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JZAR Research article

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First observations on the courtship, mating, and nest visit behaviour of the Philippine crocodile (*Crocodylus mindorensis*) at the Cologne Zoo

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Keywords:
ex situ conservation, husbandry, nest visits, reproductive behaviour

Article history:
Received: 6 December 2013
Accepted: 12 September 2014
Published online: 31 October 2014

Abstract

The aim of this study was to gain a better understanding of the social and in particular reproductive behaviour of the Critically Endangered Philippine crocodile. *Crocodylus mindorensis* has been a focus for international conservation breeding measures for about two decades. Since little scientific data have been gathered on the biology and ecology of the species so far, its breeding remains a challenge. In order to identify behavioural patterns that trigger courtship behaviour, and to determine when sociopositive interactions increase and the animals are ready for reproduction, a pair of two adult *C. mindorensis* at Cologne Zoo was systematically observed between August 2011 and July 2012 for a total of 583 hours. Observations took place using all occurrences recording and scan sampling, focusing on pre-, post- and actual mating behaviour. We present a detailed documentation of copulations with behaviours such as growling, roaring, and bubbling. Bubbling in both sexes was observed prior to copulations and decreased with the end of the mating season, supporting the assumption that it can be referred to as courtship behaviour. Behaviours that indicate the approach of the breeding season, such as approaches to the dividing slide, bubbling and nest building, could be distinguished. Our findings should help to improve breeding efforts under captive husbandry conditions and thus contribute to the conservation breeding of this highly endangered and difficult to keep crocodilian species.

Introduction

The Philippine crocodile is a relatively small freshwater crocodile endemic to the Philippines. It was once found all over the Philippines, but due to commercial exploitation and habitat destruction, natural populations are highly fragmented and declining (Banks 2000). The species is probably the most severely threatened crocodilian worldwide with an estimated population size of 100 to 250 mature individuals in the wild (Tarun et al. 2004) and is listed as Critically Endangered by IUCN (Crocodile Specialist Group 1996) and on CITES Appendix I.

Nationally, the Philippine crocodile and its habitat are protected by the Philippine Wildlife Act since 2004. The Mabuwaya Foundation, in collaboration with the University of San Mariano, manages the only currently successful *in situ* conservation programme for the Philippine crocodile on the Philippine Island of Luzon (van der Ploeg and van Weerd 2004).

Ex situ captive breeding programmes under Memoranda of Agreement with the Philippine Government are underway in the US, Australia and recently also in Europe (Ziegler et al. 2013a). Due to its fragile status in the wild and on the recommendation of the IUCN Crocodile Specialist Group (CSG) for ex situ management, the Philippine crocodile has top priority in the Regional Collection Plan of the Taxon Advisory Group (TAG) within the European Association of Zoos and Aquaria (EAZA). Recently, EAZA has established a conservation breeding programme (European studbook, ESB) for those individuals kept in Europe, which is managed by Cologne Zoo (Ziegler et al. 2013a). Recent molecular studies have revealed the existence of hybrids between *C. mindorensis* and *C. porosus* among farms in the Philippines (Tabora et al. 2012), underlining the importance of scientifically led captive breeding management to maintain genetic integrity (Hauswaldt et al. 2013).

In order to start the first Philippine crocodile captive breeding programme in Europe, 15 young individuals were imported on loan from the Philippine Government from the Palawan Wildlife Rescue and Conservation Centre (PWRCC) in 2006 and allocated across six European institutions (currently 14 remaining individuals are kept at Bergen Aquarium, Cologne Zoo, Krokodille Zoo Eskilstrup, London Zoo, Paignton Zoo, and Zurich Zoo); additional *C. mindorensis* are held at the crocodile zoo in Protivin, Czech Republic (Ziegler et al. 2013a).

