

VEGETATION COMMUNITIES AS NESTING HABITAT FOR THE SALTWATER CROCODILES IN THE NORTHERN TERRITORY OF AUSTRALIA

YUSUKE FUKUDA¹ AND NICHOLAS CUFF

Northern Territory Department of Land Resource Management, PO Box 496, Palmerston,
Northern Territory 0831, Australia

¹Corresponding author, e-mail: yusuke.fukuda@nt.gov.au

Abstract.—Crocodilians have a variety of reproductive strategies. While different species have different requirements for nesting sites, most crocodilians, including the Saltwater Crocodile (*Crocodylus porosus*) which is highly adapted to saline environments, predominantly select freshwater habitats for nesting. Using the locality data of 4,537 nests observed between 2000 and 2011 in the Northern Territory of Australia, we examined nesting sites in relation to vegetation communities with different salinity regimes. Despite potential bias in the heterogeneous distribution and abundance of the nests introduced by some anthropologic factors, the dataset covered the majority of coastal, sub-coastal, riparian, and wetland regions across the Northern Territory (21 catchments) and approximately 57% of the vegetation communities available in these regions. Within these vegetation communities, 87.7% of nests (3,978 out of 4,537) were found in freshwater or hypo-saline (mild brackish) habitats (89.7% of total habitat area), and 12.3% (559 out of 4,537) were found in saline habitats (10.3% of total habitat area). The most commonly used vegetation community was tall, closed tussock grassland with *Oryza* species (36.2% of nests) that represented 15.5% of the total habitat area. Other common vegetation communities included open forest or woodland with *Eucalyptus*, *Melaleuca*, and *Pandanus* species with tussock grassland or sedgeland ground layers. Nest site selection seems to be influenced by multiple factors, including freshwater habitats being more available than saline habitats, physiological advantages of freshwater to nesting females and/or hatchlings, and the suitability of the ground layer vegetation for constructing mound-like nests. Vegetation communities may be used to assess the suitability of nesting habitat for management and conservation purposes.

Key Words.—brackish; *Crocodylus porosus*; floodplain; freshwater; *Oryza*; salinity

INTRODUCTION

Crocodilians including alligators, caimans, crocodiles, and gharials have a variety of reproductive strategies (Lance 1989; Webb and Manolis 1989; Hussain 1999; Brazaitis and Watanabe 2011; Wang et al. 2011). Some species build mound nests from vegetation (e.g., the American Alligator *Alligator mississippiensis*, the Saltwater Crocodile *Crocodylus porosus*) and others excavate a hole in which to lay eggs (e.g., the Australian Freshwater Crocodile *Crocodylus johnstoni*, the Gharial *Gavialis gangeticus*). While these species have different requirements for nesting sites, most crocodilian species, including Saltwater Crocodiles appear to select freshwater habitats for nesting (Webb and Manolis 1989; Brazaitis and Watanabe 2011).

A number of early studies from the Northern Territory of Australia reported that the nesting of Saltwater Crocodiles was strongly associated with freshwater habitats (Webb et al. 1977, 1983; Magnusson et al. 1978; Magnusson 1980), although the species is highly adapted to saline environments (Grigg et al. 1980, 1998; Taplin and Grigg 1981; Taplin 1985). However, these studies were confined to a few river systems (Adelaide, Finnis/Reynolds, and

Liverpool/Tomkinson Rivers) and the generality of these observations is not known. It was also difficult to generalize their nest site selection because the populations in these rivers at the time of the studies were depleted and still recovering from overhunting in 1940s–1960s (Magnusson 1980; Webb et al. 1984). Populations of Saltwater Crocodiles have shown a large increase since protection from commercial hunting in 1971 and the abundance of the species is reaching pre-hunting levels in the Northern Territory (Webb et al. 2000; Fukuda et al. 2011). Australia now has one of the largest Saltwater Crocodile populations in the world (Webb et al. 2010) and the Northern Territory has the highest population in Australia (Webb et al. 1984; Fukuda et al. 2007).

This study examines the characteristics of nesting sites of one of the largest populations of Saltwater Crocodiles using the most comprehensive data available from different river systems across the Northern Territory. More specifically, we analyze the location of numerous nests, located between 2000 and 2011, in relation to vegetation communities. This allows us to infer the salinity regimes of crocodile's breeding habitats and describe the vegetation communities to a species level where most nests were found.

