Courtship behaviour of American Alligators *Alligator mississippiensis*

KENT A. VLIET, Ph.D.[1]

Courtship behaviour was observed in a captive group of about 150 individually-marked, adult American alligators *Alligator mississippiensis* over a three year period. Analysis concentrated on static and sequential analyses of behavioural acts, seasonal and temporal periodicity in courtship interactions, and the effects of size and gender as they relate to courtship behaviours. Behaviours represent four functional groups: those of introduction; movement and orientation; tactile interactions; and behaviours associated with mounting. All of the acts described were performed by both sexes. Tactile interactions consisted of contacts made almost entirely to the head and neck of the partner. Significant sequential associations were primarily between adjacent tactile zones. Courtship was typically observed from early April through the end of May in north Florida. Activity was greatest in early morning and late afternoon. Interactions averaged 319 seconds in length, 68 seconds before mounting. Mounts averaged 113 seconds in length. Pre-mounting courtship and mounting lengths were not significantly correlated. About 90% of all males and 75% of females courted in a season. The estimated active season length for males was approximately twice as long as that of females and was positively correlated with body length in both sexes. Courtship-like interactions between males were commonly observed.

INTRODUCTION

THE excellent pioneering work of Leslie Garrick and Jeffrey Lang (Garrick and Lang 1977a; Garrick *et al.* 1978) provided us with the first detailed analyses of crocodilian social behaviour. These investigators not only systematically described social signals and associated behaviours in adult American alligators (Garrick 1974, 1975; Garrick and Lang 1975, 1977b) but also provided valuable comparative studies of the American crocodile (Lang 1976), and incorporated the existing knowledge of the Nile crocodile into a synthesis of crocodilian behaviour (Garrick and Lang 1977a). In all three species, these studies noted complex patterns of social communication involving visual, auditory, and tactile signals and provided objective evidence of the highly advanced nature of these animals. The results are especially remarkable for the similarity of the behaviours catalogued in all three species.

Alligator courtship

Garrick and Lang (1975, 1977b) and Garrick *et al.* (1978) described in detail the courtship activities of the captive American alligators they studied in south-central Florida. These studies showed that courtship consists of a complex and variable sequence of tactile, visual, auditory, and possibly olfactory cues. After attraction and initial approach, alligators engage in an extended set of pre-copulatory manoeuvres involving mutual snout contact and attempts at pressing the heads of each partner under water. Both animals make "cough-like" vocalizations during this phase of courtship. One animal will submerge underneath the head of the other and blow streams of bubbles up around the latter. This is described as a form of subtle stimulation. Both animals repeatedly mount and ride each other. At some point in this mounting, the male rolls to the side of the female and mates. Dominant males were able to court and mate more frequently than were subordinant males. Females approached these males to initiate courtship. In these studies, all behavioural acts described for the American alligator were shared by both sexes. The authors also noted that it is rare to observe a complete courtship sequence leading to copulation in the American alligator.

Alligator courtship is not easily observed in the wild. Few accounts of wild alligator behaviour make any mention of courting behaviours. Fogarty (1974) mentioned "vigorous swimming" by both sexes prior to mounting but made no note of any pre-mounting contact between the animals. Silverstone (1972) observed courtship once between two wild alligators near Fort Pierce, Florida. He was apparently able to see the pair clearly enough to note approaches, contacts and mounting in these animals. Detailed observations of these behaviours, however, have been made only in the past three decades by study of animals primarily under captive conditions

[1]University of Florida, Department of Zoology, Gainesville, Florida, USA.

Pages 383–408 *in* CROCODILIAN BIOLOGY AND EVOLUTION ed by Gordon C. Grigg, Frank Seebacher and Craig E. Franklin. Surrey Beatty & Sons, Chipping Norton. 2000.

(Joanen and McNease 1971; Garrick and Lang 1977a; Garrick *et al.* 1978).

The study described herein utilized a large population of individually marked animals. By initiating this study, I hoped to corroborate and expand the findings of Garrick and Lang in a larger captive population of alligators. In this chapter I will quantify courtship behaviour in the American alligator, including such aspects as the number of courtship interactions or the number of mountings by an individual in a season, or if males have more partners in a season than do females. I also define behavioural acts and analyse sequences of acts during courtship, paying special attention to tactile behaviours. I will also describe temporal patterns of courtship, such as the length of time partners participate in courtship before mounting and the relationship of pre-mounting interactions to the length a pair remains mounted. Lastly, I will objectively analyse the effects of gender and of size on courting activity.

MATERIALS AND METHODS

Alligator courtship data were collected over a three year period at the St Augustine Alligator Farm and Zoological Park, St Augustine, Florida (29°53'N, 81°18'W). The alligator farm is a commercial tourist attraction that maintains a captive population of several hundred alligators. The study population consisted of captive-born, adult (i.e., >185 cm total length) American alligators, of unknown age. The alligators were maintained primarily on a diet of chicken, with occasional supplements of fish and red meat.

Study population

The total number of study animals and the sex ratio of the study population changed between seasons. Through the course of the study, males averaged about 260–270 cm total length. Females averaged between 220 and 230 cm in length. During the 1981 study season, the lake contained 168 alligators in a ratio of 1.15 males per female. Several males exceeded 310 cm in length. By the beginning of the 1982 study season, there was a shift in the sex ratio to 0.92 males per female for 144 study animals, due to removal of large males and introduction of new animals. The largest male in the 1982 population was 298 cm in total length. Further removal of animals prior to the 1983 season reduced the population size to only 128 alligators with a sex ratio of 1.06 males per female. Complete description of the size class distribution of the study population is given in Vliet (1987).

Prior to the three study seasons, each alligator in the study population was captured and measured to the nearest centimeter along the dorsal surface from the snout to the tip of the tail. Gender was determined by cloacal probing. Alligators were permanently marked with numbered metal, self-piercing tags in the webbing of a hind foot and visually marked by large, numbered plastic cattle ear tags, affixed to one of the anterior-most single caudal scutes on the tail.

Study site

The study site was a small lake with a surface area of approximately ¼ hectare, surrounded by another ⁴⁄₁₀ hectare of enclosed land surface. Fresh water input into the lake was provided by a deep ground well and runoff from other wells on the alligator farm. The well water inflow remained relatively constant year-round at about 22°C. Vegetation surrounding the lake consisted primarily of southern live oak *Quercus virginiana,* southern magnolia *Magnolia grandiflora,* and cabbage palms *Sabal palmetto,* over a brush of southern red cedar *Juniperus silicicola,* yaupon *Ilex vomitoria,* and saw palmetto *Serenoa repens.*

Logistically, the lake is ideal for behavioural observations of alligators as it is traversed by a large, wooden boardwalk allowing easy movement and close observation of most of the study area. Additionally, the alligators are habituated to the continual presence of humans on the boardwalk and appear to behave quite normally when humans are present.

Study methods

Study periods

Behaviour was observed and recorded for three courtship seasons from 1981 to 1983. Regular observations began in the first or second week of April and extended into the middle of June. These periods encompassed the whole of the courtship season and extended up to the time of nesting and egg laying. Observations were made primarily during daylight hours from first light intermittently to dark, but were concentrated at those morning and evening hours when courtship activity was at its peak.

Data collection

Data on courtship and other social behaviours of alligators, collected by Dr Walter Auffenberg at the St Augustine Alligator Farm in the spring of 1980, were used to compile a catalogue of behavioural acts. The acts in this catalogue were mutually exclusive and exhaustive in the sense of Altmann (1965) and Sackett (1978). Observations of alligator courtship behaviours were made *ad libitum* (Altmann 1974) and recorded as concurrent act dyads, that is, pairs of simultaneous observable motor acts between the two courting partners. Only courtships observed from initiation (i.e., first contact) were recorded. Data collection continued until the participants ceased interacting for more than 5 minutes, separated and departed from one another, or until the interaction was disturbed by other alligators. In the majority of courtships recorded, behaviours were timed to the nearest second. With the exception of the length of mounting behaviours and submergence due to pressing, the duration of behaviours was not recorded. Data collection was thus event-based rather than time-based (Bakeman and Gottman 1986).

Most observations were made from the boardwalk over the lake, usually from four to 15 meters from the alligators. Binoculars (8 × 20) were used opportunistically to view greater detail and to ascertain identification numbers. All pertinent information was recorded with microcassette tape recorders for later transcription. Visual records of courtship and other social behaviours were made with 35 mm film, 8 mm movie film, and ½" black and white video recordings. Recordings of vocalizations and other audible behaviours were made with a Nagra IV recorder and a Sennheiser shotgun microphone. Sound spectrographs of auditory signals were produced with a Kay Elemetrics Sona-Graph Model 7029A (see Lehner 1979 for a description of this device and the interpretation of sound spectrographs).

Data analysis

The analysis concentrated on static and sequential analyses of behavioural acts in courtship, seasonal and temporal periodicity in courtship interactions, and the effects of size and gender as they relate to courtship behaviours.

Courtship data were encoded as a series of concurrent act dyads. Such encoding allowed behaviours to occur simultaneously although two behaviours by one individual could not be initiated simultaneously. For the purposes of this study, courtships were defined as all interactions leading to mounting, or tactile interactions of at least 15 recorded act dyads. In interactions among more than two courting alligators, courtship data were reduced to paired interactions before the data were encoded. Data from each study season were divided into weekly groups for analysis of trends in courtship activity.

Identification of sequences of acts used in alligator courtship was made using a technique called "lag sequential analysis" developed primarily by Sackett (1978, 1979). The technique is basically a stochastic analysis, comparing the observed values of behaviours separated by a certain lag, in transition matrices, with expected lag probabilities and testing, with the binomial test, to see if one behaviour follows another more often than expected by chance. The number of lags is the number of behavioural acts or time units separating the behaviours being associated. The technique relies solely on conditional probabilities of the associations between behaviours. In this study, only single-lag associations were computed, that is, only associations between a behaviour and the act that immediately preceded or immediately followed it. Details of this technique and the calculation of expected probabilities are given in Vliet (1987).

Although the catalogue developed for this study represents a mutually exclusive and exhaustive list of the behavioural acts involved in alligator courtship, some acts are not independent of one another. For instance, the lateral *roll* is necessary for tail searching to occur and thus the behavioural act *tail search* is a combination of lateral roll and tail-searching, thus making this category mutually exclusive (Gottman and Bakeman 1979). This property of mutual exclusivity and completeness is essential for proper interpretation of lag-sequential analysis (Gottman and Bakeman 1979).

A large series of transition matrices were constructed for purposes of sequential analysis. Lag counts are made for each recorded courtship and then summed in a transition matrix as a quantification of preceding behavioural acts to following acts. Acts of interest, either tactile interactions or behaviours of orientation and movement, were highlighted in the matrix while all remaining acts were lumped into broader categories. For each of the three study seasons, up to ten transition matrices were constructed. All of the transition matrices compiled in this study are shown in Vliet (1987). The different types of matrices were calculated with dyadic pair associations for entire courtships, emphasized either tactile or movement/orientation behaviours, and represented either intraindividual sequences (acts performed in order by one individual on the partner) or interindividual interactions (act performed by one alligator and the responding act of the other partner). For intraindividual sequence analyses, only those behavioural act associations that were highly significant ($p < 0.001$) in data from at least two of the three study seasons are represented in the figures. For the interindividual comparisons, cells significant at the $p < 0.05$ level in at least one study season are discussed. For a full discussion of the construction of these transition matrices, their analysis and the statistical assumptions underlying their use, see Vliet (1987).

The active courtship season for each alligator in the study population was estimated by defining the courtship season as the time between the first and last days for which that particular animal was observed in courtship or mounting activities. Plots were then created by summing, for each day, the total number of males and females with active seasons included on that day.

Student t-test scores were used to test changes in various courtship parameters by week through each season as well as patterns in courtship data based on size of the alligator. Unpaired t-tests were used to analyse differences between sexes in season length, number of courtship interactions, and number of courting partners. Interrelationships between gender, tactile behaviours and act modifiers were tested with a 3-way analysis of variance.

RESULTS

Study periods totalled 870 hours of observation from which recorded data were used in the analysis of courtship behaviour. Data were collected on a total of 912 sequences observed from the initiation of the interaction. These included observations on 680 interactions in which the identity of both animals was known. In addition to the courtship data, data on 3 944 mountings were recorded.

General description of alligator courtship

Following introductory behaviours, alligator courtship consists primarily of touching and pressing the head and neck of each partner. Most of these behaviours are performed from a face-off orientation, one in which the heads of the two partners are parallel but opposite to one another. Following tactile behaviours, one animal presses and mounts the other. Therefore, it is convenient to group the behavioural acts involved in alligator courtship into four functional categories: behaviours related to the *introduction* of partners; behaviours of *orientation and movement;* the *tactile interactions* of the courting pair, including pressing and other physical contest behaviours; and behaviours associated with *mounting*. These functional groups are not necessarily sequential in alligator courtship as acts from different categories are often intermixed. All acts involved in alligator courtship, including tail searching and apparent copulatory movements, are shared by both sexes.

Introductory behaviours

Alligator courtship is instigated by one animal swimming to another and either initiating tactile interactions or remaining motionless until the second animal begins interactions. Visual communication is very important during the introductory phase of courtship. Alligators communicate visually by means of the relative amount and posture of the head and body exposed above the surface of the water. As an alligator intent on courtship approaches another, it must communicate its intentions to the potential partner. Typically, this involves the former swimming forward quite slowly toward the latter and positioning its body very low in the water, with only the nostrils, eyes and cranial table exposed (Fig. 1A). The very low body profile above the water surface assumed by an approaching animal seems to be perceived as a non-aggressive signal by the second alligator. The latter often rises noticeably in the water as the former draws near (Fig. 1B), exposing the snout and the lateral surfaces of the head. If it is unreceptive to the former's approach, the latter rises further out of the water, indicating possible stress or aggression, or turns away.

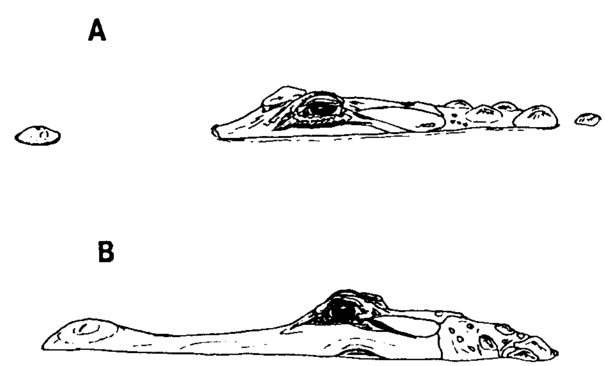

Fig. 1. Head profiles of alligators in courtship. A) A low profile often assumed by an alligator as it approaches another during initiation of courtship; B) head profile assumed by an alligator being approached by another.