Little is known about the reproductive behaviour of *C. mindorensis* either in the wild or in captivity. Reproductive behaviour includes courtship, mating, nesting, incubation and hatching. Courtship and mating consist of a sequence of attraction and advertisement behaviours followed by pair formation, precopulatory behaviours and copulation (Lang 1987). Most information about reproductive behaviour has been obtained from observations of captive Philippine crocodiles. Both females and males become reproductively active in captivity at an average length of 1.5 m and at a body weight of about 15 kg (van Weerd 2010). According to Ross and Alcala (1983), females become mature at the age of ten years and a length of 1.3 m, whereas males reach sexual maturity later, at 15 years of age and a length of 2.1 m. A few months prior to the onset of the breeding season, the gathering of nesting materials is initiated (Sumiller and Cornel 2008). During the dry season and after mating, females generally build mound nests in the vicinity of water from a mixture of sand, mud and plant material consisting of organic matter such as dried leaves, branches and twigs (Alcala et al. 1987; Akmad and Pomares 2008). Nest building is performed during both day and night, but mostly at night, from February to April or May (Alcala et al. 1987). Nesting activities occur daily within the breeding season (Sumiller and Cornell 2008). In addition, multiple nesting has been observed in a small number of pairs in captive breeding facilities during the months of February to October (van Weerd 2010). Mating can be observed starting in January at the beginning of the dry season both in the wild and in captivity (van Weerd 2010). According to Alcala et al. (1987), courtship, nest building and mating occur between January and May in captive Philippine crocodiles. Copulations in this species occur between 0400 and 0700 in the water and are accompanied by acoustic communication such as groaning and bellowing sounds (Alcala et al. 1987). According to Sumiller and Cornell (2008), some females were observed to lay eggs three to five weeks after copulation. Oviposition in the wild takes place in April and May with an incubation period of 65–78 days. Mean clutch size is 20.1 to 26 eggs (van Weerd 2010). In captivity, oviposition occurs from April to August (Alcala et al. 1987). Average clutch size is 15.7 (7–25) to 26 (18–33) with an extended incubation period of 77–85 days. Eggs are laid during the night or in the early morning (Alcala et al. 1987). Females carry out routine nest visits in the late afternoon and early morning (Akmad and Pomares 2008). *C. mindorensis* exhibits temperature-dependent sex determination and under artificial incubation females are predominantly produced at 30–32° C and males mainly at 33° C (Sumiller and Cornell 1998).

Generally, it is difficult to breed Philippine crocodiles since they tend to be highly aggressive in captivity (Yuyek 2008). Pairing time is very critical due to incompatibility, which often results in fighting and high mortality rates (Sumiller and Cornel 2008). Fighting and aggression has been found to be minimised by exposure to a mate only in late February until early March (Sumiller and Cornel 2008). Consequently, breeding mates should be held separated out of the natural breeding season in order to prevent fighting, and adults should be kept separate until a suitable time for mating.

As it is not yet known which external or internal factors trigger seasonal breeding in *C. mindorensis*, it cannot be assumed that mating occurs during the same period in individuals kept at differing latitudes out of their natural habitat. Successful breeding in captivity requires a good understanding of the species' reproductive biology and its behavioural requirements. In order to build up a stable population in European zoos, it was necessary to assess when sociopositive interactions increase, such that potential mates can be introduced.

Thus a long-term study on the reproductive behaviour of a breeding pair at Cologne Zoo was conducted starting in August 2011, with the objective of identifying behavioural patterns leading to courtship in order to provide optimal conditions for successful breeding in captive Philippine crocodiles. Thus, behavioural observations of the breeding pair at Cologne Zoo took place prior, within and after the natural breeding season between August 2011 and August 2012, focusing on social interactions and nest visit behaviour. As mates were kept separately out of the breeding season, nest visits by the female, sounds and approaches to the slide dividing the enclosures were used to provide evidence of the start of courtship behaviour. Accordingly, introductions of the pair and mating were observed in February 2012.

Material and methods

Animals and housing

The study group consisted of a pair of two adult Philippine crocodiles, transferred from a Philippine breeding facility to Cologne Zoo Aquarium in 2007 based on a Memorandum of Agreement with the Philippine Government (Hauswaldt et al. 2012; Ziegler et al. 2013a). At the beginning of the study, both animals were of a sexually mature size and age. The female (Mindo) was 13 years old, with a length of 153 cm and a weight of 11.6 kg, measured in May 2011. The male (Pinoy) was 11 years old, but was slightly bigger, with a length of 161 cm, and a weight of 16 kg, likewise measured in May 2011 (Ziegler et al. 2011).

Figure 1. Philippine crocodile exhibit at Cologne Zoo: A) Male exhibit (photo T. Ziegler); B) female exhibit (photo T. Ziegler) with slide in middle of facility (the nesting area on the right side is not visible, see Fig. 2D).

