Alien plant threatens Nile crocodile (*Crocodylus niloticus*) breeding in Lake St. Lucia, South Africa

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Abstract

We observed that the majority of Lake St. Lucia's nesting Nile crocodiles (*Crocodylus niloticus*) selected open, sunny, sandy areas in which to deposit their eggs. Nests were only found in shaded sites in the Mpate River breeding area and these nests were shaded primarily by an alien plant *Chromolaena odorata*. Soil temperatures of shaded sites at 25-cm depth, were on average 5.0–6.0°C cooler than in sunny sites at the same depth. They were well below the pivotal temperature for nests of St. Lucia's Nile crocodiles, i.e. they probably produced a female-biased sex ratio, and may have prevented embryonic development altogether. Many females abandoned nesting sites when they encountered the fibrous root mats of *Chromolaena odorata* while digging egg chambers. When additional nesting sites were experimentally created, the percent of sites utilized increased, indicating that suitable nesting sites were in short supply. This alien plant is posing a very serious threat to the continued survival of the Nile crocodile in Greater St. Lucia Wetland Park, and unless immediate action is taken, a female-biased sex ratio will result in eventual extirpation of the species from this recently acclaimed Word Heritage Site. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Crocoldylus niloticus; Lake St. Lucia; *Chromolaena odorata*; Alien plant species

1. Introduction

The process of colonization or invasion of a new habitat by a species has three principal elements. First, the colonizing species must overcome the barriers to dispersal between its native habitat and the new one; secondly, on arrival it must withstand the rigours of the new habitat; and thirdly, if the habitat allows growth and reproduction, then the colonizer must survive the adverse interactions with resident competitors, inhibitors or predators (Kruger et al., 1986). Invasive species are currently thought to be one of the proximate causes of biodiversity loss worldwide (Czech and Krausman, 1997). This has threatened key ecological functions in many systems, and has had far reaching implications for many other activities (Holling, 1992; Heywood, 1995). Most ecosystem types — terrestrial, fresh-water and marine — have been impacted to a greater or less extent by invasions (Williamson, 1999). Ecosystems vary in

their susceptibility to invasion and some of the more susceptible systems include mixed island systems, lake, river and near-shore marine systems (Heywood, 1995). Susceptibility also depends on human behaviour, land use, demographic, market and institutional structures and the control strategies adopted. In particular, habitat fragmentation, habitat conversion and agricultural disturbance are all argued to have increased the susceptibility to invasion (Williamson, 1999).

Chromolaena odorata is one of South Africa's many alien plant species and is thought to have been mistakenly introduced to the Province of Kwazulu-Natal, in seed-contaminated packing materials off-loaded at Durban Harbour during World War II (Liggitt, 1983), but its exact origin is unknown (Erasmus, 1985; Kluge, 1991). The maximum rate of spread of the plant recorded for the period 1975–1980 was in the region of 2000% (Liggitt, 1983). By 1986, invasion by this species had reached alarming proportions in the Kwazulu-Natal coastal region (Erasmus, 1986). These infestations occurred primarily in undisturbed conservation areas, such as the Greater St. Lucia Wetland Park (GSLWP), suppressing the indigenous plant communities and

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thereby posing a very real threat to species diversity (MacDonald and Jarman, 1985).

The largest semi-aquatic predator and keystone species in the GSLWP is the Nile crocodile (*Crocodylus niloticus*). It is widespread throughout the African continent, south of the Sahara Desert but is absent from much of the extreme south and southwest. Nile crocodiles were heavily exploited throughout much of Africa in the 1950s and 1960s (Cott, 1961; Parker and Watson, 1970). Many populations were reduced to low numbers, not only due to the skin trade but also to rapidly expanding human populations and the corresponding destruction of riverine habitat for agricultural purposes. The reduction in available nesting sites made the decline of crocodiles inevitable and they were exterminated from many natural areas within South Africa. Cott and Pooley (1971) reviewed the status of crocodiles in Africa. As a result, the Nile crocodile was listed at the Washington plenipotentiary conference in 1973, and was already on Appendix I of CITES (Convention of International Trade in Endangered Species of Wild Fauna and Flora) before it came into force in 1975 (Hutton, 1992). Legal protection resulted in significant recoveries of crocodiles in several areas in Africa and remaining populations in South Africa are now confined to the northeastern corner of the country, including the Kruger National Park, Ndumo Game Reserve and Lake St. Lucia within the GSLWP. In 1996, the Nile crocodile in South Africa was transferred from Appendix I to Appendix II of CITES in 1996, pursuant of Resolution Conf. 3.15 (ranching criteria) placing the animal on the threatened list.