MATERIALS AND METHODS

Study area.—The study area was the northern coastal and sub-coastal regions of the Northern Territory of Australia, including associated islands (e.g., Tiwi Islands; Fig. 1). The study area encompasses the distribution of Saltwater Crocodiles in the Northern Territory and contains a wide range of wetland types including palustrine and lacustrine water bodies, floodplains, riverine, estuarine, and marine systems (Cowardin et al. 1979; Blackman et al. 1992). The climate is tropical monsoonal with distinct wet (November–April) and dry (May–October) seasons. Some of these wetlands are temporary, typically fed by heavy rainfall and run-off during the wet season and others are perennial with significant spring water inflow from shallow aquifer systems associated with particular regional geologies (Australian Nature Conservation Agency 1996). Salinity levels associated with these wetlands range from persistent saline and freshwater through a full range of stable and fluctuating hypo- (brackish) and hyper-saline levels. In some instances, there is dramatic transition between prevailing freshwater and saline water regimes on temporal scales ranging from days to months (seasons). The wetland systems are accordingly dominated by a variety of different vegetation communities, covering a range of broad structural and floristic formations typical of northern Australia (Wilson et al. 1990). These range from aquatic forblands, graminoid (grass-like) dominated formations, and chenopod shrublands through a range of woody tree and shrub dominated formations, such as *Melaleuca* species and Eucalypt (*Eucalyptus/Corymbia* species) woodlands and open-forests, to evergreen closed-vine-forests (monsoon forests and jungles) and mangrove closed-forests.

Data and analysis.—We compiled data of Saltwater Crocodile nests harvested in the period 2000–2011, originally supplied by permitted harvesters as a part of the Northern Territory Government management programs of Saltwater Crocodiles (Leach et al. 2009; Fukuda et al. 2012). The dataset contained 7,153 nests harvested during the period throughout the Northern Territory. We excluded nests that were reported without GPS coordinates. Some GPS coordinates were duplicated between different years because the most favorable breeding sites

are repeatedly used by dominant females (Wildlife Management International 2007). We included these points because they were different nests in different years whether or not made by the same females, reflecting the suitability of the sites for nesting.

Vegetation communities and/or associated biogeographic regionalization have a long history of utilization as surrogates for assessing the habitat requirements of species across Australia and elsewhere (Sattler and Willams 1999). Standardized spatial data and attributes for vegetation communities are available for much of Australia via the National Vegetation Information System (NVIS; ESCAVI 2003). We used extant vegetation mapping data from NVIS (DSEWPC 2012), compiled for the Northern Territory at approximately 1:1,000,000 scale and developed over the past 30 years, using a range of methods and approaches to the development of spatial vegetation information. Generally, surveys of primary importance to this study used field methods consistent with McDonald et al. (1990), Brocklehurst et al. (2007), and National Committee on Soil and Terrain (NCST 2009).

The NVIS dataset comprises a polygon layer of spatial data supporting a complete hierarchy of NVIS data attributes ranging from Class (broadest) to Sub-Association (most detailed; ESCAVI 2003; NCST 2009) and provides a uniform coverage across the entire study area. It should be noted that the vector and attribute data associated with many of the Broad Floristic Formations hypothesized to be important for crocodile nesting were developed at scales larger than this (i.e. more detailed), with this being reflected in the detail present within the NVIS dataset. We assessed the NVIS Sub-Formation (Level 4) and Association (Level 5) as the most appropriate levels in the hierarchy on which relationships between crocodile nesting habits and vegetation/habitat types could be assessed. The Sub-Formation level in the hierarchy details “dominant growth form, cover-class, height and dominant genus for each of the three traditional strata” and is able to be assessed rapidly and accurately from aerial survey platforms during crocodile nest surveys (Brocklehurst and Van Kerckhof 1994; Brocklehurst and Lynch 2009).