Table 1. Observation periods divided into pre-mating, mating and post-mating periods based on the timing of the natural mating season.

Observation period	Time schedule	Method
Pre-mating	15 August 2011 – 07 December 2011	Direct observations by day
Mating	07 February 2012–26 March 2012 05 March 2012 – 29 March 2012	Direct observations by day Video recordings by night
Post-mating	13 July 2012 – 04 August 2012 16 July 2012 – 26 July 2012	Direct observations by day Video recordings by night

The public enclosure design (Fig. 1) was based on current recommendations for crocodile husbandry (Jensch et al. 2009); for details see Ziegler et al. (2011). The structure of the enclosure simulates a natural river landscape. The overall surface area measures 62 m^2, consisting of land sectors totalling 22 m^2 and an s-shaped water area of 40 m^2 with a maximum depth of 80 cm. Constantly high water quality is ensured by a sand-filter, a UV-filter and a heat exchanger. The entire water volume is exchanged eight times a day and water temperature is held constant at 28 °C. Two slider systems enable separation into at least two and at most three parts. The slides are 40 cm high, consist of metal and are perforated to enable visual, olfactory, acoustic and probably also tactile contact by means of vibrations underwater. The whole exhibit is surrounded by 2 m x 22 m laminated safety glass. The exhibit area is covered by a glass roof, such that sunlight has an influence on light regime and temperature. The enclosure is equipped with two heat plates (300 watt), three Osram Ultravitalux lights (300 watt) and three Radium-HRI lights, which create a wide spectrum of different thermal sources that allow for behavioural thermoregulation. The additional light sources are switched on for 12 hours, and the heat plates for 24 hours a day and held at a constant temperature of 26° C. Integrated plants on land and bogwood inside the water provide appropriate conditions to retrieve, to avoid thermal sources and also facilitate the transition from water to land. The enclosure sector inhabited by the female contains a nesting side provided with organic material and soil. The animals are fed during target training, based on operant conditioning techniques through positive reinforcement, that provides for behavioural enrichment and enables to easily separate them, for example in case of intraspecific aggression, such that stress can be kept at a minimum.

Data collection

The study took place between August 2011 and August 2012, conducted by four different observers on 106 days for a total of 583 hours of direct observations. Night-time observations were made using video recording via a camera system (AXIS Camera Station) and were analysed separately using the software AXIS Camera Station Client.

During direct observations, the daily time frame was divided into two shifts, one extending from 0700 to 1230, the other one from 1230 to 1800, such that each time period was equally represented in the final sample (Martin and Bateson 2007). Inter-observer reliability assessment was conducted between consecutive observers, who monitored the animals simultaneously to ensure comparable data sets. Inter-observer values over 97% were considered unbiased and reliable (Martin and Bateson 2007).

In order to assess changes in behaviour patterns over time, and to determine the timing when aggression is low and the animals are predisposed to introduction, all social behaviours and signs of nesting activity were collected. The behaviours recorded were socio-positive interactions (approaches to the dividing slide even when the conspecific was absent or on the opposite side of the slide), intraspecific communication (bubbling, i.e. emitting air blisters through nostrils or mouth, occurring exclusively under the water surface), and nesting activities (nest visits, gathering nesting material, or scratching nest material with hind legs). Behaviours of both individuals were recorded by behaviour sampling using all occurrences recording (Martin and Bateson 2007). Behaviour sampling is mainly used for recording rare but significant types of behaviour, such as fights or copulations, where it is important to record each occurrence and where rare behaviour patterns would tend to be missed by focal or scan sampling (Martin and Bateson 2007). It was expected that behaviours in both sexes, such as approaches to the slide and acoustic or visual signals, including bubbling and vocalisations, as well as nest visiting in the female, would be prevalent during the natural mating season. Furthermore, it was hypothesised that the female would visit the nest more often in the morning and the evening than during the rest of the day.

Based on preliminary results obtained from behaviour sampling, indicating a high degree of bubbling and approaches to the slide performed by both sexes, as well as an increasing occurrence of nesting behaviour, the first introduction occurred. Introductions took place on 3, 6 and 7 February 2012. The behaviour during the introductions was recorded via ad libitum pilot observations (Martin and Bateson 2007), recording each occurrence of each type of social behaviour.