A characteristic vocalization, a soft flutter, is often made by one or both of the alligators during the introductory phase or during the following tactile interaction phase of courtship. The flutter may be produced by an animal as it approaches another or as it is being approached. The fluttering signal is made in short bursts and produces ripples in the water surrounding the head of the alligator. A sound spectrograph of this auditory signal (Fig. 2) reveals a very low frequency signal, predominantly below 50 Hz with little signal recognizable above 0.1 kHz. The flutter is probably produced by forcing air from the lungs over the fleshy edge of the epiglottis. In close observation, it is apparent that the flutter is perceived tactilely by the second animal when they are in contact. It is difficult to hear by a human observer at a distance of greater than 10 meters. No discernible reaction to this signal has been observed.

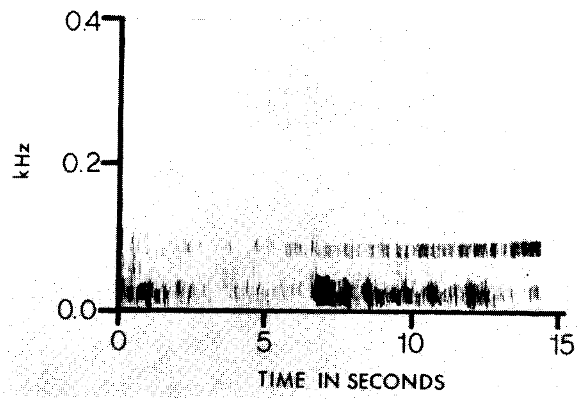

Fig. 2. Sound spectrograph of "flutter" produced by #009, a 279 cm male, as he approached #265, a 254 cm female, in courtship on June 5, 1982.

Introductory behaviours may include the initiating animal blocking the progress of a moving alligator. Courtship may also be initiated by an alligator swimming parallel (Fig. 3A) to another, eventually overtaking the second. This persistence may stimulate the latter to slow or stop, and then begin courtship.

Alligators are frequently attracted to one another by social displays, especially bellowing vocalizations (Vliet 1989). During the courtship season, alligators move toward bellowing animals of the opposite sex. Introduction and courtship may follow though most of the interactions observed during the course of this study were not associated with periods of bellowing choruses. Females occasionally approach males following the males' performance of head-slap displays, an assertion display commonly produced by alligators (Garrick and Lang 1975; Vliet 1989), as well.

Orientation and movement

Alligators entering into courtship interactions assume a characteristic orientation that I refer to as a "face-off" (Fig. 3B), in which their heads are parallel but opposite to one another. From this position, tactile contacts are made by turning the head or rotating the body (Fig. 3C). The pair repeatedly return to the face-off orientation throughout the tactile phases of courtship. This is a strong indication that alligator courtship is a co-operative procedure, with both animals performing acts that help maintain the interaction. Alligators move into a face-off on the opposite side by backing and switching, turning and circling, or submerging and passing under the chin of the partner.

In courtship, a pair of alligators is rarely active simultaneously. Rather, one animal actively courts the other for some time and then the other becomes active. As a result, most often one animal remains still while the other is performing the active part of the interaction. The behavioural act *still* is thus by far the most common act recorded in courtships. This act of doing nothing is an important element in stimulating and perpetuating courtship behaviours by the active animal. Non-receptive animals typically submerge or move away rather than remaining still.

Alligators, especially females, frequently submerge under water during courtship. The partner typically remains still until the submerged animal resurfaces. This behaviour allows an alligator to control the pace of a courtship encounter. Alligators also appear to submerge voluntarily and rise under the chin of the partner, as if to invite pressing behaviours. This stimulates the partner into further courtship.

Tactile interactions

Alligator courtship preceding mounting consists primarily of tactile interactions between the partners. Garrick and Lang (1975) referred to this stage as "contact-greeting." Tactile acts are most commonly initiated by the approaching animal. If the recipient is receptive, mutual contact occurs. Tactile interactions include touches, bumps, and rubs made almost entirely to the head and neck of the partner. Contacts are usually discreet acts, with the performer moving back and then forward again for the next contact. Contacts may also be made by rubbing from one specific point to another. These contacts are usually made with the anterior-most part of the premaxillary but, if the animal rides up on to the snout or the roof of the cranium (cranial table) of the other, contact is made with the lower surface of the jaw. If an alligator approaches another head-on, the premaxillary is often the first area touched. If the approach is made from the side, alligators frequently make contact at the articular region of the lower jaw as the site of first contact. In active bouts of

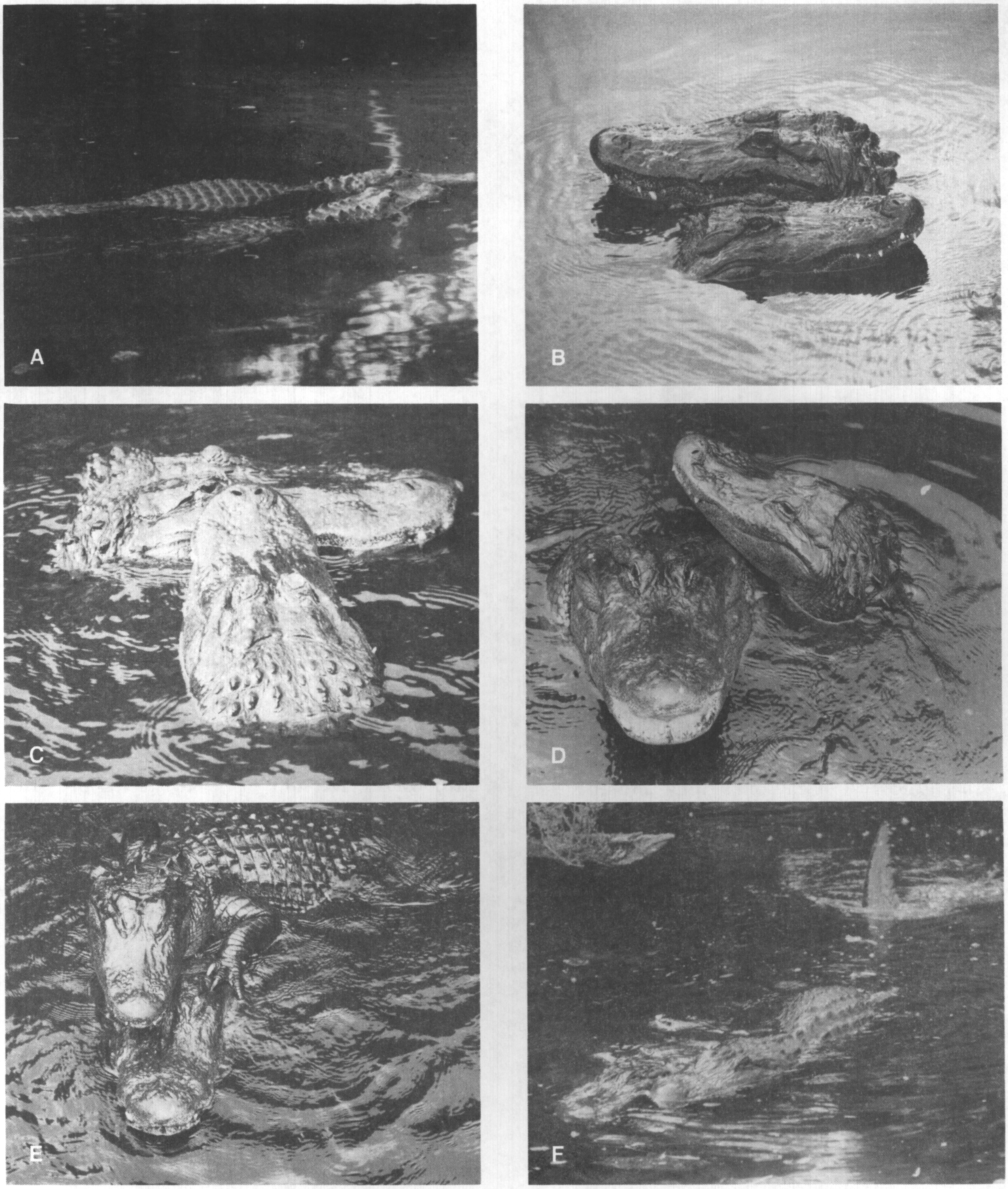

Fig. 3. Elements of courtship behaviour of the American Alligator. A) Alligator (below) swimming parallel with a potential courting partner; B) male (above) and female in face-off orientation C) tactile interactions in courtship — lower animal contacting *below the eye* of other; D) pressing behaviour in courtship — female (above) snout pressing on other; E) female mounting male during courtship. F) male mounted on female.

courtship, alligators will rub or chin back and forth over the head and neck of a partner. Tactile interactions, in association with the pressing behaviours described below, can continue for long periods of time. In extreme cases, alligators may interact tactilely for up to four hours without mounting or attempting to mate.

Pressing Behaviours. Pressing behaviours are a more vigorous form of the tactile interactions. Presses occur when a courting alligator rises up on the dorsal surface of a tactile zone of another, usually the snout cranial table (Fig. 3D), or nuchal scales, and attempts to press the other under the water surface. Presses may be visibly resisted. Thus, pressing interactions constitute a form of physical contest between the two courting individuals. Intense courtship interactions involve repeated attempts at pressing, as well as pushing laterally by one partner on another. Occasionally, both alligators forcibly push the other during face-offs. This results either in the pair circling one another while maintaining the face-off or the pair's heads rising out of the water in an act called "jaw fencing" (see Fig. 5B).

If one courting partner successfully presses another underwater, it may attempt to keep the latter from resurfacing by straddling over the head of or mounting fully on the submerged animal. The submerged animal usually backs or turns out from under the former and rises to the surface. Alligators are frequently held under water for periods of up to five minutes although presses average less than 30 seconds (27.8 sec. in 1983, N = 200). Being pressed under often seems to stimulate an alligator into further courtship, rather than diminishing its interest. Both animals usually move directly back into a face-off to continue courtship.

Mounting

Following pressing behaviours, one alligator mounts another by lifting one forelimb over and pulling itself into a dorsal recumbency over the other. Pressing behaviours are generally continued following mounting. From its overlying position, the upper animal is often able to press the lower under water and prevent it from surfacing for several minutes. If the lower animal does surface, it is often quickly and deliberately pressed under water again. Mounted alligators often move forward continuously. Pressing appears to cause the mounted animal to keep moving. This may act to tire the animal and make it more responsive to mating. However, if an alligator is moving forward too rapidly, copulation is not possible.

Female alligators often mount males during courtship (Fig. 3E). This often seems to stimulate the male into further courtship with the female. Mounted females perform all of the acts males do, occasionally rolling and tail searching and rarely even getting the tail underneath that of the male. There is no evidence that copulation took place while females were mounted on males.

If the lower animal is relatively still and is receptive, copulation may take place. Embracing the female with his forelegs and balancing his weight with a hindlimb, the male slides to a lateral surface of the female and rotates his tail until it is arched under that of the female (Fig. 3F). When the male arches his back and brings his tail forward, apposition of the cloacae is accomplished and copulation can occur. A receptive female will arch her tail dorsally, apparently assisting the male in placing his tail underneath hers. Presses on the head of the female by the male also appear to cause the female's tail to be raised. As noted elsewhere (Garrick and Lang 1977a; Vliet 1986), copulation is very difficult to detect in alligators. It was thus impossible to take accurate measures of the lengths of copulations during the course of this study. Copulation seemed to be quite short, usually less than 30 seconds.

Quantitative description of alligator courtship

Catalogue of behavioural acts

The behavioural act catalogue developed in association with this study consisted of a total of 49 acts directly related to courtship interactions (Table 1). As one specific goal in this analysis of alligator courtship was to obtain an understanding of the tactile behaviours in courtship, 18 acts in the catalogue (1–18) consist of specific areas of the body, I referred to as "tactile zones" (Fig. 4), that are contacted during tactile interactions. The "act" is the action of one animal contacting a particular tactile zone

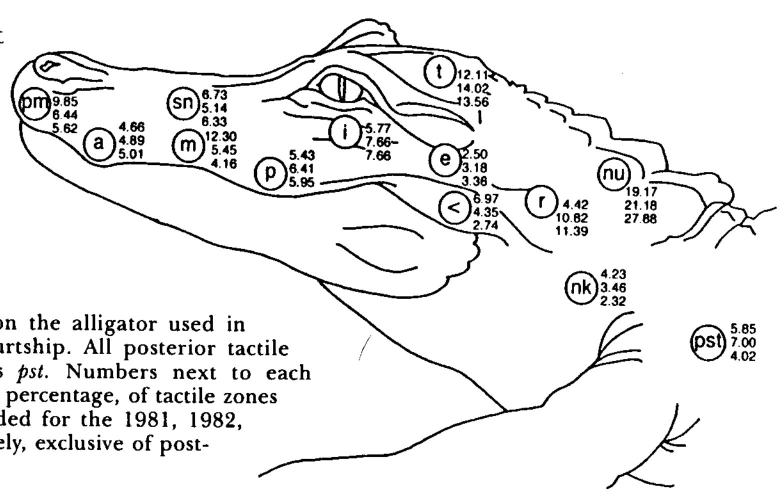

Fig. 4. Locations of the 13 tactile zones on the alligator used in recording tactile contacts during courtship. All posterior tactile zones are lumped together here as *pst*. Numbers next to each represent the relative frequencies, as a percentage, of tactile zones contacted during all courtships recorded for the 1981, 1982, and 1983 courtship seasons, respectively, exclusive of post-mounting contacts.

Table 1. The catalogue of behavioural acts defined for this study, including the letters used to record these acts and the modifiers appropriate for each. Modifiers associated with many of these acts are indicated. See the text for a definition of these modifiers.