To investigate how many catchments and vegetation communities the nest dataset covered, we imported and intersected the nest dataset with the GPS coordinates, the catchment dataset (Geoscience Australia 2004) and the vegetation

dataset (DSEWPC 2012) into a Geographic Information System (GIS), using ArcGIS Version 10.1 (Esri, Redlands, California, USA). We classified the vegetation Sub-Formations and Associations from polygons that contained observed crocodile nests into the habitat types of freshwater (< 0.1% salinity), hypo-saline (or brackish) water (0.1–3% salinity, typically < 1%), saline water (> 3% salinity), or unknown (salinity unknown), based on the detailed description of each vegetation association available in DSEWPC (2012) and the known tolerance to salinity of the plant species in the association. Vegetation Sub-Formations and Associations, likely to experience fluctuating salinity levels depending on the time of a year, were classified on the basis of the expected water salinity during the crocodile breeding season in typical years. Saltwater Crocodile breeding is highly seasonal coinciding with the wet season (Webb et al. 1983; Webb 1991) when the water salinity can dramatically change because of the large amount of rainwater and run-off flushing into catchments. Under prevailing annual monsoonal conditions resulting in flooding events, freshwater inflows to predominantly saline supra-tidal habitats results in extended periods of lowered standing water salinity in these habitats. We determined the extent of the breeding season of Saltwater Crocodiles by plotting the number of nests harvested in each

month during 2000–2011, in relation to rainfall during the same period. We used the average monthly rain (mm) derived from five weather stations across the Northern Territory (Fig. 1).

We identified the total area of each Sub-Formation in known and predicted habitats for Saltwater Crocodiles (Fig. 1). We predicted the habitat extents based on the methodologies outlined in Fukuda et al. (2004) and Fukuda et al. (2007). The criteria for the habitats were 250 m buffer from features categorized as waterbody in GEODATA TOPO 250K Series 3 (Geoscience Australia 2006) under 55 m elevation in the Australian Height Datum (AHD), and 1 km buffer from the nests found in 2000–2011. We set these buffers in accordance to the scales of the GIS datasets used to derive potential habitat extents (1:250,000) and the cartographic scale tolerance of the vegetation data used in the analyses (1:1,000,000). We also identified the most dominant vegetation species (Vegetation Association) in each Sub-Formation identified to contain a nest.

RESULTS

Of the 7,153 nests compiled from the historical harvest records, 4,537 nests were reported with GPS coordinates. The 4,537 nests with GPS coordinates were contained in 21 catchments, across coastal, sub-coastal, and riverine regions of the ‘Top End’ of the Northern Territory (Fig.

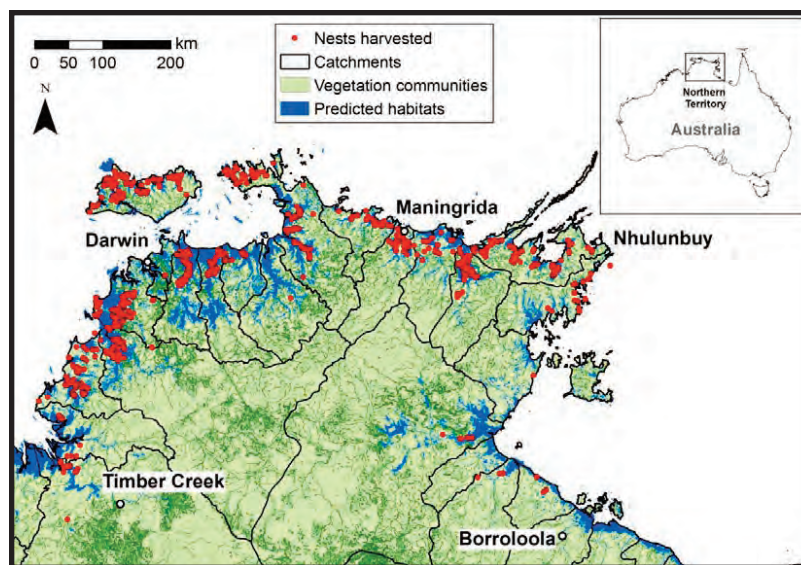


FIGURE 1. Nests of Saltwater Crocodile (*Crocodylus porosus*) harvested 2000–2011 and reported with GPS coordinates in the Northern Territory, Australia. The vegetation communities and catchments were derived from DSEWPC (2012) and Geoscience Australia (2004), respectively. The predicted habitats were generated based on Fukuda et al. (2004) and Fukuda et al. (2007; see text for criteria). The weather stations from which we extracted the average monthly rainfall for 2000–2011 are Borroloola, Darwin, Maningrida, Nhulunbuy, and Timber Creek.