Data analysis

The data were divided into pre-mating, mating, and post-mating periods (Table 1). Observation periods were selected based on the timing of the naturally occurring mating season. For each behaviour recorded, frequencies per 30 minutes were calculated and compared within the three observation periods. In addition to direct observations, video observations were analysed in order to calculate differences in the occurrence of nesting behaviour during day and night. Due to the small sample size and because the data were neither normally distributed nor independent, nonparametric tests were applied. Changes in behaviour between the different observation periods were compared using Wilcoxon signed-rank tests for paired samples and Friedman tests for more than two paired samples (Lamprecht 1992). The Mann–Whitney U-test was used to assess individual differences (Lamprecht 1992). Differences were considered significant at $P < 0.05$ (Lamprecht 1992).

Results

Courtship behaviour

Nest visits and nesting activities (scratching with hind feet) were first observed in mid-January 2012. The prefabricated nest was shaped like a hill, with a height of 60 cm and a diameter of 1 m. The temperature within the nest varied between 25 °C and 34 °C.

Introductions of the pair (Figure 2) took place at the beginning of February 2012, corresponding to the beginning of the mating season in the natural habitat. Introductions took place on 3 February (7 h 57 min), 6 February (3 h 53 min), and 7 February (2 h 15 min). At the beginning of the introduction both individuals showed acoustic and visual signals, such as roaring and bubbling.