The Nile crocodile usually breeds once a year and the timing of breeding is affected by locality (Cott, 1961; Graham, 1976). In the St. Lucia region eggs are laid in November, shortly after the spring rains and hatchlings emerge in February. The incubation period ranges from 75–90 days (Cott, 1961; Blomberg, 1976). Like other crocodilians, turtles and some lizards (Bull and Charnov, 1989; Janzen and Paukstis, 1991; Wibbels et al., 1992) this species has temperature-dependent sex determination (Hutton, 1987; Leslie, 1997). The temperature that produces a 1:1 sex ratio under constant temperature incubation has been termed the pivotal temperature (Mrosovsky and Pieau, 1991), which has become a "benchmark" temperature for comparisons between species and among populations of the same species (reviewed by Standora and Spotila, 1985). The critical period for sex determination is termed the thermosensitive period. Identification of the thermosensitive period permits ecologists to analyze the relationship between environmental temperatures during the appropriate time of incubation and sex ratios of natural nests.

The Lake St. Lucia ecosystem represents the southernmost extent of the breeding range of the Nile crocodile in the world, and it is also one of three major breeding areas for this threatened species within the boundaries of South Africa. The lake itself has six main nesting areas including a 2-km section of the Mpate River which flows into the southern end of the lake (Fig. 1). We observed that the majority of St. Lucia's nesting Nile crocodiles selected open, sunny, sandy areas in which to deposit their eggs (Leslie, 1997). Nests were found in shaded sites only in the Mpate River breeding area and these nests were shaded primarily by *Chromolaena odorata*.

The primary objective of this study was to determine the impact of *Chromolaena odorata* on crocodile nest site selection, nesting success and resultant hatchling sex ratios in the Mpate River breeding area in the GSLWP, Kwazulu-Natal, South Africa. A secondary objective was to conduct a mitigation experiment in order to possibly alleviate this threat.

2. Methods

2.1. Study area and alien plant

The GSLWP is a protected natural area located in the province of Kwazulu-Natal, South Africa (Fig. 1). In December 1999, the park was awarded World Heritage Status. Lake St. Lucia lies at the southern extremity of the Mozambiquan coastal plain, which extends along eastern Africa from Kenya to Kwazulu-Natal. The lake itself is located between latitudes 27° 34′ S to 28° 24′ S and longitudes 32° 21′ E to 32° 34′ E. It comprises c. 80% of the estuarine system of Kwazulu-Natal Province, and is the largest estuarine system in Africa (Begg, 1978). The climate is sub-tropical. Mean annual rainfall on the eastern shores of the lake system is 1500 mm and on the western shores is 700 mm.

Chromolaena odorata is a herbaceous perennial native to the Neotropics of the family Asteraceae, and it occurs in most suitable areas below 1000-m altitude from southern Florida to northwestern Argentina. It is typically a plant of secondary succession with an extensive fibrous root system, capable of rapidly invading clearings and persisting until shaded out by the overgrowth of forest trees. Where agriculture and human activity prevent forest regeneration, *Chromolaena odorata* persists as a typical plant of forest edges and paths, abandoned fields and pastures, building sites and along roads, railways and streams. Regrowth occurs after slashing and burning, and up to 1,300,000 seeds are annually produced by each plant (Erasmus, 1986). The botany and the phenology of the species has been described by King and Robinson (1970) and Rai (1976). In the New World, *Chromolaena odorata* is common in most habitats except in undisturbed rainforest, but is seldom weedy and is never the target of specific weed control measures. It does not invade pasture nor compete successfully with plantation crops. This reduced aggres-