(1) *Premaxillary* [pm] — the tip of the snout. Modified by [psh] and [pr].
(2) *Anterior maxillary* [a] — the anterior-most portion of the maxillary region, encompassing the first convex area of the toothrow. Modified by [psh].
(3) *Mid-maxillary* [m] — the center portion of the maxillary, the concave part of the maxillary toothrow. Modified by [psh] and [pr].
(4) *Posterior maxillary* [p] — the remaining portion of maxillary, the area around the second convex portion of the toothrow. Modified by [psh] and [pr].
(5) *Below the eye* [i] — represents touches to the jugal bone below the eye. Modified by [psh], [pr], [pru], and [ch].
(6) *Below the ear* [e] — below the external ear flap. Modified by [psh], [pr], and [ch].
(7) *Angle of the jaw* [ang] — the fleshy area over the articulation of the jaws. Modified by [psh] and [pr]. Represented as [<] in Figure 4.
(8) *Articular* [r] — includes touches to the angular process of the lower jaw. Modified by [psh], [pr], and [ch].
(9) *Neck* [nk] — the lateral surface of the neck. Modified by [psh] and [pr].
(10) *Snout* [sn] — the dorsal surface of the snout including all touches anterior to the eyes. Modified by [pr], [pru], and [ch].
(11) *Cranial table* [t] — the bony plate composing the dorsal surface of the cranium. Modified by [pr], [pru], and [ch].
(12) *Nuchal scales* [nu] — dorsal surface of neck. Modified by [pr], [pru], [ch], and [psh].
(13) *Dorsum* [dor] — the dorsal surface of the torso. Modified by [ch], [pr], and [pru]. Included within [pst] in Figure 4.
(14) *Forelimb* [arm] — any touch to the shoulder or the anterior appendage. Modified by [psh]. Included within [pst] in Figure 4.
(15) *Side* [side] — the entire lateral surface of the torso. Modified by [psh]. Included within [pst] in Figure 4.
(16) *Hindlimb* [leg] — the posterior appendage. Included within [pst] in Figure 4.
(17) *Pelvis* [pel] — the dorsal area between the hindlimb insertions. Modified by [pr], [psh], and [ch]. Included within [pst] in Figure 4.
(18) *Tail* [tail] — any area along the length of the tail, posterior to pelvis. Modified by [ch]. Included within [pst] in Figure 4.
(19) *Still* [st] — remaining still or do nothing. This was recorded as a behavioural act in the sense of Hazlett and Bossert (1965).
(20) *Forward* [for] — moving forward or moving toward another animal.
(21) *Back* [bk] — backing away from another animal.
(22) *From* [from] — moving away from another.
(23) *To* [to] — moving back to another.
(24) *Follow* [fol] — moving toward an animal that is moving away.
(25) *Directed swim* [dir] — one alligator forcing another to swim in a certain direction.
(26) *Away* [away] — leaving an interaction.
(27) *Face-off* [fo] — a very common orientation in which the heads of both animals are parallel but opposite to one another (Fig. 5A). Modified by [psh] and [cir].
(28) *Sixty-nine* [six] — a face-off orientation to the full body length of the animals. Modified by [cir].
(29) *Jaw fencing* [jf] — in vigorous pushing by both animals during a face-off, the heads of both animals rise up out of the water (Fig. 5B).
(30) *Switch* [sw] — backing from a face-off and then moving forward into a face-off on the other side (Fig. 5C).
(31) *Circle* [cir] — turning and rotating into a face-off on the other side (Fig. 5D).
(32) *Pivot* [piv] — using a tactile zone, most usually the pre-maxillary, on the other animals' head as a fulcrum to pivot into a face-off.
(33) *Submerge* [sub] — submerge underwater.
(34) *Under chin* [uc] — following submerge, moving forward underneath the chin of the other animal.
(35) *Surfacing* [up] — rising to the water surface after submerging or being pressed under.
(36) *Leg over* [lo] — raising a leg up over the other animal to pull up into a mount (Fig. 6A).
(37) *Straddle* [str] — one animal pulls itself on top of another without assuming a proper mounted position.
(38) *Mount* [mount] — dorsally mounting on another animal (Fig. 6B).
(39) *Roll* [rl] — following mount, while grasping the lower animal, the upper animal rolls its body laterally to tail search.
(40) *Tail search* [ts] — following rolling, the mounted animal attempts to move its tail underneath that of the lower animal.
(41) *Tail under* [tu] — with tail search, the upper animal hooks its tail underneath the lower animal and brings the cloacae into apposition (Fig. 6C).
(42) *Tail not under* [tnu] — after tail under is broken off.
(43) *Tail arch* [raise] — when receptive to mating attempts, the lower animal arches its tail facilitating the upper animal getting its tail under.
(44) *Off* [off] — the upper animal drops off the lower, ending a mount or straddle.
(45) *Flutter* [fl] — a soft airy acoustic signal produced by one or both animals primarily during the initiation of courtship.
(46) *Bellow growl* [belgr] — a bellowing vocalization without the characteristic body posturing of the normal bellowing display, produced by females and occasionally by small males, often attracts animals and thus leads to courtship.
(47) *Bellow* [bel] — a highly stereotyped vocal display produced by both males and females, often attracts members of the opposite sex.
(48) *Resist* [res] — one animal resists being pressed by another.
(49) *Bubbles* [bub] — an exhalation of air, usually associated with submergence or pressing under.

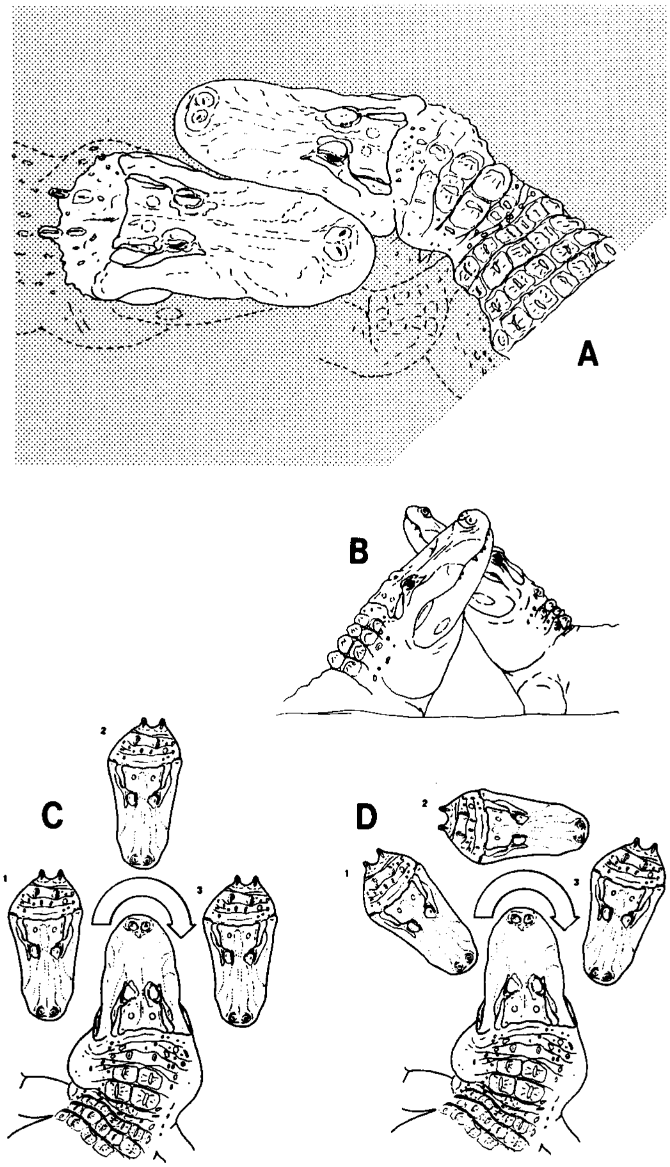

Fig. 5. Behaviours in alligator courtship associated with orientation. A) Alligators in a "face-off orientation; B) jaw fencing; C) movements as one alligator "switches" into a face-off on the other side; D) movements as an alligator "circles" into a face-off on the other side.

of the partner during courtship. Seventeen of the acts (19–35) have to do with movement and orientation during courtship. Nine acts are associated with mounting behaviours (36–44). Three acts (45–47) are vocalizations associated, at least in part, with courtship. Lastly, there are two miscellaneous acts (48 and 49), quite infrequent, associated primarily with tactile interactions in courtship.

The tactile zone acts and a few of the orientation acts occur alone or in association with certain modifiers. These modifiers are:

1. *press* [pr] — one animal topping another and pressing down on the latter's head.

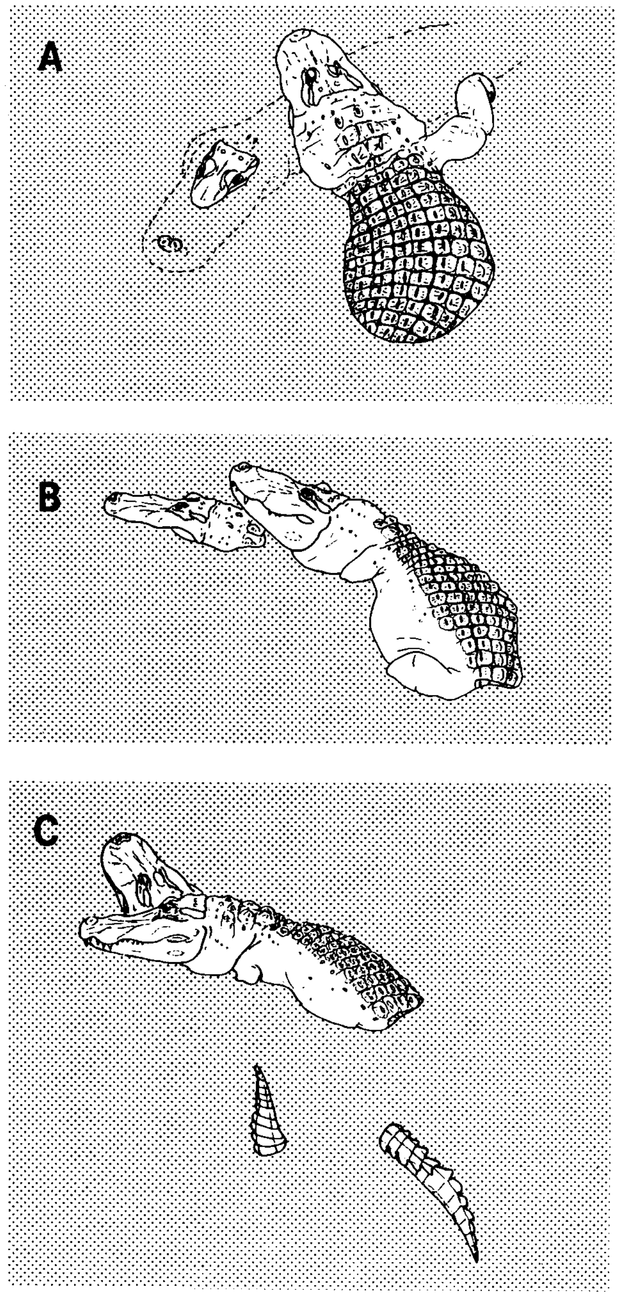

Fig. 6. Behaviours in alligator courtship associated with mounting. A) Mounting animal puts a "leg-over"; B) pulls up into a fully mounted position; and C) rolling laterally and with tail underneath that of the lower animal, in a mating position.

2. *press under* [pru] — one animal forcing another's head underwater.
3. *push* [psh] — forcing another animal in a lateral direction.
4. *chinning* [ch] — rubbing with the under side of the jaw over a specific area.
5. *circling* [cir] — simultaneous behaviours by both animals in which both maintain their orientation to the other while rotating.

Static analysis of courtship behavioural acts

BEHAVIOURAL ACT FREQUENCIES

The relative frequencies of tactile zones contacted during courtship for the three study seasons, with post-mounting behaviours eliminated, are illustrated in Figure 4. Tactile interactions in alligator courtship are oriented strongly to the head of the partner. Generally, about 94% of all contacts that I recorded between courting alligators are on the head and neck. The posterior tactile zones are rarely touched and have thus been lumped together as [pst] in the figure. *Nuchal scales* [nu] are contacted frequently during courtship, both in mounting attempts and during pressing interactions. The frequency with which zones are contacted differs noticeably between some adjacent areas. For instance, while *below the eye* [i] is commonly touched, the nearby *below the ear* [e] is infrequently contacted.

Many of the behavioural acts involved in alligator courtship are combined with several act modifiers that were identified with the catalogue above. All of the tactile zone acts are modified at one time or another. Several of the acts involved with orientation during courtship are similarly modified. Specific modifiers associated with each of these behavioural acts are listed in the catalogue.

Table 2 lists the tactile zones and the percentage of these acts recorded with modifiers from the courtship data in 1981, 1982 and 1983. In general, dorsally located tactile zones are highly modified, roughly 80% of the time, chiefly by *press* and *press under*. Much of this occurs during mounting or mounting attempts. Lateral tactile sites are much less likely to be acted upon by modifiers and are usually modified by *push* or *chinning*. These sites are typically pressed or pushed upon less than 20% of the time.

Tactile behaviours accounted for only about 17–20% of the 44 500 acts recorded during the study (Table 3). Acts of movement and orientation both precede and follow tactile behaviours and are much more frequent than tactile acts. After mounting, the upper animal usually presses the lower one on the cranial table, nuchal scales or, more rarely, the snout.

SEXUAL DIFFERENCES IN ACT FREQUENCIES

Some differences exist between sexes in the frequency of which certain tactile zones are contacted. Analysis of the total number of tactile acts recorded for males and females in 1982 and 1983 indicated some sexual differences in the frequency with which some tactile zones are contacted. Data used in the analyses included only courtships of known individuals and included behavioural acts after mounting. Following contingency table analysis of male and female behaviours, acts with the highest Chi-square values were removed until differences between males and females where not significant (Zar 1974). In both 1982 and 1983, females contacted *snout* significantly more often than expected by a random model and touched *nuchal scales* and *cranial table* less frequently than expected. Males contacted *snout* less frequently than expected in both years. In addition, in the 1982 season, females executed the act *articular* significantly less often than expected and *below the eye* and *posterior maxillary* more frequently than expected. Males touched the *nuchal scales* more often than predicted.

Percentages of behavioural acts performed with act modifiers by males and females (Table 4) appear to suggest that females attempt pressing slightly less often than males and are less likely to be able to press under than are males. Males also seem to push slightly more often than females. However, results of a 3-way analysis of variance test between males and

Table 2. Percentages of each tactile zone act performed with modifiers in data from entire courtships from the 1981, 1982 and 1983 study seasons. The total number of records of each tactile zone (N) also is given. Acts *dorsum, forelimb, side, pelvis, hindlimb,* and *tail* make up [pst].

	1981		1982		1983	
ACTS	%	N	%	N	%	N
pm	6.3	205	16.2	253	8.4	119
a	5.2	97	16.1	192	15.7	106
m	10.9	256	16.8	214	15.9	88
p	4.4	113	17.1	252	14.3	126
i	11.7	120	11.0	301	16.7	162
e	3.8	52	19.2	125	21.1	71
ang	10.3	145	9.4	171	15.5	58
r	19.6	92	18.4	425	11.2	241
nk	4.5	88	8.8	136	8.2	49
sn	85.2	135	62.9	202	60.4	134
t	80.6	252	86.4	551	87.5	287
nu	75.3	397	96.6	526	64.4	590
pst	9.8	122	13.8	276	7.0	85

Table 3. Observed frequencies of behavioural acts, and the per cent of total for recorded acts from data on entire courtships from the 1981, 1982 and 1983 study seasons. All tactile behaviours lumped as [tac]. Acts *tail arch* and *resist* included with *still* [st]. Acts *follow* and *directed swim* lumped with *forward* [for]. *Jaw fencing* is included with *face-off* [fo]. *Roll, tail search, tail under,* and *tail not under* are grouped into [mnt]. *Bellow growl, bellow, bubbles,* and *away* not included.