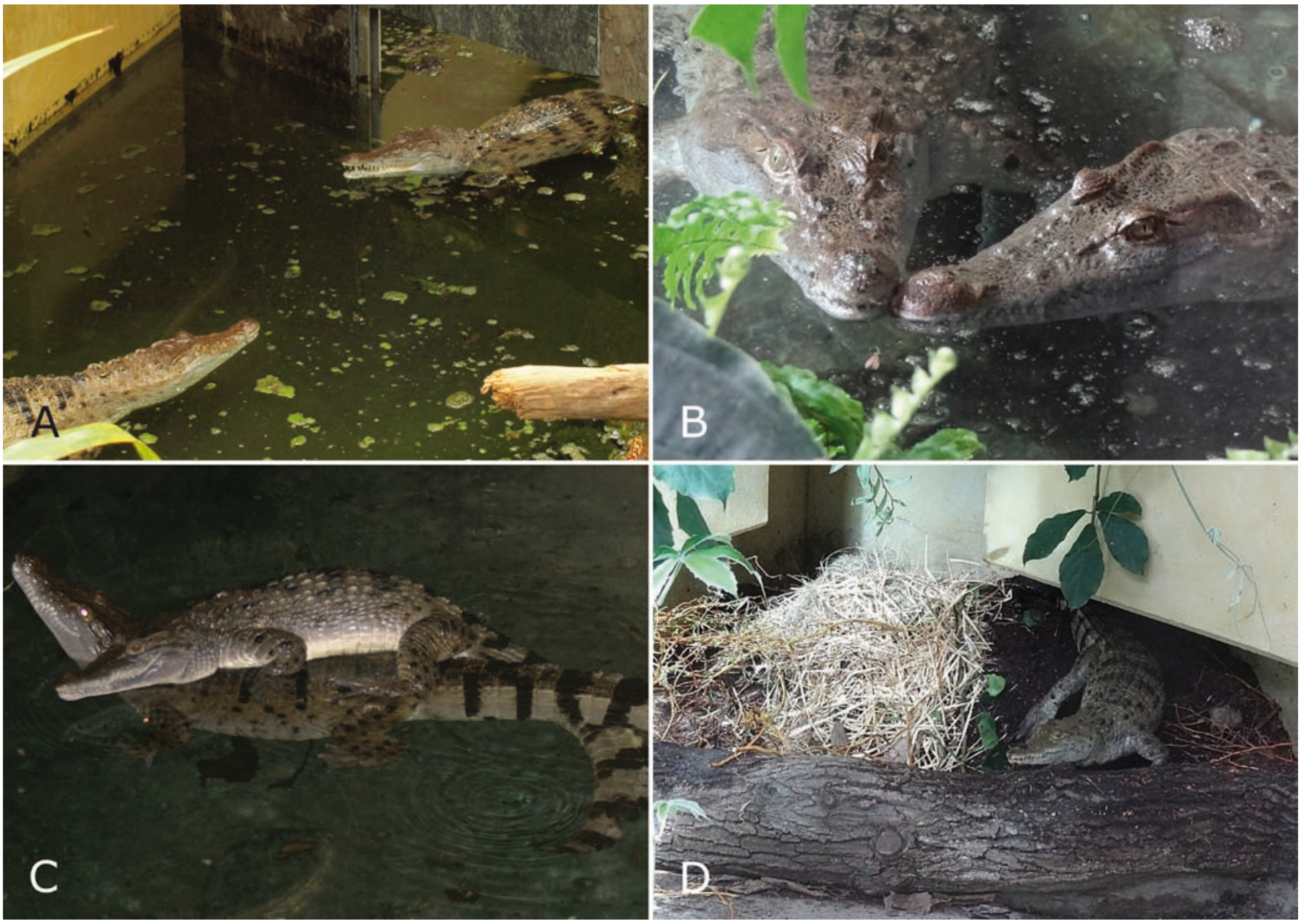

Figure 2. Reproductive behaviour patterns observed at the Cologne Zoo: A) Approaching of sexes at the opened slide between male (left) and female (right) exhibits (photo D. Karbe), B) Snout tip contact (photo A. Rauhaus), C) Copulation at night of 3 February 2012 (photo T. Ziegler), D) female scratching on top of nest (photo A. Rauhaus).

Pair-formation was shown as cycling movements of both animals round one another in the water. In most cases the female swam around the male, sometimes beneath or above him. Pre-copulation behaviour included mounting or growling when one of the animals displayed dominating behaviour. In such cases, both individuals swam together, submerged and re-emerged again. The male especially would dive beneath the female before and during mounting. The female responded with bubbling.

Copulations took place after these behaviours. The animals wrapped their tails around one another and alternately submerged and emerged. The general procedure for copulations observed during three days in 2012 was as follows. The first approach started with mutual recognition. Mostly, the animals were located face to face and kept one another under observation for at least a few minutes. Then, one of the crocodiles, or sometimes both of them, approached slightly. During the first introduction it was 50 minutes until the first physical contact was observed. First physical contact usually started with the tips of the snouts or positioning of their heads in parallel with one another. Meanwhile, at least one of the animals, but generally both of them, kept bubbling.

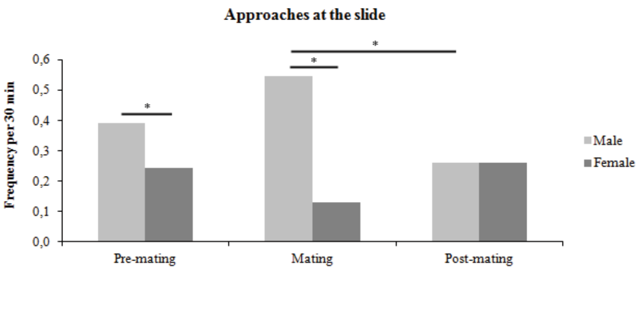

Figure 3. Mean frequencies of approaches to the dividing slide (* $P < 0.05$, Friedmann test respectively Mann–Whitney U-test).

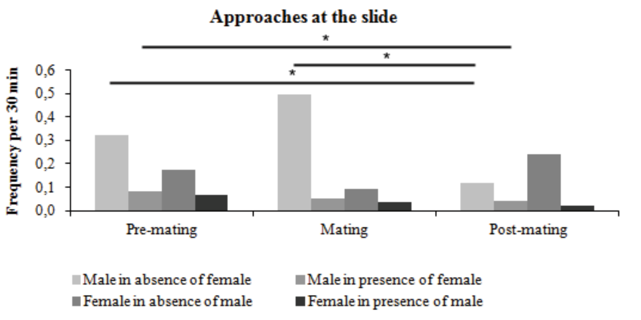

Figure 4. Mean frequencies of approaches to the dividing slide, with respect to the presence or absence of the respective conspecific (*$P < 0.05$, Friedmann test).

Figure 5. Female (with male on top) bubbling through nostrils (photo A. Rauhaus).

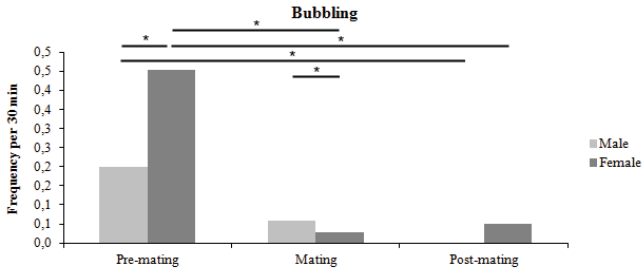

Figure 6. Mean frequencies of bubbling (* p<0.05, Friedmann test respectively Mann–Whitney U-test).