siveness is due to attack by a large complex of insects, other arthropods and diseases, together with competition with related plants (Ambika and Jayachandra, 1990). In the Neotropics, *Chromolaena odorata* is therefore largely controlled by these biotic factors. However, due to the absence of these species-specific biotic factors, *C.*
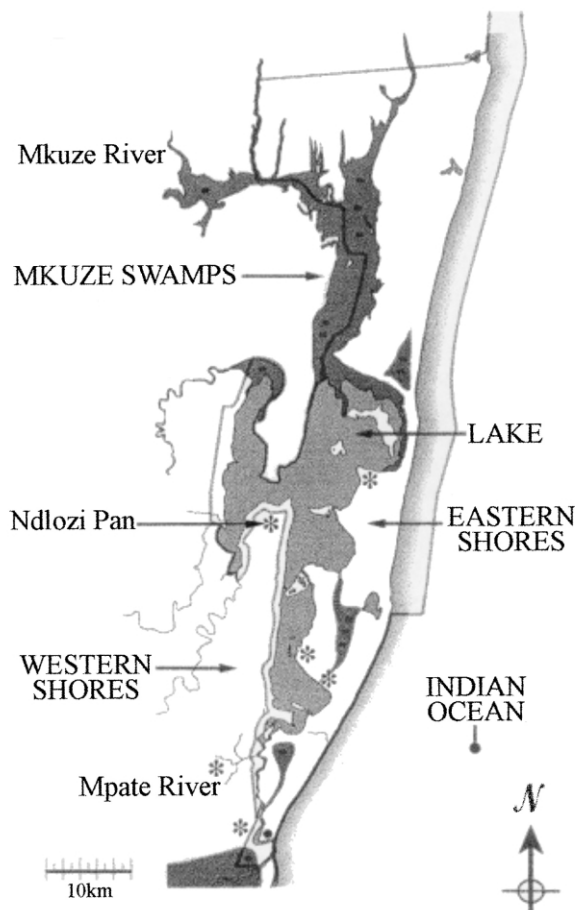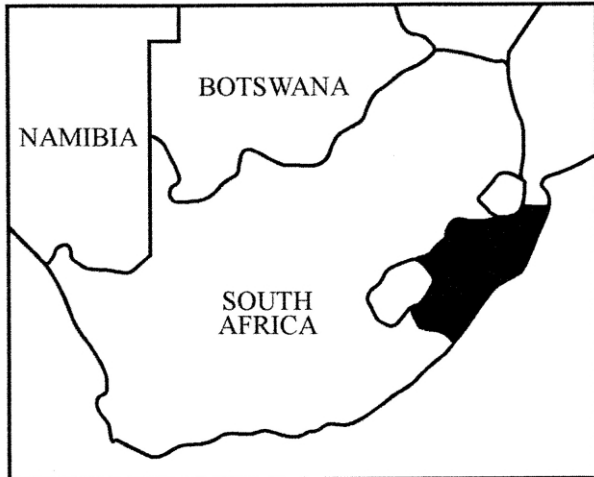

Fig. 1. The Greater St. Lucia Wetland Park is located in the Province of Kwazulu-Natal, South Africa, at the extremity of the Mozambiquan coastal plain which extends along eastern Africa from Kenya to St. Lucia. The lake system is home to c. 800 adult Nile crocodiles. *Six main breeding areas.

odorata has thoroughly colonized parts of Africa, India, Sri Lanka, Indochina, Malaysia and Indonesia where it is a very successful exotic species and a noxious weed (Ambika and Jayachandra, 1990).

Chromolaena odorata currently occurs in large densities on the western shores of Lake St. Lucia, and is also abundant in the south and the north. The isolated nature of the eastern shores and regular clearing programmes along parts of the western shoreline of the narrows has effectively kept *Chromolaena odorata* within the plantations of the western shores. Low light levels in these areas decrease the flowering potential of the plant, thereby reducing overall density (A. Blackmore, personal communication). Although densities of *Chromolaena odorata* on the eastern shores are fairly low, invasion of virgin areas by this species is a progressive and stepwise process (Blackmore, 1991), and some control measures are being undertaken.

2.2. Crocodile nesting surveys

Annual nesting surveys of the entire lake system were carried out from 1993 to 1997. During the 1993/1994 breeding season, we noticed that many previously utilized crocodile nesting sites in the Mpate River area were not being used by females. Egg shell fragments take a number of years to deteriorate so it was difficult to estimate when particular sites were last used. Moreover, we noticed that many sites were either partially or totally shaded by *Chromolaena odorata*, and a number of sites were virtually completely overgrown with this plant. Subsequent surveys revealed that some crocodiles were actually nesting in these overgrown, shaded and thus cool nesting sites, and that some females had attempted to dig nest chambers in other shaded sites, but for some reason had abandoned the process. This raised the question as to what effect *Chromolaena odorata* was possibly having on crocodile nest site selection, nesting success and hatchling sex ratios.