	1981		1982		1983	
Act	Obs.	%	Obs.	%	Obs.	%
tac	2 081	20.2	3 930	18.1	2 116	17.3
st	4 753	45.9	10 316	47.3	5 709	46.4
for	887	8.6	2 322	10.6	1 229	10.0
bk	337	3.3	745	3.4	408	3.3
from	125	1.2	247	1.1	189	1.5
to	46	0.4	63	0.3	81	0.7
fo	732	7.1	849	3.9	562	4.6
six	14	0.1	63	0.3	31	0.3
sw	43	0.4	76	0.3	46	0.4
cir	134	1.3	211	1.0	165	1.3
piv	7	0.1	43	0.2	29	0.2
sub	193	1.9	298	1.4	110	0.9
uc	47	0.5	55	0.3	28	0.2
up	326	3.1	660	3.0	397	3.2
lo	155	1.5	575	2.6	322	2.6
str	44	0.4	78	0.4	89	0.7
mount	138	1.3	507	2.3	280	2.3
mnt	147	1.4	356	1.6	209	1.7
off	126	1.2	349	1.6	268	2.2
fl	26	0.3	82	0.4	44	0.4

females, tactile behaviours, and act modifiers on the data for entire courtships from the 1982 and 1983 study seasons indicated that there was no statistically significant difference between the sexes in the frequency with which acts were modified. That is, statistically neither males nor females seem more likely to exert force to their tactile behaviours.

Table 4. The percentages of tactile acts performed with modifiers by males and by females from data on entire courtship interactions from the 1982 and 1983 study seasons.

	1982		1983	
Modifier	Male	Female	Male	Female
press	6.54%	7.77%	6.01%	6.24%
press under	6.10%	4.06%	7.53%	3.13%
push	8.16%	6.43%	8.34%	5.21%
chinning	2.96%	2.29%	1.50%	3.21%
unmodified	76.1%	79.45%	78.22%	76.65%

INITIAL ACTS IN COURTSHIP

The frequencies with which tactile zones are contacted during the initiation of courtship differ from those presented above. Tabulated frequencies of the first three zones contacted during a courtship encounter show very clear trends. Generally, for males, very high values are found for the *premaxillary* and the *articular,* as well as the *nuchal scales* (Fig. 7). If a male approaches from the front, it frequently touches the *premaxillary* before making other contacts or moving into a *face-off*. If the initial approach is from the side or immediately into a face-off, the *articular* region is frequently contacted first. The high values for the *nuchal scales* are due to alligators attempting to mount immediately, without preliminary tactile interactions. If this mount is unsuccessful, the animal may then begin tactile behaviours. The

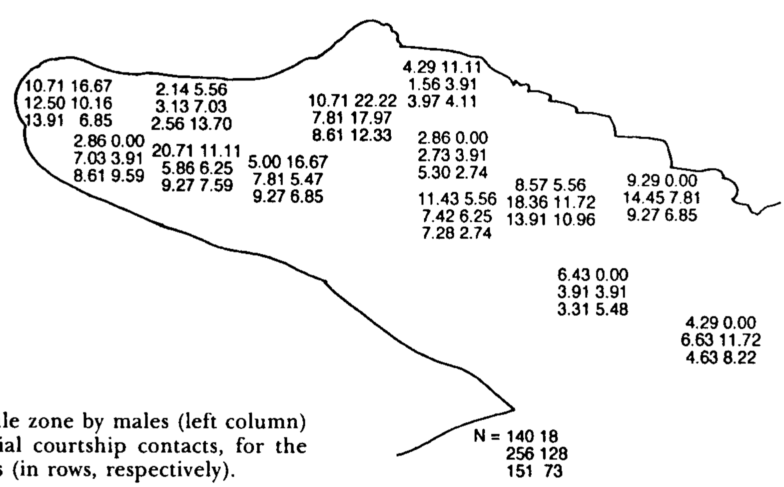

Fig. 7. Percentage of contacts to each tactile zone by males (left column) and females (right column) in initial courtship contacts, for the 1981, 1982, and 1983 study seasons (in rows, respectively).

pattern is generally the same for females except females also seem to touch *below the eye* and the *snout* frequently. These tendencies are shown throughout the tactile interaction. Relatively high percentages of contacts also are recorded for the posterior tactile zones during these initial few contacts. Posterior contacts seem to be made as the alligator is approaching the head of the partner. Once oriented to the head, posterior contacts are rare.

Sequential order of courtship behaviours

Results of analyses of intraindividual transition matrices related to tactile interactions (Fig. 8), indicate that, in courtship, alligators move along the side of the head and neck contacting zones regularly. All of the tactile zones along the lateral surface of the head have numerous associations with other nearby zones. Some zones, such as *posterior maxillary* [p], *below the eye* [i], and *articular* [r] are very frequently used, with several significant associations leading to, and from, these sites.

Dorsal sites on the head are significantly associated with mounting behaviours. The *cranial table* [t] and *nuchal scales* [nu] are contacted immediately before or after mounting. This is to be expected as a mounting alligator must usually press on a dorsal site in order to gain the leverage to pull itself up into the mounted position. Once mounted, the upper animal occupies itself with chinning or pressing the *cranial table* [t].

The *face-off* [fo] orientation is assumed repeatedly during tactile interactions. After contact with the *premaxillary* [pm], alligators move into a face-off position significantly more frequently than predicted by chance alone. From this orientation, they then move up to press on the *nuchals* [nu] or turn the head and bump into the *articular* [r].

Matrices emphasizing tactile acts for interindividual associations (that is, one act performed by an individual and the following act of the partner) reveal significant associations between tactile acts and those of orientation, submergence, and the flutter vocalization (Fig. 9). Tactile acts associated with orientational movements (*face-off* [fo], *circle* [cir], *switch* [sw], etc.) are numerous. Several acts, touches to the *premaxillary* [pm], *below the eye* [i], or to the *articular* [r], lead to orientational movements by the courting partner. Orientational movements by one alligator, frequently lead the other to contact the *snout* [sn], *below the ear* [e], *angle of the jaw* [ang], *articular* [r] or *nuchal scales* [nu]. The high number of both preceding and following significant transitional associations with orientational movements, indicates the importance of these, especially the *face-off* [fo] orientation, in perpetuating a courtship interaction.

Contact to dorsal tactile zones, the *snout* [sn] and *cranial table* [t], often lead to the *submergence* [sub] of the courting partner. *Submergence* [sub] consequently leads to *mounting* [mnt] and presses to the dorsal sites. *Submergence* [sub] appears at times to be an invitation for the courting partner to press the *cranial table* [t], or possibly even to *mount* [mnt].

Fluttering [fl] vocalizations occur sporadically in alligator courtship. Flutters usually are produced only when animals are very close to one another, usually within 50 cm, and often when actually in contact. As a consequence, fluttering is strongly associated with tactile behaviours. Contact with the *premaxillary* [pm] and *anterior maxillary* [a] are often replied to with a flutter. Fluttering by one alligator leads to touches to the *premaxillary* [pm],

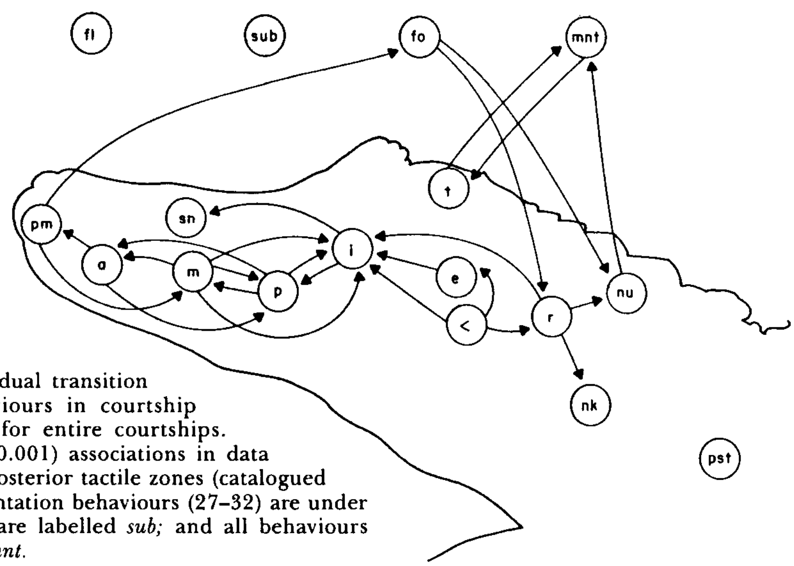

Fig. 8. Results of single-lag, intraindividual transition matrix analyses of tactile behaviours in courtship interactions for both sexes and for entire courtships. Arrows indicate significant ($p < 0.001$) associations in data from all three study seasons. All posterior tactile zones (catalogued acts #13–18) are labelled *pst;* orientation behaviours (27–32) are under *fo;* those of submerging (33–35) are labelled *sub;* and all behaviours related to mounting (36–44) are *mnt.*

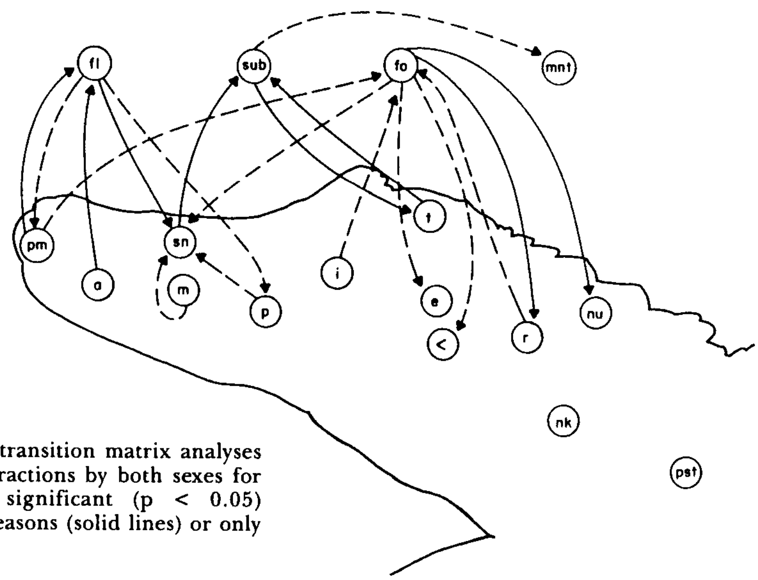

Fig. 9. Results of single-lag, interindividual transition matrix analyses of tactile behaviours in courtship interactions by both sexes for entire courtships. Arrows indicate significant (p < 0.05) associations in data from at least two seasons (solid lines) or only a single study season (broken lines).

anterior maxillary [a], *snout* [sn], and *posterior maxillary* [p] by the partner.

Analyses of transition matrices compiled for behaviours performed by males and by females once again show many similarities to the general pattern discussed above. However, some insight as to differences between the sexes was demonstrated. Several preceding tactile acts of the male lead to *submergence* [sub] by the female. Although commonly performed by both sexes, submergence, as a means of terminating interactions, or temporarily pausing the courtship, is a frequent behaviour of females. Several behaviours were associated with fluttering by the male. There is a greater tendency for males to flutter than females. So, not only do contacts by the female result in fluttering by the male, but male fluttering also was associated with a number of following acts by the female.

The matrices emphasizing movements, orientations, and mounting behaviours, provide information of the logistical movements surrounding the tactile interactions. Results from intraindividual matrices (Fig. 10), clearly show associations between the tactile acts and orientation, movement, and mounting behaviours. The sequence of behavioural acts involved in mounting is clearly shown. *Tactile* interactions lead to either *straddling* [str] or *leg-over* [lo], either then leading to a full *mount. Mounting* is followed by the post-mounting behaviours [mnt] (pressing, rolling and tail searching, etc.), or by a dismount [off].

The importance of the *face-off* [fo] in orientation and movement surrounding courtship is also obvious. The face-off orientation is assumed by *switching* [sw], *circling* [cir], or *pivoting* [piv] into place. Once assumed, tactile contacts can be made.

Sequences of behaviours involving submergence are also obviously defined. Courting alligators often submerge during interactions. Frequently following *submergence* [sub], alligators move forward *underneath the chin* [uc] of the courting partner, apparently inviting

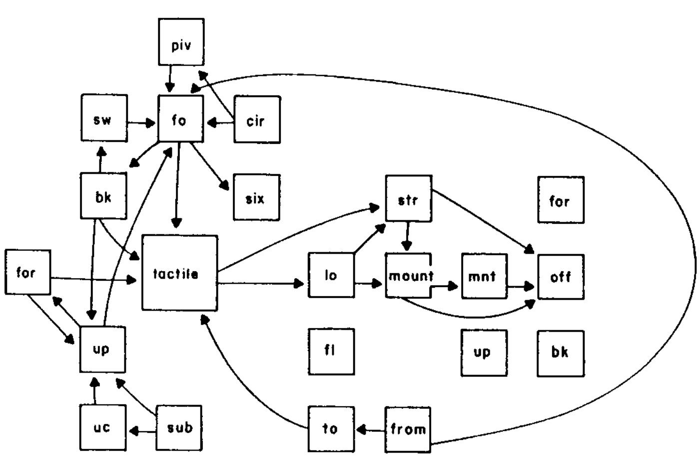

Fig. 10. Results of single-lag, intraindividual transition matrix analyses emphasizing behaviours of movement and orientation in courtship interactions for both sexes and for entire courtships. Arrows indicate significant (p < 0.001) associations in data from at least two study seasons. All tactile behaviours (1–18) were lumped as *tactile.* Follow and directed swim (24 and 25) were lumped with forward [for]. Face-off [fo] included jaw-fencing (29). All post-mounting behaviours — roll, tail search, tail under, tail not under, and tail arched (39–43) — were included in *mnt.*

presses to the dorsal tactile zones, or possibly mounting. Submerged alligators either move forward to rise [up] into a face-off on the other side, or *back* [bk] up and emerge on the surface where they were before.

Analyses of the interindividual matrices (Fig. 11) related to orientation elucidate recognizable sequences of courtship manoeuvres. After *tactile* interactions, one animal *backs* [bk], the other *switches* [sw] to the other side, the former moves forward into a *face-off* [fo] and they then return to *tactile* behaviours. The *face-off* [fo], as well as *leg-over* [lo], are also associated with *fluttering* [fl].

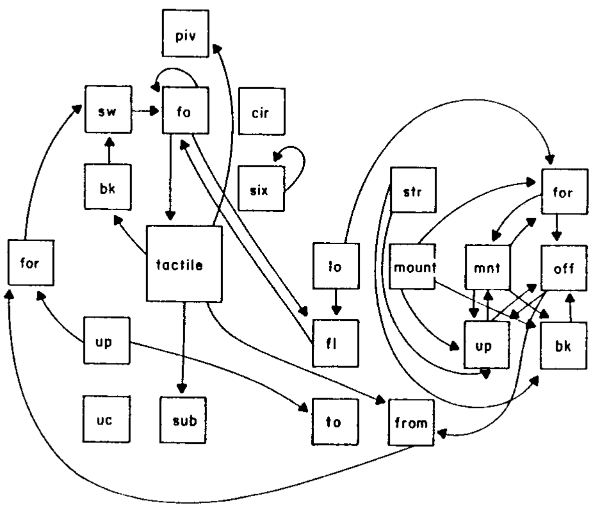

Fig. 11. Results of single-lag, interindividual transition matrix analyses emphasizing behaviours of movement and orientation in courtship interactions for both sexes and for entire courtships. Arrows indicate significant ($p < 0.05$) associations in data from at least two study seasons.