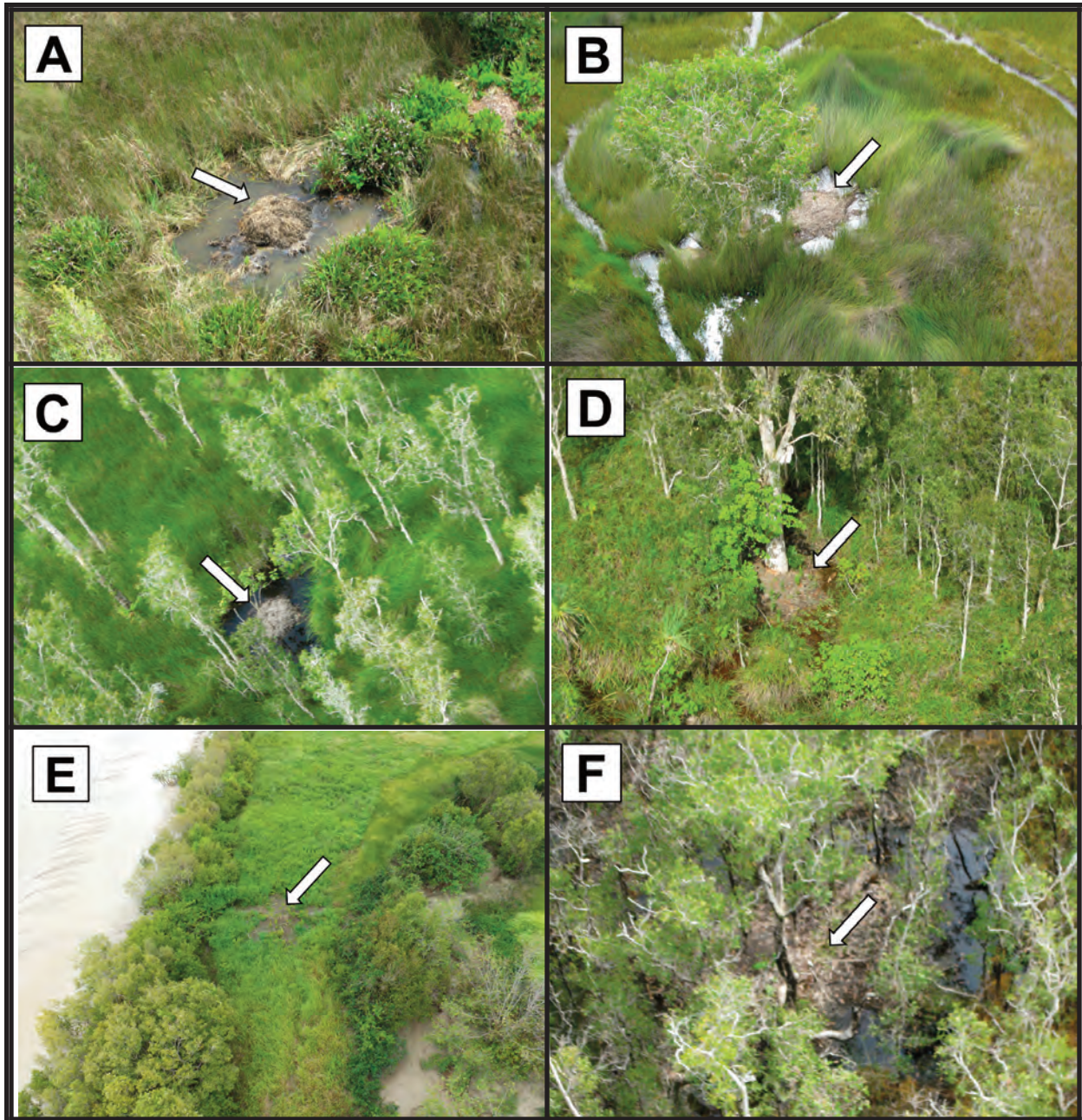


FIGURE 2. Nests (arrows) of Saltwater Crocodiles (*Crocodylus porosus*) in different vegetation communities in the Northern Territory, Australia. Nests occurred in A) tall closed tussock grassland, B) inundated floodplain with *Oryza* species, C) open woodland with *Melaleuca* species, D) closed forest with *Eucalyptus*, *Melaleuca* and *Pandanus* species, E) salt tolerant grassland fringing mangroves, and F) *Eucalyptus miniata* dominated mid open forests. (Photographed by Yusuke Fukuda).

1). Some catchments had fewer nest records than others for various reasons (e.g., difficult to access in remote areas, harvest legally banned in Kakadu National Park).