Commonly both animals raised their heads with mouth wide open. While snouts were in contact, growling and roaring took place. Subsequent to the acoustic signals, the animals alternately held their head laterally pressed into the nape of the other's neck. The animal which exhibited this behaviour, usually the male, also started mounting. The female was pressed deeper into the water and continued to bubble. During the pre-mating procedure, they alternately submerged and emerged, or sometimes swam around each other. Subsequently, the male turned into a dorsolateral position and actual copulation took place. During copulation both tails were erected and slung around one another. After mating, the animals rapidly retreated from each other. Between copulations both crocodiles often approached, lay, swam, or submerged close together. During the first two introductions, 16 and nine copulations were recorded respectively. Copulations lasted on average 3.3 min and were observed up to twice per hour.

The third introduction resulted in aggressive behaviour by the female. Only one copulation took place during this morning; thereafter, the female was observed following the male, which frequently moved away from her, and mountied him several times, showing the same behaviour as the male had previously, e.g. pressing him under water. Subsequently, the male entered the land section and the nest. The female positioned herself next to the male, blocking the way back into the water. Both animals started roaring and the female slapped her tail against the male, which snapped in her direction while trying to leave the nest. After some bites by the female against the male's neck, the animals were separated.

Approaches by each sex to the dividing slide

The mean frequencies of approaches towards the dividing slide are given in Figure 3. During the pre-mating period as well as during mating season, the male approached the slide significantly more often than the female ($P < 0.05$). Approaches during the post-mating period were almost identical in both individuals. The male approached the slide significantly more frequently during the mating season than during the post-mating period ($P < 0.05$). The female showed a tendency towards a lower degree of approaches to the slide before and after the mating season but the differences were not statistically significant (Figure 3).

When the female was present, the male displayed a significantly higher amount of approaches to the slide during the post-mating period than during the pre-mating period ($P < 0.05$). When the female was absent, the male approached the slide significantly more often during the mating season compared to the post-mating period ($P < 0.05$). There was also a significant difference in frequency in the pre-mating period compared to the post-mating period ($P < 0.05$). Interestingly, the male stayed close to the slide more often whenever the female was absent. However, the differences between the pre-mating and post-mating seasons were not significant. In contrast, the female did not show any significant differences in approaching the dividing area, regardless of whether or not the male was present (Figure 4).

Bubbling

The occurrence of bubbling (Figure 5) during the different observation periods is shown in Figure 6. The female performed bubbling significantly more often during the pre-mating season compared to the mating and post-mating period ($P < 0.05$). In contrast, the male showed a decrease in the frequency of bubbling over time with a statistically significant difference between the pre-mating and the post-mating period ($P < 0.05$). In general, the female performed bubbling significantly more often than the male during the pre-mating period ($P < 0.05$), whereas the male showed a significantly higher degree of bubbling than the female during the actual mating season ($P < 0.05$). During the post-mating

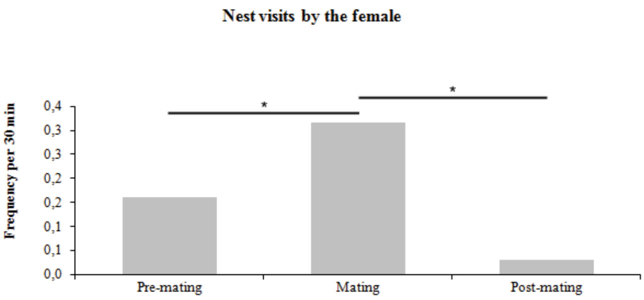

Figure 7. Mean frequencies of nest visits by the female (* $P < 0.05$, Friedmann test).