The study was divided into two parts: (1) a comparison of soil temperatures at various depths and distances from the water, in both sunny and shaded sites, and (2) a mitigation experiment in which we cleared existing nesting sites of *Chromolaena* and created a number of new nesting sites within dense stands on the banks of the Mpate River.

2.3. Soil temperature study

We measured vertical thermal profiles along two transects on the south bank of the Mpate River, using thermocouple probes mounted on wooden dowels at 15, 20 and 40 cm depths. One transect was in full sun and one in full shade, mainly from *Chromolaena odorata*. Four stations were sampled along each transect, located at increasing distances from the water's edge, i.e. 4 m (low lying), 7 m (slight incline), 10 m (fully exposed) and

13 m (near forest fringe). Thermocouples were connected to a CR-10 datalogger (Campbell Scientific, Inc., USA) which was buried underground and powered by a solar panel. Soil temperatures were recorded hourly for the entire breeding season and data were downloaded weekly. Climatological data, including maximum and minimum air temperature and rainfall, were recorded at the St. Lucia Crocodile Centre a few kilometres away, at 0800 and 1400 daily.

We used the JMP Macintosh software package to analyze soil temperature data by performing a repeated measures analysis of covariance (ANCOVA) with replication on two treatments (sun versus shade), four distances per treatment (4, 7, 10 and 13 m from the water), three depths per distance (15, 25 and 40 cm), over a 4-month period (November–February using 2-week mean temperatures). Treatment and distance were the between-individual variables while period and depth were the within-individual variables. Soil temperature was the response variable and air temperature provided the regressor for the analysis. We compared temperature data for the sunny versus shaded sites from the 1994–1995 and 1996–1997 nesting seasons.

2.4. Mitigation experiment

We observed the behaviour of a number of breeding female crocodiles in the Mpate River area during the nesting seasons from 1993/1994 to 1996/1997. In 1994/1995, three females dug a number of test holes ("attempted dig") at their chosen nest site. We noticed that while digging their egg chambers, the females had encountered roots from *Chromolaena odorata*. Being unable to dig through the fibrous mat of roots, these sites were abandoned.

Sixteen nesting sites were used in this experiment in the 1994/1995–1996/1997 nesting seasons. Five had been used as nesting sites in the 1993/1994 season and were left unaltered. We cleared *Chromolaena odorata* from another five previously utilized nesting sites that had been abandoned and enlarged them. We also created six new nesting sites within dense stands of *Chromolaena odorata*, manually removing as much of the root stock as possible and without use of chemicals. These sites were c. 4×4 m in size. Clearing had to take place every season due to the vigorous regrowth of the plant. A number of foot and boat surveys, and an aerial survey in mid-December each season, confirmed utilization of the nesting sites.

3. Results

3.1. Soil temperatures

In the 1994/1995 nesting season treatment (i.e. sun versus shade) distance, depth and period had significant effects on soil temperature ($P < 0.0001$). The two-way interactions of treatment with distance, depth and period had significant effects on soil temperature ($P < 0.0001$), as did the two way interactions of distance×depth and depth×period ($P = 0.0114$ and $P = 0.0062$ respectively). The three way interactions of treatment×distance× depth; treatment×distance×period; treatment×depth× period and distance×depth×period were not significant ($P = 0.1547$, $P = 0.3610$, $P = 0.9699$ and $P = 1.000$, respectively). The four-way interaction of treatment× distance×depth×period was also not significant ($P = 0.1309$). Air temperature ($P < 0.0001$) and rainfall ($P < 0.0001$) both had significant effects on soil temperature.

Due to the lack of functional probes in the 1996/1997 nesting season, soil temperatures at some depths were not recorded, including those at the station 4 m from the waters edge in the shade transect. The depth variable was therefore removed from the analysis. These data indicated that treatment ($P < 0.0001$), distance ($P < 0.0001$) and period ($P < 0.0155$) had significant effects on soil temperature. When comparing weekly average soil temperatures in the sun transects at 25-cm depth, at various distances from the water's edge, in the 1995/1996 and 1996/1997 seasons (7 December–3 March), the significant effects of distance from water on soil temperatures becomes apparent. During both nesting seasons, soil temperatures 4 m and 13 m from the water were lower than those 7 and 10 m from the water (Fig. 2). Soil temperatures 4 m from the water's edge were no doubt influenced by the nearby river, whereas those 13 m from the waters edge were lower due to the encroaching vegetation. There were significant two-way interactions of treatment×distance ($P < 0.0061$) and treatment×period ($P < 0.0001$). Air temperature and rainfall both had significant effects on soil temperature ($P < 0.0001$), while, unlike the 1994/1995 season, the three-way interaction of treatment×distance×period was also significant ($P = 0.0009$).

