement and other physical needs, thus this energy is available for other activities. Under these circumstances, one often sees increased play in mammals, so it should not be surprising to find reptiles responding in a similar manner. In this study, social rather than object play may have been further facilitated by the Spartan environment; animals may have engaged

in social interactions to increase arousal levels. CAINE & O'BOYLE (1992) found that frequencies of various types of play in tamarins were distorted and play sequences were less varied when animals played on broad, flat, horizontal surfaces, unnatural for an arboreal species. Social play is believed more prominent in mammals with a complex social system (although this putative relationship is far from established: BURGHARDT 1984); this may also be true for turtles.

Ethologists tend to focus on the more easily observable or striking behaviour patterns, such as the titillation display in these pond turtles. It is possible that titillation may be used in a variety of social contexts, which we are confusing because we are not attentive to more subtle behaviour occurring synchronously or expressed in modes outside of our direct sensory abilities (e.g. chemically). Nevertheless, the results reported here are consistent with the hypothesis that, in juvenile *P. nelsoni*, courtship behaviour has been incorporated in a rudimentary form of play. As untidy as it may seem, if this behaviour is part of rudimentary play, not finding an obvious benefit for it is not surprising, nor is the performance of it by both sexes. Given the elegant model for the stages of evolution of precocial courtship to social play in rodents developed by PELLIS (1993), it would be useful to carry out more observations of social interactions of a wide number of aquatic emydid turtles both in captivity and in the field.

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