Significant transitional associations of behaviours involved with mounting are apparent. *Leg-over* [lo], *mounting* [mount], or post mounting [mnt] behaviours cause the subordinant animal to move *forward* [for] or to *back* [bk] up. *Straddling* [str], *mounting* [mount], and post-mounting [mnt] behaviours frequently involve pressing the lower animal under the water surface and are, thus, followed by that animal rising [up] again to the surface. *Forward* [for], *surfacing* [up] or *backing* [bk] movements by the lower animal lead to dismounting [off] by the upper animal, that consequently leads to the former terminating the interaction and swimming *away*.

Temporal description of alligator courtship

Seasonal patterns in courtship activity

Courtship is generally observed in St Augustine from the second week of April through the first week of June. Variation in time of onset and in the intensity of courting activity was observed in the three years of the study. Estimates of the effective size of the daily courting population for the 1981, 1982, and 1983 seasons (Fig. 12), visually define the season of courtship of the alligator. In each case, most of the males that were to be active in a season had already been observed in courtship by the first of May. The majority of females active in a season became active later, usually after the first of May.

Most animals end courtship activities at about the same time. This fact causes the effective courting population to grow throughout most of the courting season, reaching a climax during the last two weeks of May and dropping off rapidly thereafter.

The distribution and frequency of mounting behaviour, as an indicator of courting activity, recorded during the 1983 breeding season further illustrates this seasonal pattern (Fig. 13). In the early part of the breeding season, courtship and mounting are uncommon and

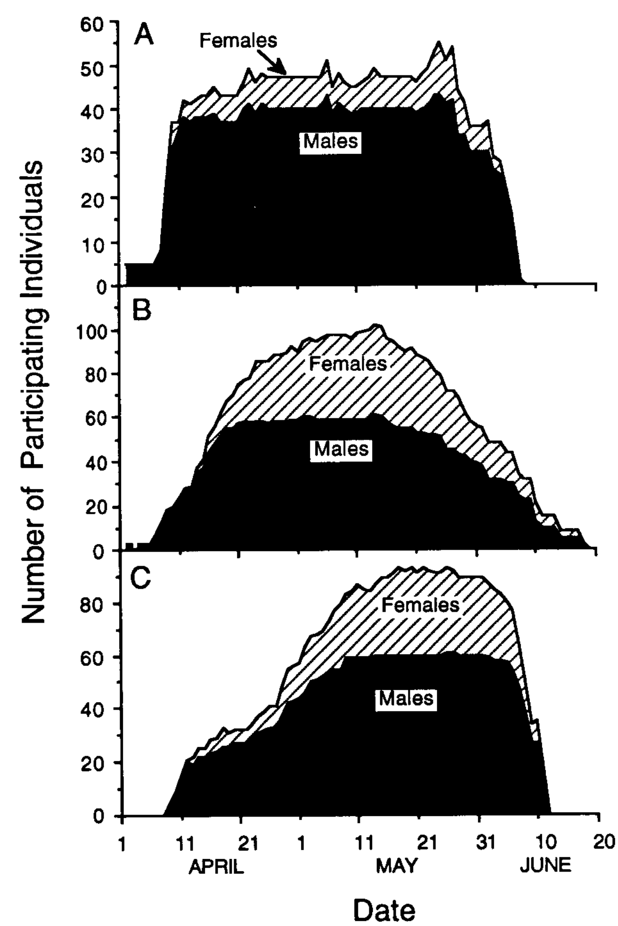

Fig. 12. Estimated size of the courting population, by day, for the: A) 1981, B) 1982, and C) 1983 study seasons. See Results for explanation of population estimation.

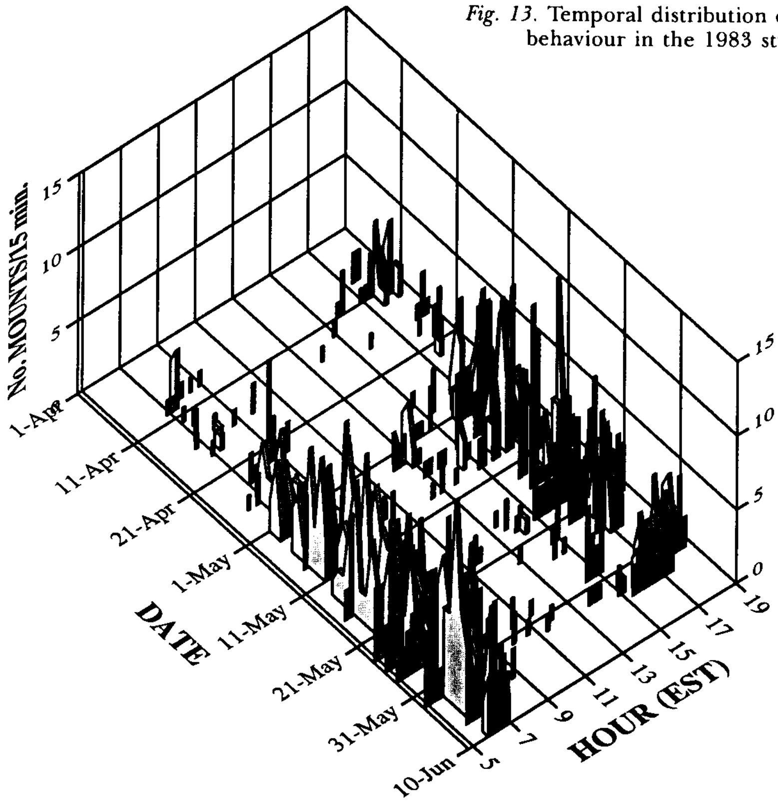

Fig. 13. Temporal distribution of observed mounting behaviour in the 1983 study season.

sporadic from first light until sunlight reaches the preferred basking areas of the lake. Most of the alligators halt interactions at this point and leave the water for these basking sites. Some sporadic courting activity is again apparent when the basking areas are cast into shadow at the end of the day.

Activity becomes more frequent and widespread as the season progresses, with a peak in activity in mid to late May. Ambient air and water temperatures are warmer at this time and alligators spend significantly less time on land basking. Courting activity is most common in the early morning and late afternoon hours with the morning activity being the most intense. Some interactions occur around midday as well. Courtship also occurs sporadically throughout the night. Courting activity seems to drop off sharply at last light in the evening, remains fairly low throughout the night and then increases noticeably about one hour before sun up.

Intensity of courting activity varied greatly between the study seasons. During the 1981 study season, courtship activity was much more vigorous, in terms of length of courtships, than in the following two study seasons. Late winter and early spring weather conditions, especially night time low temperatures and the subsequently lower water temperatures in 1982 and 1983, might be responsible for the reduced activity noted in the latter two study seasons.

Cadence of courtship interactions

Courtship interactions are highly variable in length and so are difficult to describe temporally. The duration of a courtship may be rather easily quantified by measures of either the length of time of the interaction or the number of behavioural act dyads recorded before the first mounting or in the entire interaction. There were minor differences in the average number of act dyads in recorded courtships from the three study seasons (Table 5). Interactions leading to mounting recorded in this study, including post-mounting behaviours, averaged about 34.2 dyads in length in 1981, 32.4 in 1982 and 36.6 in the 1983 study season. If post-mounting acts are excluded, the average length of an interaction drops to 13.4, 16.7 and 14.9 recorded act dyads, respectively.

Courtship in alligators does not always involve an extended period of tactile interactions between the courting pair. Commonly, an alligator will mount another without any preliminary contacts. These "immediate mounts", here defined as courtship interactions in which mounting occurred within the first five recorded act dyads, were recorded as courtships because the interaction resulted in a mounting, but the inclusion of these mounts in analyses of the lengths of courtship interactions can significantly lower the average number of acts recorded for courtships. Although not uncommon in the 1981 study

Table 5. Average number of act dyads recorded for courtship sequences, for the 1981, 1982, and 1983 study seasons: A) for entire courtship sequences including post-mounting behaviours and immediate mounts; B) for courtship sequences excluding post-mounting behaviours, including immediate mounts; C) for courtship sequences excluding post-mounting behaviours, excluding immediate mounts.

Study season	Ave. No. act dyads	Standard error	Minimum	Maximum	Total number
A					
1981	34.18	± 5.31	8	122	28
1982	32.44	± 2.76	5	183	150
1983	36.61	± 5.16	6	332	86
B					
1981	13.39	± 4.04	3	73	18
1982	16.69	± 2.13	3	144	118
1983	14.94	± 2.50	3	87	62
C					
1981	18.08	± 5.65	6	73	12
1982	25.01	± 3.19	6	144	71
1983	27.38	± 4.23	6	87	29

season, immediate mounts represented more than half of all interactions recorded in the 1982 and 1983 study seasons (Fig. 14). Removal of immediate mounts from the analyses resulted in higher, roughly-similar average pre-mounting courtship lengths between the three seasons of 18.1 dyads in 1981, 25.0 in 1982, and 27.4 in 1983. Not all courtship interactions, even lengthy ones, result in mounting. For the purposes of this study, only those interactions greater than 15 act dyads in length were considered, if no mounting occurred. These courtships naturally had very high averages in number of act dyads recorded.

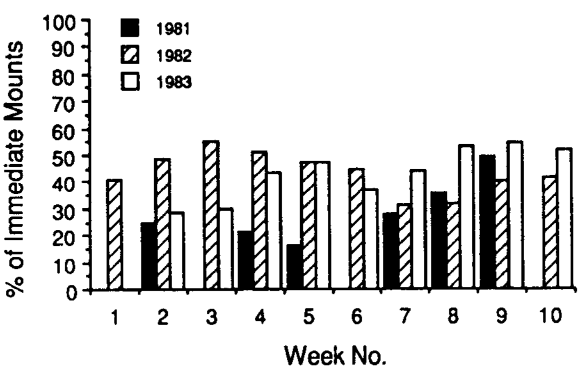

Fig. 14. Frequency of immediate mounts, by week beginning April 1, as a percentage of the total recorded mounts, for the 1981 (black bars), 1982 (striped) and 1983 (white) study seasons.

Weekly variation courtship parameters

Changes in the average length of premounting courtship interactions calculated for each week of the study season were discernible through the course of each season, but the direction of these changes varied between study seasons. The average number of act dyads recorded for courtship interactions decreased slightly but significantly (t-test, $p < 0.05$, $r = -0.71$) through the 1981 season (Fig. 15). A similar pattern for the 1983 study period was also significant (t-test, $p < 0.02$, $r = -0.77$). However, the pattern was reversed in data from the 1982 season. The average number of act dyads in a courtship significantly increased (t-test, $p < 0.02$, $r = 0.76$) in that season.

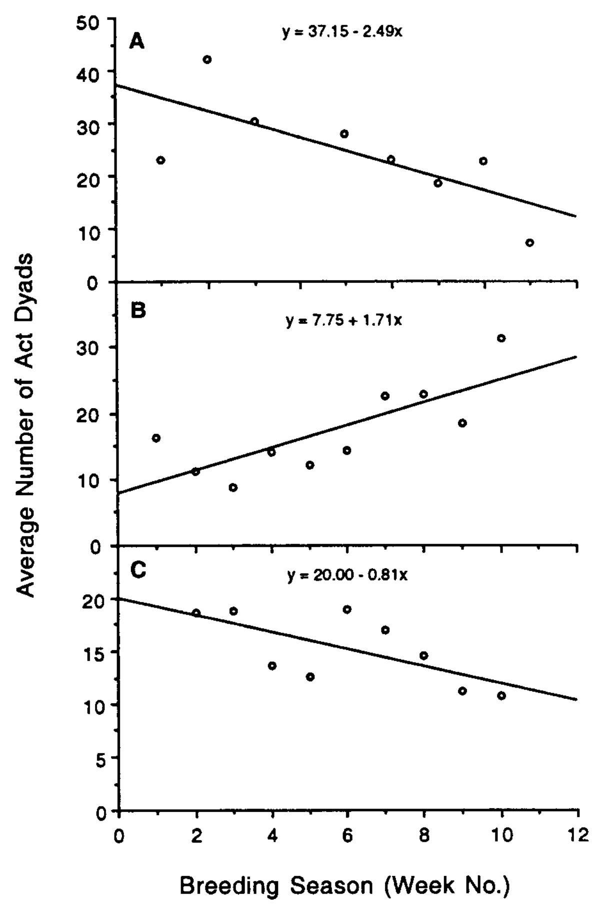

Fig. 15. The average number of acts dyads performed for entire courtships without mounting or prior to the first mount, exclusive of immediate mounts, by week, beginning April 1, through the A) 1981, B) 1982 and C) 1983 study seasons.

Length of time in courtship interactions

Courtship interactions in the 1983 study season averaged about 5 minutes (307.7 seconds, S.D. = 266.3, N = 75) in length, although courtships of more than 24 minutes (1 460 seconds) in length were recorded. Pre-mounting interactions averaged about 65.2 seconds. Interactions averaged a rate of one act dyad every 3 seconds. This rate is highly variable however. There were no significant changes in these values by week.

Mounting was also highly variable in length. In 1983, mount length averaged 2 minutes (119 seconds) with a standard deviation of 2.5 minutes (150.6 seconds) (N = 61). Although most recorded mounts were less than two minutes in length, some lasted more than 24 minutes. Mounts were frequently disturbed by other alligators. About 12.4 % of mounts recorded in courtship interactions during the 1983 study season (N = 226) were interrupted by other alligators. Averages are thus probably lower than they would be for alligators maintained in lower densities.

Interestingly, there was no correlation between the amount of time spent in pre-mounting courtship activities and the length of the mount that followed. This is true even if immediate mounts are removed from the analyses.

Courtships often involve multiple mountings, either by the same individual or by both courting animals. Rarely, a courting pair may mount as many as six times during an interaction. The proportion of courtships with multiple mountings varied between study seasons from a low of 11.8% in 1982 to a high of 17.5% in 1981. Recorded courtships without mounting varied from a low of 13.5% in 1983 to a high of 29.2% in 1981. No weekly changes in these proportions were noted.

Demographic patterns in courtship

Patterns based on gender

Most of the alligators in the study population were active in courtship during some point of the season. Generally, more than 90% of the male study animals were observed in either courtship or mounting activity during the course of the study while less than 75% of the females were (Table 6). Even fewer females participated actively in courtship. For instance, in 1983, 5 of the 46 courting female alligators (21.7%) were observed in only one courtship encounter. Males and females differed greatly in the average length of their active courting season. Males, in general, begin courtship interactions much earlier in the season than do females (refer again to Fig. 12). As most courting terminates at about the same time (during the first week of June), males consequently have a much longer courting season than do females. The effective courting population grows throughout most of the courting season, reaching a climax during the last two weeks of May and dropping off rapidly thereafter.