Soil temperature profiles at all four shade transect stations at all four depths in the 1994/1995 season, had temperatures well below the calculated lower pivotal temperature of 31.7 °C for Nile crocodiles at St. Lucia. The same pattern was apparent for soil temperatures at all depths at the sunny transect stations in the 1996/ 1997 season. Although temperatures at 15-cm depth were warmer than at both the 25- and 40-cm depths, there was very little temperature variation between depths at all stations. A comparison of sun versus shade (treatment) daily mean soil temperatures at a depth of 25 cm, 10 m from the water's edge, showed that the shaded site was 5.0–6.0°C cooler than the sunny site in the 1994/1995 and 1996/1997 nesting seasons (Fig. 3). Mean shaded site temperatures were 26.1°C (range = 21.8–28.3°C) and 25.6°C (range = 21.2–33.4°C) in the 1994/1995 and 1996/1997 seasons respectively.

3.2. Mitigation experiment

The total number of crocodile nests in the Mpate River breeding area was 10, 6, 14 and 11, in the 1993/1994, 1994/1995, 1995/1996 and 1996/1997 nesting seasons, respectively. The use of current nesting sites decreased from 100% in the 1993/1994 season, to 60, 40 and 40% in the 1994/1995, 1995/1996 and 1996/1997 nesting seasons, respectively. Many sites became overgrown with

Chromolaena odorata and were abandoned by nesting females. The use of abandoned nesting sites remained at 40% in the 1993/1994 and 1994/1995 seasons, but increased to 80 and 60% in the 1995/1996 and 1996/1997 nesting seasons, respectively. This increase was due to the fact that we had cleared *Chromolaena odorata* from these nesting sites (Table 1). In the 1994/1995 nesting season, 33% of the created nesting sites were used by female crocodiles. This percentage increased to
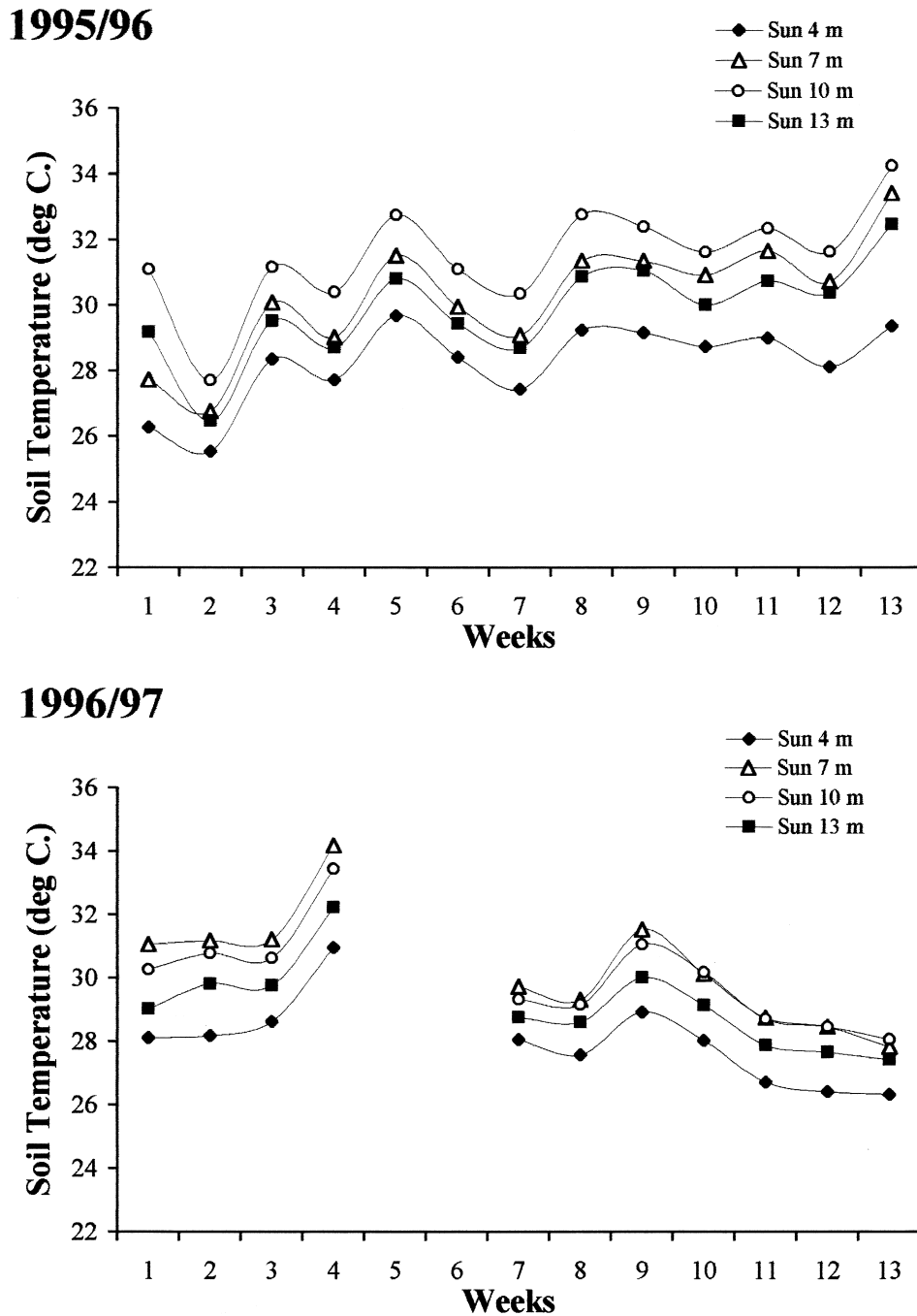