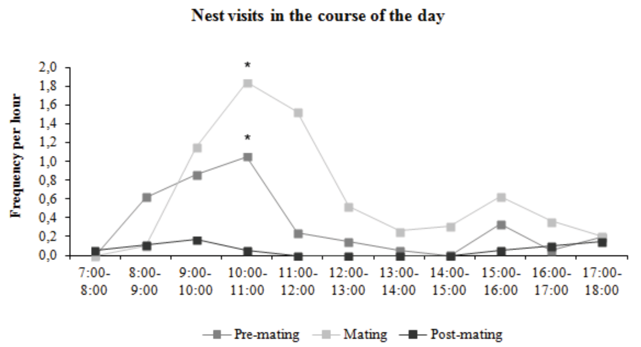

Figure 8. Mean frequencies of nest visits by the female in the course of the day (*$P < 0.05$, Wilcoxon signed-rank test).

period, the male showed no bubbling at all, but the difference between the sexes was not statistically significant (Figure 6).

Nest visits
There was a significant difference in the frequency with which the female visited the nest during the mating season compared to both the pre-mating and the post-mating period ($P < 0.05$; Figure 7). Nest visits were observed more frequently during the post-mating than the pre-mating season, but the differences were not statistically significant. A closer look at nest visits over the course of the day (Figure 8) showed that the female displayed the highest frequency of nest visits between 1000 and 1100 during both the pre-mating and mating season. During the rest of the day, the frequency of nest visits was lower, with a slight increase in the afternoon, but with no statistically significant differences between different times of day. Differences between day and night during the mating and post-mating period were not statistically significant.

Discussion

The Philippine crocodile pair at Cologne Zoo was introduced at the beginning of 2012 and multiple copulations were observed subsequently. This supports the assumption that the courtship and mating season in captivity, even at different latitudes, correlates with the beginning of the breeding season in the wild (e.g. Alcala et al. 1987; Akmad and Pomares 2008; van Weerd 2010). Size and body weight of both sexes kept at Cologne Zoo generally conformed with the measurements given by van Weerd (2010) for reproductively active individuals; however, the male at Cologne Zoo was three years younger than the age indicated by Ross and Alcala (1983) for sexual maturity in males. In addition, Ziegler et al. (2013a) described an eight-year-old pair kept at Krokodille Zoo (Eskilstrup) that was already showing reproductive behaviour (including oviposition), so body size seems to be of greater relevance in reaching sexual maturity than age.

In general, all crocodilian species have particular intraspecific communication signals, which are also used as advertisement calls, presumably mainly during the mating season (Dinets 2013). Garrick and Lang (1977) subdivided mating sequences into three successive parts: (1) attraction and advertisement signals, (2) pair formation and (3) precopulatory behaviour, which were also observed in the Philippine crocodiles kept at Cologne Zoo. Precopulatory behaviour observed at Cologne Zoo was also in accordance with the findings of Alcala et al. (1987), i.e. physical contact (snout tip contact and rubbing, positioning of heads parallel to each other) combined with acoustic signals (bubbling, growling and roaring) and movements (female swimming across and below the male, alternately emerging and submerging). Garrick and Lang (1977) also described the initial approach and interaction between a potential breeding pair as a mutual snout contact on specific regions of the head.

Vocalisations between adults, such as bellowing or roaring, are associated with establishment and maintenance of social relationships and are performed predominantly during seasonal reproductive activities (Lang 1987; Ross 1998). According to Wang et al. (2007), such acoustic communication systems in crocodiles can include long-distance signals (bellowing) and short-distance messages (tooting, mooing, whining and bubbling). Such social signals may include some form of percussion, vibrations and olfactory messages, and also body posture or direct interactions (Brazaitis and Watanbe 2011). As Wang et al. (2007) showed that some acoustic signals can be heard over large ranges and thus might be particularly important for more solitary species, such acoustical communication could also be an important adaptation in *C. mindorensis,* which has a predominantly solitary mode of life (van Weerd 2010). However, at Cologne Zoo these signals could only be recorded when individuals were approaching one another or were already close. Alcala et al. (1987) showed that the female Philippine crocodile emits a series of brief high-pitched groaning or bellowing sounds and the male responds by producing similar but lower pitched sounds. Usually roaring is emitted by males and apparently functions similarly to bellowing in attracting females (Cott 1961, 1975).