For known individuals in which interactions were observed, males had significantly (unpaired t-test, $p < 0.001$) longer estimated courting seasons than did females in each of the three study seasons (Table 6). Averages differ dramatically between the three study seasons, but the average male courting season length is between 1.7 (1982) and 2.9 (1981) times as long as that of the average female. Males were active on average for an estimated six and a half weeks in 1982 and 1983, while the average estimated courting season length for females was less four weeks. Males also averaged a highly significantly (unpaired t-test, $p < 0.001$) greater number of interactions (observed courtships or mountings) than did females in each of the three years. In 1982 and 1983, males participated on average in about three and a half times more interactions than did the average female (Table 6). Similarly, males interacted with a highly significantly (unpaired t-test, $p < 0.001$) greater number of partners than did females. Males averaged 18 to 20 courting partners in 1982 and 1983 while females were observed in courtships or mountings with an average

Table 6. Variation in courtship activity by gender. Average estimated courting season length, in days (standard deviation in parentheses), average number of observed courting interactions, average number of courting partners, and the percentage of courting animals of the total for males and females in the 1981, 1982, and 1983 study seasons. Only animals known to be active in courtship were included in the calculations. Values include all interactions recorded, including homosexual interactions and mounting. All differences between male and female parameters are highly significant (Unpaired t-test, $p < 0.001$, 104 d.f in 1981, 119 d.f. in 1982, 107 d.f. in 1983).

Study season	gender	Ave. season length (days)	Ave. number interactions	Ave. number partners	Total number	% of Total
1981	Males	32.17 (± 23.41)	6.92 (± 5.94)	4.07 (± 3.64)	71	78.9
	Females	10.97 (± 14.68)	2.69 (± 2.23)	1.81 (± 1.17)	35	44.9
1982	Males	47.14 (± 17.55)	28.80 (± 17.55)	18.22 (± 10.68)	65	94.2
	Females	27.52 (± 17.87)	8.27 (± 7.61)	5.07 (± 4.14)	56	74.7
1983	Males	45.22 (± 14.31)	31.76 (± 22.84)	20.07 (± 11.19)	63	95.5
	Females	24.93 (± 17.37)	8.67 (± 10.70)	5.89 (± 6.70)	46	74.2

of only five or six alligators. These estimates of the average length of the courting season, the average number of interactions and the average number of courting partners include data from all recorded interactions. These include courtship-like encounters or mounting between males or between females, as well as courtships involving a male and a female.

Data from this study clearly show that, as the season progresses, females begin to become active and interact with the active males. By the most active period in the season, the last half of May, females are not only interacting with males but are initiating the majority of the courtship interactions recorded (Fig. 16). There is a definite positive trend in the proportion of mounts involving females as the season progresses in both 1982 and 1983 (Fig. 17). Additionally, the percentage of mounts, analysed by week, made by females on males rises dramatically in the latter half of the courtship season in these two study seasons (Fig. 18). In summary, the pattern seems to be that, early in the season, male/male mounts are common; as the season progresses, there are more male/female mounts; and, towards the end of the season, the frequency of female/male mounts increases. The 1981 data base was insufficient to perform similar analyses.

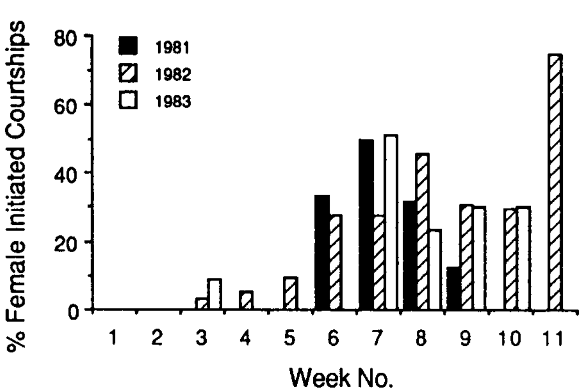

Fig. 16. Courtships initiated by females, by week beginning April 1, as a per cent of the total courtships recorded, for the 1981, 1982 and 1983 study seasons.

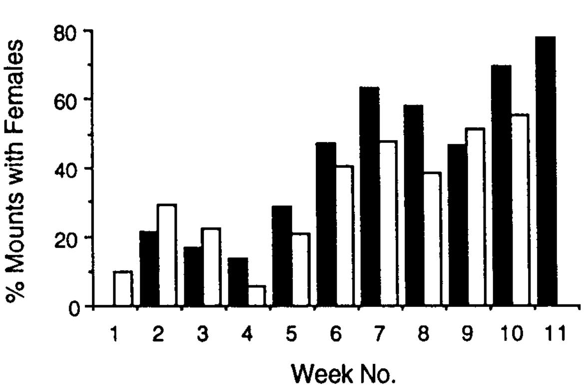

Fig. 17. Proportion of mounts involving females, as a percentage of total number of mounts, by week beginning April 1, for the 1982 (black bar) and 1983 (white bar) study seasons.

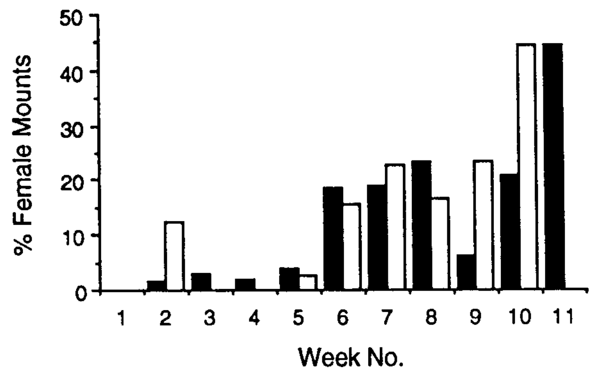

Fig. 18. The percentage of mounts, by week beginning April 1, made by females on males, for the 1982 (black bar) and 1983 (white bar) study seasons.

Patterns based on size

Larger animals seem to be more active and are active for a longer period of time than are small animals. The length of the estimated active courting season of an animal was significantly positively correlated with the alligator's total body length in the 1982 data for both males (t-test, 64 d.f., $p < 0.001$) and females (t-test, 55 d.f., $p < 0.05$) (Fig. 19). The length of the courting season was not significantly correlated with body length for males or females in either 1981 or 1983 however. The number of interactions an animal was observed to partake in was also positively correlated with body length for males (t-test, 64 d.f., $p < 0.001$) and females (t-test, 55 d.f., $p < 0.05$) in 1982 (Fig. 20) and for males (t-test, 62 d.f., $p < 0.02$) in 1983. No such association was found for either sex in 1981 or for active females in the 1983 study season. It should be noted, however, that the 1982 data base for these calculations was much stronger than that in 1981 or 1983 due to the very large number of interactions recorded in 1982.

Male-male interactions

Courtship-like interactions between males were commonly observed in this study. In fact, they make up the majority of the interactions recorded. Mounts between males represented between 63.2% in 1982, and 72.4% in 1981, of all mounts observed (Table 7). These interactions are indistinguishable from those between the sexes. They involve all of the behaviours discussed herein, including tactile interactions, mounting and copulatory attempts. Quantitatively, in terms of act frequency, sequence and cadence, these

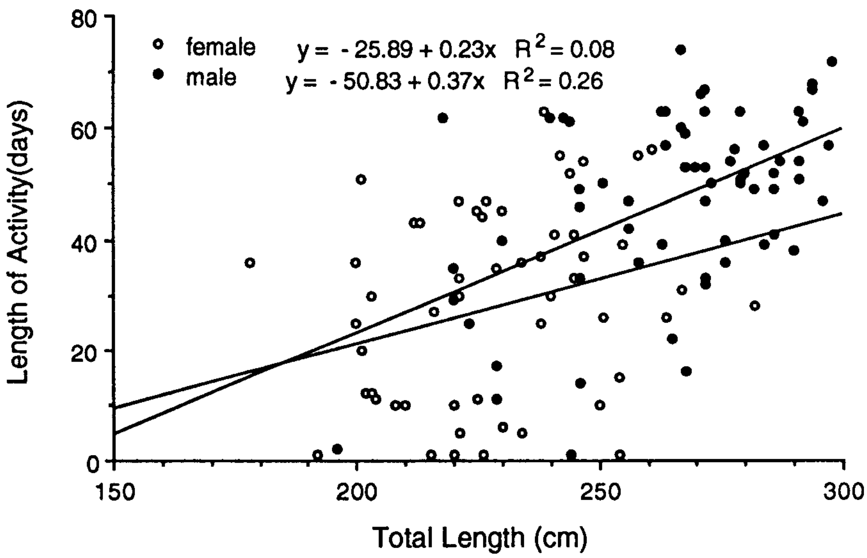

Fig. 19. Estimated length of the courting season, in days, of individual males (closed circles) and females (open circles), by total body length, for the 1982 study season.

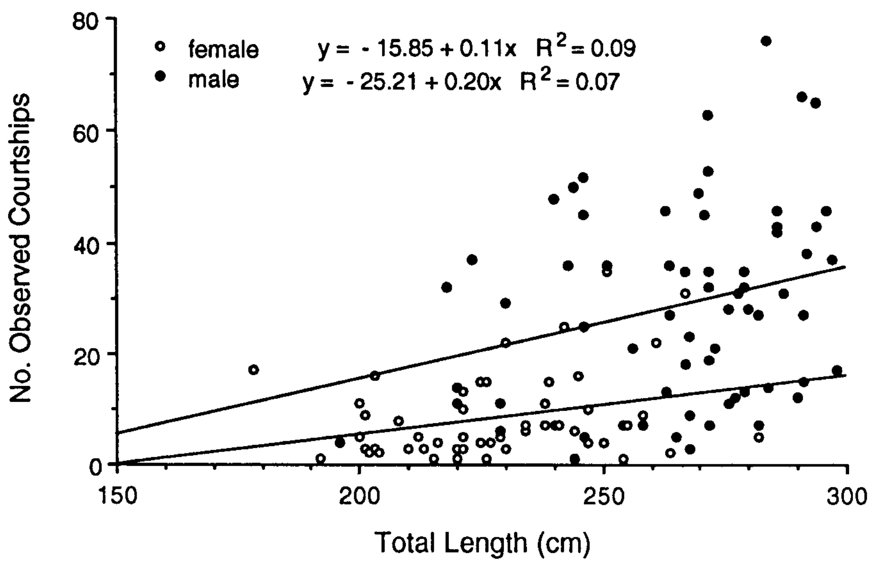

Fig. 20. Total number of recorded courtship interactions of individual males (closed circles) and females (open circles), by total body length, for the 1982 study season.

interactions are not different from those of courtship between opposite genders. Perhaps as a result of the much earlier start of the courtship season for males relative to females, males must interact with other males. However, even after females become active and readily interact in courtship with males, homosexual interactions between males continue to be common. The longest courtship-like interaction (2 205 sec.) and the longest mount (1 060 sec.) observed in this study were between two males.

In contrast, females rarely interact with one another. Intrasexual mounting by females was

Table 7. Observed frequency, and percentage of total, for recorded mounts of known individuals, by mount type (gender of upper alligator/lower alligator) for the 1981, 1982, and 1983 study seasons. Male/male[1] signifies that the upper male is equal to or larger than the lower male. Male/male[2] signifies a smaller male mounted in the upper position.

Mount type	1981 (%)	1982 (%)	1983 (%)
male/female	28 (16.5)	248 (25.9)	219 (20.1)
female/male	15 (8.8)	90 (9.4)	121 (11.1)
male/male[1]	78 (45.9)	329 (34.4)	420 (38.5)
male/male[2]	45 (26.5)	276 (28.8)	314 (28.8)
female/female	4 (2.4)	14 (1.5)	17 (1.6)
TOTAL	170	957	1 091

quite rare, as low as 1.5% in 1983 to only 2.4% in 1981.

Courting groups

In captive situations, a courting pair is very conspicuous and often attracts the attention of other alligators. Ultimately, these animals may become involved in the interaction and a "courting group" is formed. Courting groups of up to twelve individuals were observed during this study. Interactions within these groups seem to be essentially random with male-male and male-female encounters occurring frequently. Males engaged in courtship with a female readily terminate that interaction and initiate interactions with males. Courting groups are not static entities. Rather, their composition changes continuously as animals emigrate, alone or as mounted pairs, and new animals become incorporated. Mounting occurs frequently in these groups but is typically of short duration due to disturbance from other animals. I witnessed only a single case in which a male alligator clearly attempted to dislodge the upper individual from a mounted pair. Mounted alligators commonly dropped off of the lower alligator to initiate courtship with a recently arrived individual.

DISCUSSION

Detailed observations of behaviours such as those described in this chapter would be difficult to study under wild conditions. However, while the study of animals in captivity allows close observation of behaviours, caution must be taken in accepting these observations (Kaufmann and Kaufmann 1963). Captive animals may be under different stresses and conditions than are those in the wild. Often captive populations are of much higher density and this crowding may affect social structure, hormone cycling, reproductive behaviours, movement patterns, and many other factors associated with social behaviour (Morris 1964, 1966). Behaviours observed in captivity thus may differ greatly from those of wild animals. Still, observation of captive animals is often the only means of studying certain behaviours in detail, and thus provide a basic understanding of an animal's social behaviour that may or may not be validated by study of wild populations. I know of no equivalent data sets on the behaviour of wild alligators to which my results could be compared.

Behavioural acts in courtship

Acts involved in the introduction of potential mates are the most poorly understood of alligator courtship behaviours. Some authors refer to "vigorous swimming" by both sexes prior to tactile encounters (Joanen and McNease 1971; Silverstone 1972; Fogarty 1974). However, this was not observed in this study. If an alligator approaches a moving animal, it swims parallel with it, often apparently leading or pushing the other forward (Garrick and Lang 1977a; Garrick *et al.* 1978; Vliet 1986), an act I refer to as a "directed swim." This may serve to tire the alligator and make is more receptive to courtship.

The means by which alligators locate or attract mates are not well understood. Auditory and olfactory channels of communication are thought to serve these purposes. Many authors have suggested that bellowing by either sex serves, at least in part, to attract members of the opposite sex (Kellogg 1929; Harper 1930; LeBuff 1957; Fogarty 1974; Garrick 1975; Garrick and Lang 1977a; Garrick *et al.* 1978; Vliet 1986, 1989). Animals often pair up and bellow simultaneously near, or in contact with, one another. During the spring months, many of these interactions proceed into courtship encounters. Joanen and McNease (1971, 1975) suggest that alligators in Louisiana's coastal bayous use bellowing vocalizations to attract others into the open bodies of water where courtship occurs. Carr (1976) mentions bellowing by a wild female causing the approach of a male from about 300 yards. The pair then proceeded to interact. The majority of courtships, however, observed during the course of this study occurred outside of bellowing choruses.