Fig. 2. Difference between 25-cm depth soil temperatures (middle of nest depth) in the sun transects at various distances from the waters edge in the 1995/1996 and 1996/1997 nesting seasons, recorded at the Mpate River nesting site, Lake St. Lucia, South Africa. The missing data points in the 1996/1997 season indicate when the datalogger was stolen.

50% in 1995/1996 and to 66.7% in the 1996/1997 season. In the 1994/1995 season, a number of test holes were observed at two additional created sites. One site had three holes. A similar situation occurred at one of the abandoned but cleared sites, where four test holes were found.

4. Discussion

4.1. Shading of nesting sites and altering of sex ratios

Data from our first experiment confirmed that *Chromolaena odorata* had a shading effect on nesting sites, and that this shade reduced incubation temperatures. Shaded site temperatures at 25 cm depth, were 5–6°C cooler than sunny site temperatures at the same depth. Nests in shaded sites would, therefore, be well below the

pivotal temperature for Nile crocodiles at St. Lucia and would therefore be expected to produce a female-biased sex ratio (Leslie, 1997). Skewed sex ratios among reptile populations are, however, not unusual. Mrosovsky et al. (1984) determined that for both species of sea turtles studied, there were seasonal changes in the sex ratio of hatchlings. Dutton et al. (1992) estimated the sex ratio of leatherback sea turtles at Sandy Point, St. Croix to be 75–100% male in all nests, and Spotila et al. (1987) computed a sex ratio for the green turtle nesting season to be 67:33 female to male. Morreale (1983) concludes that the combination of the relatively mild tropical coastal climate and the depth of the nests contributed greatly to the stability of the nesting environment for the green sea turtle.