Bubbling is known to be a communicational signal triggering precopulatory behaviours (Wang et al. 2007). Such non-vocal sounds appear to be transmitted through the water to animals at the surface as well as to those underwater (Lang 1987). The occurrence and role of bubbling in terms of reproduction and precopulation behaviour has also been observed in other crocodile species, such as the Nile crocodile (*Crocodilus niloticus*) (Garrick and Lang 1977), as well as in the American alligator (*Alligator mississipiensis*) (Vliet 1989). Mata (unpubl.) suggested that bubbling should also be defined as courtship and mating behaviour in *C. mindorensis*. In the current study, bubbling was observed prior to copulations, and the frequency of bubbling was significantly higher during the pre-mating season compared to the mating and post-mating periods, which supports the assumption that it can be referred to as courtship behaviour.

Head raising with opened mouth, which was displayed by the Philippine crocodile pair at Cologne Zoo during approaches, might serve as a visual advertisement signal, but could also be related to olfactoric signalling, as the scent glands are presented in this posture. Such olfactory signalling is documented by Garrick and Lang (1977). The Philippine crocodiles at Cologne Zoo also held their heads laterally pressed into the nape of the other's neck, followed by mounting. According to Garrick and Lang (1977), copulation followed predictably when the pair had begun with cycling movements and mounting. This was also observed in the present study. The mating sequence observed in the Philippine crocodiles held at Melbourne Zoo (Gilbert and Banks 2013) was almost identical.

Before the aggressive behaviour initiated by the female during the third day of introduction, she was observed following and mounting the male in the water; the male tried to increase the distance by moving away from her. Thus, mounting may also be defined as dominance behaviour, which may be followed later by aggressive interactions between conspecifics (see also Gilbert and Banks 2013). The fact that the aggressive behaviour towards the male (tail slapping, biting) took place on top of the nest could be interpreted as nest guarding behaviour, which is known in the species both from the wild and from captivity. However, aggressive and dominant behaviour, sometimes resulting in serious injuries or even death (Banks 2005, Ziegler et al. 2013a) is commonly seen in Philippine crocodiles during, before and after breeding (Mata unpubl.). Furthermore, nest guarding usually occurs after egg deposition between April and July (Banks 2005) and the following and mounting behaviour of the female took place away from the nest in the water, so the behaviour observed at Cologne Zoo was probably not related to nest guarding.

The hypothesis that the female would visit the nest more often in the morning hours and in the evening than during the rest of the day, as reported by Akmad and Pomares (2008), could only partly be confirmed, as in the current study the frequency of nesting activities was highest between 1000 and 1100 both during the pre-mating and the mating period, but with only a slight increase between 1500 and 1600.

One of the main objectives of the study was to determine when the animals demonstrate evidence of starting courtship behaviour in order to coordinate the timing of introductions and to prevent aggressive fights. It was expected that socio-positive behaviours such as approaches to the slide and acoustic signals in both sexes, as well as nest visiting in the female, would be prevalent during the natural mating season. While the expectation that approaches to the slide would increase during the mating season could not be confirmed in the female, the male showed an increased frequency of approaches to the slide during the pre-mating and mating periods that was highest during the actual mating period, particularly when the female was absent. The assumption that intraspecific communication in terms of bubbling would be prevalent during the reproductive season was confirmed; both individuals displayed a higher degree of bubbling during the pre-mating season. As expected, the frequency of nest building activities increased during the pre-mating period and was highest during the mating period. Thus the behaviours observed can be a useful tool in determining the appropriate timing of introductions in captive Philippine crocodiles.

Outlook

The aim of this study was to provide better insights into the mating behaviour of *C. mindorensis* and to provide enhanced management of the species during the reproductive activity phase and to improve the efforts of captive breeding programmes. Our study showed that introductions of captive Philippine crocodiles need to be carefully planned, and in particular careful observations of the particular behaviours that indicate potential receptiveness or interest should take place before introduction attempts. Our findings document distinct behavioural patterns such as bubbling, vocalisations and approaching that help determine the initiation and termination of courtship to improve breeding efforts under captive conditions and thus contribute to the ex situ conservation of this Critically Endangered species. Although introductions and subsequent copulations in 2012 did not lead to oviposition, introductions in the following year, which also took place at the beginning of the natural dry season in the Philippines, finally led to successful copulations, subsequent egg deposition and hatching (see Ziegler et al. 2013b). Analysis of successful reproduction in 2013 together with juvenile development is currently underway and will be presented elsewhere.

Acknowledgements

We would like to thank Natascha Behler (Bonn), Dr Lydia Kolter (Cologne), Jürgen König (Cologne) and Natascha Schneider (London) for their support.

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