In addition to repeated references to an association between bellowing activity and reproductive activity for *Alligator mississippiensis* (Schmidt 1922; Beach 1944; Fogarty 1974; Garrick and Lang 1975, 1977a; Garrick *et al.* 1978; Vliet 1989), it has also been reported in several other crocodilians, including *Caiman crocodilus* (Alvarez del Toro 1969), *Crocodylus acutus* (Alvarez del Toro 1974), *C. niloticus* (Cott 1961), *C. porosus* (Deraniyagala 1939).

It has also been suggested that alligators locate one another by following scent trails of musk, left by passing alligators (Gadow 1901). McIlhenny (1935) noted that female alligators produce increased amounts of musk from the cloacal glands during the mating season. This was most definitely evident during capture of alligators for this study.

Most accounts of seasonal movements in alligators suggest that the females move to the males during the mating season (Joanen and McNease 1971, 1972; Goodwin and Marion 1979). Kellogg (1929) noted that males are more active in the breeding season and travel large distances. Carr (1976), however, wrote of a female alligator in a small sinkhole lake being visited by a male each year during the reproductive season.

Garrick and Lang (1977a,b) and Garrick *et al.* (1978) referred to a "cough-like" or "chumpfing" vocalization produced by alligators during courtship. Although the flutter described herein is probably the same vocalization, it does not match their description of the "cough-like vocalization". Herzog (1974) described a "low growl" vocalization produced during mounting, and also to human intruders. The definition of this vocalization is confused as Herzog (1974) provided no sound spectrograph of the "low growl" and Garrick *et al.* (1978) described a vocalization, that they called a "low growl", that is contextually different from Herzog's vocalization.

This study included detailed analyses of contacts to specific "tactile zones" along the head and neck of the alligator. Interest in this was due, in part, to reports that varanid lizards, especially males, tongue flick very specific sites on the head and body of the female (Auffenberg 1981, 1983). These sites have increased numbers of swollen pustular scale organs, the function of which is unknown. Crocodilians have high concentrations of similar pigmented pustules (Laidlaw and Murray 1933) in the areas here defined as tactile zones. Although Neill (1971) considered these to be organs of taste, Von Düring and Miller (1979) showed that these structures in *Caiman crocodilus* are purely tactile.

Tactile interactions are always performed at the water surface, never submerged. This was clearly visible in the study site. Courting alligators remain at the surface until one animal has mounted the other. Following mounting, both animals often submerge. This might suggest that visual communication, in addition to tactile perception, is also important during the tactile phase of alligator courtship. However, alligators that are totally blind due to aggressive encounters are still capable of courting properly. These animals assume the face-off orientation and return to it repeatedly following tactile zone contacts during courtship, emphasizing the essentially tactile nature of alligator courtship. Courting at the water's surface may facilitate proper orientation and co-ordination of movement between the interacting animals.

Pressing behaviours should allow alligators to judge the strength, size, and possibly other measures of fitness of the potential mate, either by the strength with which its presses or resists pressing. The ability of a male to restrain a female by pressing her under water may be important in stimulating her receptivity to further courtship and mating. This has been suggested in monitor lizards (Auffenberg 1983, 1994).

A number of other behaviours have been described in the literature as acts involved with alligator courtship. Neill (1971) described courtship in captive alligators to include caressing or scratching the dorsum of the female by the male with his forelimbs. This has not been described by any other author. Several authors have observed alligators to "bubble" during courtship (Garrick and Lang 1977a,b; Garrick *et al.* 1978; Neill 1971). One animal, usually the male, lowers its head below the water surface and exhales, producing long streams of bubbles through its mouth or nostrils. The alligators at St Augustine never did this as a part of courtship. The reason for this discrepancy is unknown.

The statistics used for sequential analysis of courtship behaviours assume that acts are independent of all other acts. This assumption is clearly not met here as tactile zones are not actually independent of each other. Zones are not equidistant to one another. The proximity of one tactile zone to an adjacent one imparts a greater chance of association with the neighbouring zone than with one more distantly located. The large number of significant associations indicated by the analyses of tactile interactions undoubtedly reflect this fact. Considering this, it appears that there is little, if any, sequential nature in the order of tactile zones contacted by one individual on another during alligator courtship. Some tactile zones are contacted more frequently than others, but the sequence in which the zones are contacted is probably random, or nearly so.

Temporal patterns in alligator courtship

In St Augustine, the courtship season usually extends from the second week of April through the first week in June, with a peak in courting intensity about the third week of May. Although courtship is seen throughout this two month period, the majority of copulations resulting in successful fertilization are thought to occur in mid May. During this time, the frequency of courtship interactions and the estimated courting population, as well as the frequency of other social displays (Vliet 1989), all reach a peak. The extended length of the courting season may be necessary for the proper stimulation and co-ordination of the hormone cycles of both males and females (Garrick and Lang 1977a,b; Garrick *et al.* 1978; Vliet 1986). Alternatively, courtship by males in the early part of the season may be necessary to stimulate female receptivity in the latter part. A mechanism such as this has been documented in the lizard *Anolis carolinensis* (Crews 1975, 1978, 1980), as well as in the ring dove, *Streptopelia risoria* (Erickson and Lehrman 1964; Erickson 1970). The cumulative effect of all courtships, not only those of a single male, has been suggested to motivate females in the fish *Chromis cyanea* (de Boer 1981) into reproducing. Alligators are large, aggressive, and potentially dangerous to one another. This extended period of courtship may also serve to reduce anxiety and decrease the possibility of injury caused by close approach for courting. An extended length of courtship prior to mating has been reported in many other reptile species (e.g., Wiewandt 1977; Dugan 1982; Werner 1982). A high number of courtships relative to number of copulations is also frequent among other reptiles, especially lizards (e.g., Greenberg and Noble 1944; Harris 1964; Rand 1967; Auffenberg 1978, 1981).

The timing of alligator courtship correlates well with what is known of reproductive hormone cycles in alligators. Levels of reproductive hormones of both sexes increase rapidly in early April and peak in late April or May. Females ovulate just before the peak of the breeding season (Lance 1986; Guillette *et al.* 1997). Spermatogenesis in the males also peaks at this time (Joanen and McNease 1975, 1980a; Lance 1984, 1985). Alligator movements and basking behaviours suggest they are keenly sensitive to ambient temperatures. Unseasonable weather may cause, either hormonally or through some other physiological means, a shift in the timing or a change in the intensity of alligator courting behaviour. Mean time of egg laying is correlated with ambient temperatures of the preceding spring months (Joanen and McNease 1980b; Kushlan and Jacobsen 1990). The timing of the courting season appears to be similarly correlated.

Alligators that spend the entire year together may show courting behaviours outside of the normal reproductive season. Silverstone (1972) noted courting behaviours as late in the year as 16 November in a 3.2 meter male and a 2.1 meter female near Fort Pierce, Florida. Garrick *et al.* (1978) also noted that a few courtships are seen out of season. I have observed short interactions of courtship-like behaviour as late as November in two identifiable free-roaming alligators in the Okefenokee Swamp, near Waycross, Georgia.

No evidence of pair bonding or individual recognition was found in this study. However, pair bonding in the breeding season may occur, at least in some populations or habitats. Phil Wilkinson (pers. comm.) noted close association between individual males and females in his study of nesting ecology of coastal alligator populations in South Carolina (Wilkinson 1984). Alligators caught in snare traps were often found with an alligator of the opposite sex very near by. These animals did not move away, even when approached by humans. Pooley and Gans (1976) note that Nile crocodiles are monogamous, at least through the course of one reproductive season.

One might hypothesize that courtship interactions would be longest at the start of the season, when animals were unaccustomed to close contact, and then decrease in length through the season. This was the case in two of three seasons studied here. Many early accounts of alligator courtship make no mention of tactile interactions (McIlhenny 1935; LeBuff 1957). McIlhenny (1935) introduced a captive female into an enclosure with a captive male. Although the two alligators had never been in contact with one another, they had been near one another in separate enclosures for many months. Upon introduction of the female, the male immediately mounted and copulated with her. This occurred repeatedly for several days, always without preliminaries.

Immediate mounts, i.e., those with little or no tactile interactions preceding the mount, were commonly seen among the alligators at St Augustine and represented the majority of mounts observed in two of the three study seasons. While extended pre-mounting interactions are common in alligators, so are mounts without any preambles. In this study, the length of the pre-mounting courtship encounter and the length of the mount were not significantly correlated in either males or females. The length of the mount appears to be strongly related to the behaviour of the upper animal while mounted and the reactions of the lower animal, rather than the courtship interaction preceding mounting. Upon mounting, the upper alligator generally presses the lower under water by forcing down on the nuchal scales, cranial table, or snout. Once pressed under, the lower animal usually begins moving forward. If moving rapidly, the upper animal is unable to roll to the side and attempt to mate. Every time the lower animal rises to breath, it is quickly and deliberately pressed under again. Ultimately, the lower animal slows so that the upper can roll to the side, tail search, and attempt to mate.

Demographic patterns in alligator courtship

Early studies of alligator courtship suggested that male alligators initiate courtship and are the most active of the pair in courtship interactions (Joanen and McNease 1971; Neill 1971; Fogarty 1974). Female initiation of courtship is not commonly recognized among vertebrate groups. It is known to occur in several species of crocodilians, however. In addition to this study, initiation of courtship by female alligators has been reported by Silverstone (1972), Garrick (1975), Garrick and Lang (1975, 1977a) and Garrick *et al.* (1978). Accounts of courtship in other crocodilians include references to female initiation in *Alligator sinensis* (Brazaitis 1973), *Caiman crocodilus* (Staton and Dixon 1975, 1976), *Crocodylus acutus* (Lang 1976; Garrick and Lang 1977a), *C. johnstoni* (Compton 1981), *C. niloticus* (Pooley 1982; Kofron 1991), and in the gharial, *Gavialis gangeticus* (Whitaker and Basu 1982).

Examples of female initiation of courtship in other reptiles are few. Christian and Tracy (1982) mention that females of the Galápagos land iguana, *Conolophus pallidus* move to the males in the breeding season. Harris (1964) suggests that female rainbow lizards, *Agama agama*, seek out males for breeding. Female initiation of courtship is known also to occur in the lizards *Leiocephalus carinatus*, *Sauromalus obesus*, *Crotaphytus collaris* and *C. reticulatus* (Carpenter and Ferguson 1979), and *Varanus gilleni* (Murphy and Mitchell 1974). Interestingly, Auffenberg (1983) noted that 3.6% of observed courtships in captive Bengal monitors *Varanus bengalensis* involved females approaching males immediately after those males won combat with other males. He suggested that the females watch the contests between the males. Female wood turtles *Clemmys insculpta* also are known to approach males (Fisher 1945; Harless 1979).

Many species of crocodilians are known to have polygamous mating systems. Male alligators are known to mate with multiple females in a single reproductive season (Joanen and McNease 1971; Fogarty 1974; Garrick *et al.* 1978; this study). Pooley (1982) reported that one large male *Crocodylus niloticus* mated with four different females in a single afternoon. One male *Crocodylus palustris* was observed to mate with at least two females (Whitaker and Whitaker 1978). Whitaker and Basu (1982) described harem groups of several females to one male in *Gavialis gangeticus*.

The mating of individual females by several males has also been reported in the American alligator (LeBuff 1957; Garrick and Lang 1977a; Garrick *et al.* 1978; this study). Females living solely within the territory of a dominant male would have little choice among males with which to mate (Stamp 1983). In some crocodilians, however, females seem to be able to move freely between the territories of dominant males. This has been noted in *Alligator mississippiensis* (Garrick and Lang 1977a) and *Crocodylus acutus* (Lang 1976; Garrick and Lang 1977a). Females of crocodilians do seem to mate mostly with dominant males. This has been observed in *Alligator mississippiensis* (Garrick *et al.* 1978), *Caiman crocodilus* (Staton and Dixon 1976), *Crocodylus niloticus* (Pooley 1982). Female acceptance of these males is still crucial, however. Joanen and McNease (1971) noted that captive female alligators would kill some males introduced into the enclosure.

The meaning of the male-male interactions is unclear. I have seen similar behaviour in other collections of captive alligators in Florida. Sex recognition may not be an important function of alligator courtship behaviours as other behavioural and ecological factors, such as territorial spacing of the males, might serve this purpose. Social factors that keep males widely separated in the wild can not function in the very high densities and limited space of captivity. Males may approach other males as "supernormal females". Males might be unable to distinguish the sex of other alligators and court with any receptive animal, although this hypothesis seems unlikely. It is also conceivable that male alligators use courtship-like behaviours in non-aggressive competition for social position. Homosexual interactions of this sort has not been reported to occur in the wild. Joanen and McNease (1972) did, however, often find males in close association with one another during the breeding season in the Louisiana coastal marshes.

Homosexual courtship and mounting has been reported in the lizards *Anolis lineotropus* (Rand 1967) and *Varanus komodoensis* (Auffenberg 1981). In both cases, these behaviours were performed by young, relatively inexperienced, males. This was not the case in the present study.

There is evidence that courting alligators also form groups in the wild. Joanen and McNease (1971, 1972) reported groups of alligators in close association during the courtship season. These groups, consisting of up to ten adult alligators of various size classes, were never observed outside of the breeding season. McIlhenny (1935) also observed an alligator, presumed to be a female, being followed by several males. It is possible that in times past, when alligator population densities were much higher than today, large courting groups were the normal form of courtship encounters. A few species of crocodiles, such as *Crocodylus niloticus* (Modha

1968) and *C. acutus* (Garrick and Lang 1977a) are known to form large aggregations in the breeding season.

ACKNOWLEDGEMENTS

This work would not have been possible without the direction and assistance of Dr Walter Auffenberg, Prof. F. Wayne King, and the late Dr Archie Carr, Jr. During the 1981 study season, EARTHWATCH volunteers, provided by The Center for Field Research, assisted in collection of behavioural data. Thanks also to Mr David Drysdale, owner of the St Augustine Alligator Farm, and to his entire staff, most notably Mr Tim Williams and Mr Mark Wise, for their support, instruction and untiring assistance.

REFERENCES

Altmann, J., 1974. Observational study of behavior: Sampling methods. *Behaviour* **49**(3–4): 227–65.

Altmann, S. A., 1965. Sociobiology of rhesus monkeys. II. Stochastics of social communication. *J. Theor. Biol.* **8**: 490–522.

Alvarez del Toro, M., 1969. Breeding the spectacled caiman, *Caiman crocodilus* at Tuxtla Gutierrez Zoo. *Int. Zoo Yrbk.* **9**: 35–36.

Alvarez del Toro, M., 1974. Los Crocodylia de Mexico. Inst. Mexicano de Recursos Naturales Renovables. 70 Pp.