However, none of the above mentioned studies, for example, were carried out in so-called disturbed areas. The biological effect of spatial factors (such as sun
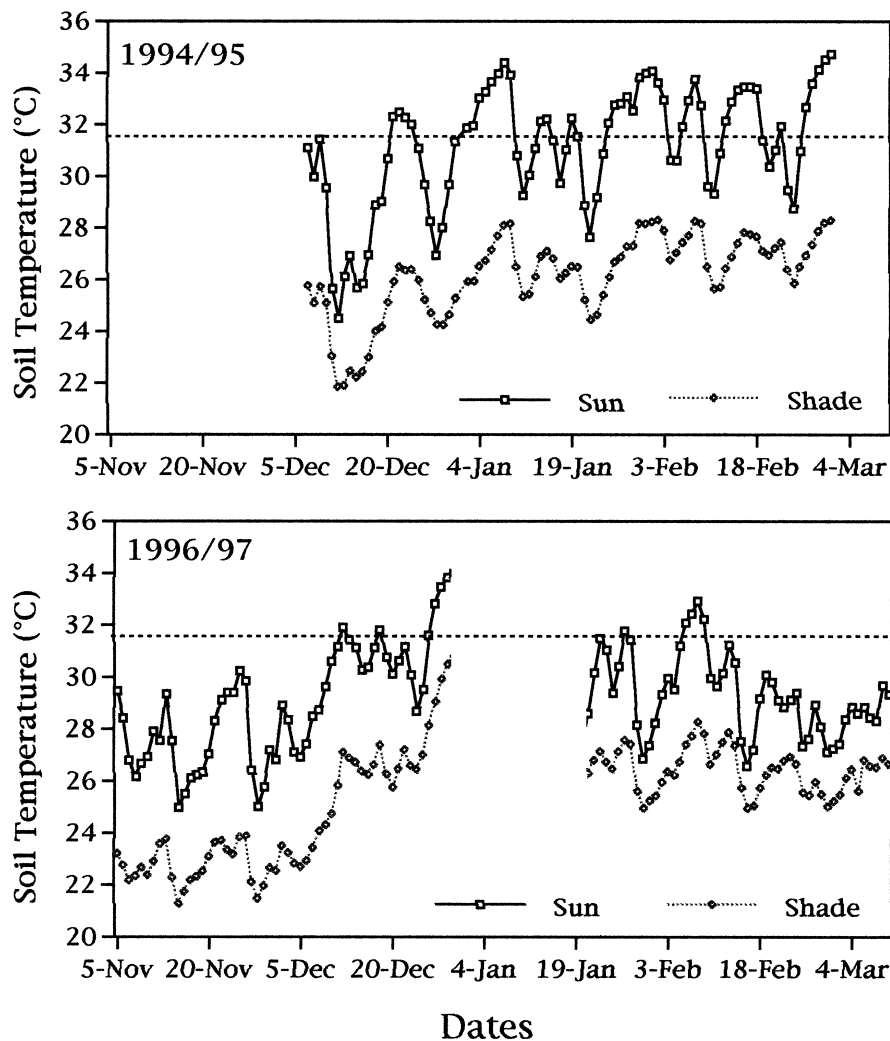

Fig. 3. Difference between sun versus shade daily mean soil temperatures at 25-cm depth (middle of nest depth), 10 m from the water's edge in the 1994/1995 and 1996/1997 nesting season, recorded at the Mpate River nesting site, Lake St. Lucia, South Africa. Shaded was created by the alien plant, *Chromolaena odorata*. Dashed line represents the pivotal temperature. The missing data points in the 1996/1997 season indicate when the datalogger was stolen.

versus shade, different depths and distances from the water) on sex determination was probably high at St. Lucia, as female Nile crocodiles nested at varying distances from the water in open, sunny sites and in sites that were either partly shaded or totally shaded by *Chromolaena*. Females who returned to the same nesting area/19site each breeding season were often forced to nest in shaded or partly shaded sites and had difficulty avoiding the alien plant's intrusion (Leslie, 1997).

Schwarzkopf and Brooks (1987) and Janzen (1994) suggest that female western painted turtles (*Chrysemys picta*) choose the thermal environment of nests, and hence the sex ratio of their off-spring: they may assess the vegetational cover on the nest site at oviposition. Shine and Harlow (1996) suggest that in some oviparous lizard species, the mothers may be able to manipulate the phenotypes of their progeny not only via direct pathways (e.g. allocation of nutrients, etc.) but indirectly, inducing particular developmental pathways through selection of nest sites, and thus incubation conditions. When given the choice, St. Lucia's breeding female crocodiles clearly selected specific oviposition sites 2–3 weeks prior to oviposition, clearly avoiding shaded or partly shaded sites, even if it meant nesting up to 100 m from the nearest water source. However, with the shortage of suitable nesting sites they had to nest in shaded or partly shaded sites.