Auffenberg, W., 1978. Social and feeding behavior in *Varanus komodoensis*. Pp. 301–31 *in* Behavior and Neurology of Lizards ed by N. Greenberg and P. MacLear. Nat. Inst. Mental Health: Washington, DC.

Auffenberg, W., 1981. The Behavioral Ecology of the Komodo Monitor. University Presses of Florida. Gainesville. 406 Pp.

Auffenberg, W., 1983. Courtship behavior in *Varanus bengalensis* (Sauria: Varanidae). Pp. 535–51 *in* Advances in Herpetology and Evolutionary Biology ed by A. G. J. Rhodin and K. Miyata. Museum of Comparative Zoology: Cambridge, Massachusetts.

Auffenberg, W., 1994. The Bengal Monitor. University Press of Florida, Gainesville. 560 Pp.

Bakeman, R. and Gottman, J. M., 1986. Observing interaction: An introduction to sequential analysis. Cambridge University Press: Cambridge. 221 Pp.

Beach, F., 1944. Responses of captive alligators to auditory stimulation. *Amer. Nat.* **78**: 481–505.

Brazaitis, P., 1973. The identification of living crocodilians. *Zoologica* **58**(3–4): 59–101.

Carpenter, C. C. and Ferguson, G. W., 1977. Variation and evolution of stereotyped behavior in reptiles. Pp. 335–554 *in* Biology of the Reptilia, Vol. 7: Ecology and Behaviour A ed by C. Gans and D. W. Tinkle. Academic Press: New York.

Carr, A. F., 1976. Excerpts from the life of an alligator: A re-appraisal of "The Alligator's Life History." Foreword. Pp. v–x *in* The Alligator's Life History ed by E. A. McIlhenny. Facsimile reprint, Society for the Study of Amphibians and Reptiles Misc. Publ.

Christian, K. A. and Tracy, C. R., 1982. Reproductive behavior of Galápagos land iguanas, *Conolophus pallidus*, on Isla Santa Fe, Galápagos. Chapter 20. Pp. 366–79 *in* Iguanas of the World: Their Behavior, Ecology, and Conservation ed by G. M. Burghardt and A. S. Rand. Noyes Publ.: Park Ridge, New Jersey.

Compton, A. W., 1981. Courtship and nesting behaviour of the fresh-water crocodile, *Crocodylus johnstoni*, under controlled conditions. *Aust. Wildl. Res.* **8**(2): 443–50.

Cott, H. B., 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile *(Crocodylus niloticus)* in Uganda and northern Rhodesia. *Trans. Zool. Soc. Lond.* **29**: 211–356.

Crews, D., 1975. Effects of different components of male courtship behavior on environmentally induced ovarian recrudescence and mating preferences in the lizard *Anolis carolinensis*. *Anim. Behav.* **23**: 349–56.

Crews, D., 1978. Integration of internal and external stimuli in the regulation of lizard reproduction. Pp. 149–71 *in* Behavior and Neurology of Lizards ed by N. Greenberg and P. MacLear. Nat. Inst. Mental Health: Washington, DC.

Crews, D., 1980. Studies in squamate sexuality. *Bioscience* **30**: 835–38.

de Boer, B. A., 1981. Influence of population density on the territorial, courting and spawning behaviour of male *Chromis cyanea*. *Behaviour* **77**: 99–120.

Deraniyagala, P. E. P., 1939. The Tetrapod Reptiles of Ceylon. Vol. 1. Testudinates and Crocodilians. Colombo. 412 Pp.

Dugan, B., 1982. The mating behavior of the green iguana, *Iguana iguana*. Chapter 18. Pp. 320–41 *in* Iguanas of the World: Their Behavior, Ecology, and Conservation ed by G. M. Burghardt and A. S. Rand. Noyes Publ.: Park Ridge, New Jersey.

Erickson, C. J., 1970. Induction of ovarian activity in female ring doves by androgen treatment of castrated males. *J. Comp. Physiol. Psychol.* **71**: 210–15.

Erickson, C. J. and Lehrman, D. S., 1964. Effect of castration of male ring doves upon ovarian activity of females. *J. Comp. Physiol. Psychol.* **58**: 164–66.

Fisher, C., 1945. Early spring mating of the wood turtle. *Copeia* **1945**: 175–76.

Fogarty, M. J., 1974. The ecology of the Everglades alligator. Pp. 367–73 *in* Environments of South Florida: Past and Present ed by P. J. Gleason. Mem. Miami Geol. Survey No.2.

Gadow, H., 1901. Amphibia and Reptiles. MacMillan and Co.: London.

Garrick, L. D., 1974. Vocalizations of adult American alligators. *Amer. Zool.* **14**: 1278. Abstract.

Garrick, L. D., 1975. Love among the alligators. *Anim. Kingdom* **79**(2): 2–8.

Garrick, L. D. and Lang, J. W., 1975. Alligator courtship. *Amer. Zool.* **15**(3): 813. Abstract.

Garrick, L. D. and Lang, J. W., 1977a. Social signals and behavior of adult alligators and crocodiles. *Amer. Zool.* **17**: 225–39.

Garrick, L. D. and Lang, J. W., 1977b. The alligator revealed. *Natural History* **June/July**: 54–60.

Garrick, L. D., Lang, J. W. and Herzog, H. A., Jr, 1978. Social signals of adult American alligators. *Bull. Am. Mus. Nat. Hist.* **160**(3): 153–92.

Goodwin, T. M. and Marion, W. R., 1979. Seasonal activity ranges and habitat preferences of adult alligators (Reptilia, Crocodilidae) in a north-central Florida lake. *J. Herpetol.* **13**(2): 157–63.

Gottman, J. M. and Bakeman, R., 1979. The sequential analysis of observational data. Pp. 185–206 *in* Social Interaction Analysis: Methodological Issues ed by M. E. Lamb, S. J. Suomi and G. R. Stephenson. University of Wisconsin Press: Madison.

Greenberg, B. and Noble, G. K., 1944. Social behavior of the American chameleon *(Anolis carolinensis* Voigt). *Physiol. Zool.* **17**: 392–439.

Guillette, L. J., Woodward, A. R., Crain, D. A., Masson, G. R., Palmer, B. D., Cox, M. C., Qui, Y. X. and Orlando, E. F., 1997. The reproductive cycle of the female American alligator *(Alligator mississippiensis). Gen. Comp. Endocrinol.* **108**(1): 87–101.

Harless, M., 1979. Social behavior. Chapter 21, Pp. 475–92 *in* Turtles: Perspectives and Research ed by M. Harless and H. Morlock. John Wiley and Sons: New York.

Harper, F., 1930. Alligators of the Okefenokee. *Sci. Monthly* **31**: 51–67.

Harris, V. A., 1964. The Life of the Rainbow Lizard. Hutchinson: London. 164 Pp.

Hazlett, B. H. and Bossert, W. H., 1965. A statistical analysis of the aggressive communication system of some hermit crabs. *Anim. Behav.* **13**(2): 357–73.

Herzog, H. A., 1974. The vocal communication system and related behaviors of the American alligator (*Alligator mississippiensis*) and other crocodilians. M.Sc. thesis, University Tennessee, Knoxville. 83 Pp.

Joanen, T. and McNease, L., 1971. A telemetric study of nesting female alligators in Rockefeller Refuge, Louisiana. *Proc. Ann. Conf. S.e. Assoc. Game and Fish Comm.* **24**: 175–93.

Joanen, T. and McNease, L., 1972. A telemetric study of adult male alligators on Rockefeller Refuge, Louisiana. *Proc. Ann. Conf. S.e. Assoc. Game and Fish Comm.* **26**: 252–75.

Joanen, T. and McNease, L., 1975. Notes on the reproductive biology and captive propagation of the American alligator. *Proc. Ann. Conf. S.e. Assoc. Game and Fish Comm.* **29**: 407–15.

Joanen, T. and McNease, L., 1980a. Reproductive biology of the American alligator in southwest Louisiana. Pp. 153–59 *in* Reproductive Biology and Diseases of Captive Reptiles ed by J. B. Murphy and J. T. Collins. Society for the Study of Amphibians and Reptiles Contr. to Herpetol., No. 1.

Joanen, T. and McNease, L., 1980b. Time of egg deposition for the American alligator. *Proc. Ann. Conf. S.e. Assoc. Fish Wildl. Agen.* **33**: 15–19.

Kaufmann, J. H. and Kaufmann, A., 1963. Some comments on the relationship between field and laboratory studies of behavior, with special reference to coatis. *Anim. Behav.* **11**: 464–69.

Kellogg, R., 1929. The habits and economic importance of alligators. *U.S. Dept. Agric. Tech. Bull.* No. **147**: 1–36.

Kofron, C. P., 1991. Courtship and mating of the Nile crocodile (Crocodylus niloticus). *Amphib. — Rept.* **12**: 39–48.

Kushlan, J. A. and Jacobsen, T., 1990. Environmental variability and the reproductive success of Everglades alligators. *J. Herpetol.* **24**(2): 176–84.

Laidlaw, G. F. and Murray, M. R., 1933. Melanoma studies III. A theory of pigmented moles. Their relation to the evolution of hair follicles. *Amer. J. Pathol.* **9**(6): 827–38.

Lance, V., 1984. Endocrinology of reproduction in male reptiles. *Symp. Zool. Soc. Lond.* **52**: 357–83.

Lance, V., 1985. Reproduction in the American alligator *Alligator mississippiensis*. Pp. 253–55 *in* Current Trends in Comparative Endocrinology ed by B. Lofts, and W. N. Holmes. Hong Kong University Press: Hong Kong.

Lance, V., 1986. Hormonal control of reproduction in crocodilians. Chapter 42. Pp. 409–16 *in* Wildlife Management: Crocodiles and Alligators ed by G. J. W. Webb, S. C. Manolis and P. J. Whitehead. Surrey Beatty & Sons: Chipping Norton.

Lang, J. W., 1976. American crocodile courtship. *Amer. Zool.* **16**: 197. Abstract.

LeBuff, C. R., 1957. Observations on captive and wild North American crocodilians. *Herpetologica* **13**(1): 25–28.

Lehner, P. N., 1979. Handbook of Ethological Methods. Garland STPM Press: New York. 403 Pp.

McIlhenny, E. A., 1935. The Alligator's Life History. Christopher Publishing House, Boston. 117 Pp.

Modha, M. L., 1968. Basking behavior of the Nile crocodile on Central Island, Lake Rudolf. *E. Afr. Wildl. J.* **6**: 81–88.

Morris, D., 1964. The response of animals to a restricted environment. *Symposia Zool. Soc. Lond.* **13**: 99–118.

Morris, D., 1966. The rigidification of behaviour. *Phil. Trans. Royal Soc. Lond.*(B) **251**: 327–30.

Murphy, J. B. and Mitchell, L. A., 1974. Ritualized combat behavior of the pygmy molga monitor lizard, *Varanus gilleni* (Sauria: Varanidae). *Herpetologica* **30**: 90–97.

Neill, W. T., 1971. The Last of the Ruling Reptiles: Alligators, Crocodiles, and their Kin. Columbia University Press: New York. 486 Pp.

Pooley, A. C., 1982. Discoveries of a Crocodile Man. Williams Collins Sons and Co.: London. 213 Pp.

Pooley, A. C. and Gans, C., 1976. The Nile crocodile. *Sci. Am.* **234**: 114–24.

Rand, A. S., 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus. Proc. U.S. Nat. Mus.* **122**: 1–79.

Sackett, G. P., 1978. Measurement in observational research. Pp. 25–45 *in* Observing Behavior. Vol. 2: Data Collection and Analysis Methods ed by G. P. Sackett. University Park Press: Baltimore.

Sackett, G. P., 1979. The lag sequential analysis of contingency and cyclicity in behavioral interaction research. Pp. 623–49 *in* Handbook of Infant Development ed by J. D. Osofsky. John Wiley and Sons: New York.

Schmidt, K. P., 1922. The American alligator. *Field Mus. Nat. Hist.* leaflet #3: 25–38.

Silverstone, P. A., 1972. Final report of a study of the behavior of the American alligator *(Alligator mississippiensis)* at the Fort Pierce, Florida Bureau of the Smithsonian Institution. Unpubl. report. 55 Pp.

Stamp, J. A., 1983. Sexual selection, sexual dimorphism, and territoriality. Pp. 169–204 *in* Lizard Ecology: Studies of a Model Organism ed by R. B. Huey, E. R. Pianka and T. W. Schoener. Harvard University Press: Cambridge, Massachusetts.

Staton, M. A. and Dixon, J. R., 1975. Studies on the dry season biology of *Caiman crocodilus crocodilus* from the Venezuelan llanos. *Mem. Soc. Cienc. Nat. La Salle* **35**(101): 237-65.

Staton, M. A. and Dixon, J. R., 1976. Breeding biology of the spectacled caiman *Caiman crocodilus crocodilus* in the Venezuelan llanos. *U.S. Fish Wildl. Service, Wildl. Res. Rep.* No. **5**: 1-21.

Vliet, K. A., 1986. Social behavior of the American alligator. Pp. 203-11 *in* Crocodiles. IUCN Publ.: New ser., Caracas.

Vliet, K. A., 1987. A quantitative analysis of the courtship behavior of the American alligator *(Alligator mississippiensis)*. Ph.D. dissertation, University of Florida, Gainesville. 197 Pp.

Vliet, K. A., 1989. Social displays of the American alligator *(Alligator mississippiensis)*. *Amer. Zool.* **29**: 1019-031.

Von Düring, M. and Miller, M. R., 1979. Sensory nerve endings of the skin and deeper structures. Chapter 6. Pp. 407-41 *in* Biology of the Reptilia. Vol. 9: Neurology A ed by C. Gans, R. G. Northcutt and P. Ulinski. Academic Press: New York.

Werner, D. I., 1982. Social organization and ecology of land iguanas, *Conolophus subcristatus*, on Isla Fernandina, Galápagos. Chapter 19. Pp. 342-65 *in* Iguanas of the World: Their Behavior, Ecology, and Conservation ed by G. M. Burghardt and A. S. Rand. Noyes Publ.: Park Ridge, New Jersey.

Whitaker, R. and Basu, D., 1982. The gharial *(Gavialis gangeticus)*: A review. *J. Bombay Nat. Hist. Soc.* **79**: 531-48.

Whitaker, Z. and Whitaker, R., 1978. Notes on captive breeding in mugger *(Crocodylus palustris)*. *J. Bombay Nat. Hist. Soc.* **75**(1): 228-31.

Wiewandt, T. A., 1977. Ecology, behavior, and management of the Mona Island ground iguana, *Cyclura stejnegeri*. Ph.D. dissertation, Cornell University, Ithaca, New York.

Wilkinson, P., 1984. Nesting ecology of the American alligator in coastal South Carolina. S. Carolina Wildland Marine Res. Dept., Div. Wildl. and Freshwater Fish. 113 Pp.

Zar, J. H., 1974. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey. 620 Pp.