Incubation temperature has also been shown to affect the probability of crocodile and alligator embryos surviving (Webb and Smith, 1984; Lang et al., 1989). Temperature also has an affect on the frequency of abnormalities among embryos and hatchlings (Webb et al., 1983; Ferguson, 1985). It can influence body size (Webb et al., 1987. Allsteadt and Lang, 1995), and the

weight of residual yolk (Webb et al., 1987, Allsteadt and Lang, 1995) at hatching. Many studies in the late 1980s also showed that hatchling pigmentation patterns (Deeming and Ferguson, 1989), post-hatching growth rates (Hutton, 1987; Webb and Cooper-Preston, 1989) and post-hatching patterns of thermoregulation (Lang, 1987) could be affected by incubation temperature. Incubation temperature is dependent upon the nest site characteristics, so the suitability of an oviposition site is extremely important. In reptiles, a continuous increase/decrease in incubation temperature does not produce a simple linear pattern of decrease/increase in the duration of the incubation period (Deeming and Ferguson, 1991). Compared to many reptiles, crocodilians have a relatively restricted range of incubation temperatures from c. 28–34°C (Ferguson, 1985). At 28°C, *Alligator missippiensis* eggs complete development but fail to hatch (Lang and Andrews, 1994). Survivorship of Chinese alligator (*Alligator sinensis*) eggs and dwarf caiman (*Paleosuchus trigonatus*) eggs is poor below 27°C (Chen, 1990; Magnusson et al., 1990), and Hutton (1987) stated that Nile crocodile eggs incubated below 27°C never hatch.

4.2. Mitigation experiment

When additional nesting sites were created and existing sites cleared and expanded, the number of sites used increased. As *Chromolaena odorata* invaded two of the control sites, so the percent nesting increased in the newly created sites. In two newly created sites and one abandoned site, where crocodiles started to dig nests but later abandoned them, close examination showed that we had failed to remove the deeper roots of *Chromolaena*.

Table 1
Results of the mitigation experiment on crocodile nesting success over four seasons 1994–1997

Category[a]	1993/1994	1994/1995	1995/1996	1996/1997
Current sites				
Site No. 14	Nest	Nest	No nest	No nest
Site No. 15	Nest	No nest	Overgrown	Overgrown
Site No. 9	Nest	Nest	Nest	Double nest
Site No. 16	Nest	Nest	Overgrown	Overgrown
Site No. 12	Nest	No nest	Nest	Nested
Abandoned sites				
Site No. 2	No nest	No nest	No nest	No nest
Site No. 4	Nested	Nested	Nested	Nested
Site No. 6	Nested	Nested	Nested	Nested
Site No. 7	No nest	Attempted dig (×4)	Nested	Nested
Site No. 5	No nest	No nest	Nested	No nest
Created sites				
Site No. 1	No nest	Nested	No nest	No nest
Site No. 3	No nest	No nest	No nest	No nest
Site No. 8	No nest	Attempted dig (×1)	Nested	Nested
Site No. 10	No nest	Attempted dig (×3)	Nested	Nested
Site No. 11	No nest	No nest	No nest	Nested
Site No. 13	No nest	Nested	Nested	Nested

[a] Abandoned and created sites are those where *Chromolaena* was removed from previously used potential nesting sites

The 1994/1995 season marked the end of a 4-year drought in the area, which may explain the exceptionally low nesting frequency (Leslie, 1997). With the exception of the latter season, the total number of nests in the Mpate River area did not differ significantly between seasons, although the use of specific nest sites varied. There was a 40% loss of suitable nesting sites over a 4-year period due primarily to invasion by *Chromolaena odorata*. Had we not created additional nesting sites, nest numbers would probably have decreased by 33, 50 and 66.7% in the 1994/1995, 1995/1996 and 1996/1997 nesting seasons respectively. Suitable nesting sites in the Mpate River breeding area were clearly in short supply because the newly created sites were readily used, and when given a choice, nesting females did not choose shaded or partly shaded sites.

4.3. Conclusions

This alien plant species is clearly posing a very serious threat to the continued survival of the Nile crocodile in the Lake St. Lucia ecosystem. *Chromolaena* already occurs in high densities in the northern, southern and western parts of the lake system (Blackmore, 1991). Of the six crocodile breeding areas in the lake system (Fig. 1), the two other areas occurring on the western shores have already been invaded by *Chromolaena odorata*, although not as extensively as the Mpate River area. If *Chromolaena odorata* remains uncontrolled and continues to spread, a similar situation could occur at Ndlozi Pan, the only other nesting area where primarily male hatchlings are produced (Leslie, 1997). Unless immediate action is taken, a female-biased sex ratio in all nesting areas will result in eventual extirpation of the Nile crocodile from the Lake St. Lucia ecosystem.

Acknowledgements

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