When intersected with the vegetation mapping data, we found the nests recorded in 46 Sub-

Formations. This represented approximately 57% of the vegetation communities available in the coastal, sub-coastal (below 55 m elevation in AHD where approximately 99.65% of nests were observed), riparian, and wetland regions of the Northern Territory (46 of 79 Sub-Formations

Herpetological Conservation and Biology

TABLE 1. The number and percentage of the nests of Saltwater Crocodile (*Crocodylus porosus*) found in the freshwater or mild brackish water vegetation communities 2000–2011. The detailed description of each vegetation association is available in Brocklehurst and Van Kerckhof (1994), ESCAVI (2003), Brocklehurst et al. (2009), and DSEWPC (2012).

Vegetation Sub-Formation	Vegetation Association	Area (km ²)	% of total habitats predicted	Number of nests	% of total nests found
<i>Oryza</i> tall closed tussock grassland	<i>Oryza</i> spp. & <i>Eleocharis</i> spp. tall closed tussock grassland	6,374	15.5	1,642	36.2
<i>Melaleuca</i> mid open forest/ <i>Melaleuca</i> low open woodland/ <i>Eleocharis</i> low open sedgeland	<i>Melaleuca cajuputi</i> & <i>Melaleuca viridiflora</i> +/- <i>Melaleuca leucadendra</i> mid open forest with <i>Melaleuca cajuputi</i> , <i>Acacia auriculiformis</i> & <i>Melaleuca viridiflora</i> low open woodland secondary tree layer and <i>Eleocharis dulcis</i> , <i>Pseudoraphis spinescens</i> , <i>Leersia hexandra</i> low open sedgeland ground stratum.	804	2.0	276	6.1
<i>Eucalyptus</i> mid open forest/ <i>Livistona</i> low sparse palmland/ <i>Heteropogon</i> tall tussock grassland	<i>Eucalyptus miniata</i> , <i>Eucalyptus tetrodonta</i> & <i>Erythrophleum chlorostachys</i> mid open forest with <i>Livistona humilis</i> , <i>Cycas armstrongii</i> and <i>Acacia oncinocarpa</i> low sparse palmland and <i>Heteropogon triticeus</i> , <i>Sorghum plumosum</i> & <i>Chrysopogon fallax</i> tall tussock grassland.	4,877	11.9	269	5.9
<i>Eucalyptus</i> mid open forest/ <i>Acacia</i> tall sparse shrubland/ <i>Sorghum</i> mid tussock grassland	<i>Eucalyptus miniata</i> , <i>Corymbia nesophila</i> & <i>Eucalyptus tetrodonta</i> mid open forest with <i>Acacia oncinocarpa</i> , <i>Acacia difficilis</i> & <i>Livistona humilis</i> tall sparse shrubland and <i>Sorghum</i> spp., <i>Pseudopogonatherum contortum</i> & <i>Chrysopogon fallax</i> mid tussock grassland ground stratum.	1,107	2.7	235	5.2
<i>Melaleuca</i> low open woodland/ <i>Pandanus</i> tall open palmland/ <i>Chrysopogon</i> mid tussock grassland	<i>Melaleuca viridiflora</i> +/- <i>Corymbia polycarpa</i> &/or <i>Corymbia latifolia</i> low open woodland with <i>Pandanus spiralis</i> , <i>Livistona humilis</i> and <i>Grevillea pteridifolia</i> tall open palmland and <i>Chrysopogon fallax</i> , <i>Themeda avenacea</i> , <i>Sorghum</i> spp. mid tussock grassland.	1,665	4.0	230	5.1
* <i>Halosarcia</i> low sparse samphire shrubland	<i>Halosarcia indica</i> , <i>Tecticornia australasica</i> & <i>Suaeda arbusculoides</i> low sparse samphire shrubland.	5,915	14.4	213	4.7
**Other	Various	16,180	39.3	1,113	24.5
Total		36,922	89.7	3,978	87.7

*This vegetation class is supra tidal but was included in the freshwater class because it largely becomes freshwater in the breeding wet season with the input of freshwater during monsoonal events (see text).

**This vegetation class contained 32 associations with the nest abundance ranging from 1 to 161.

and 46 of 81 Associations). In these vegetation communities, 87.7% of nests (3,978 of 4,537) were found in the freshwater or hypo-saline habitats that comprised 89.7% of total habitat area (approximately 36,922 km²), while 12.3% (559 of 4,537) were found in the saline habitats that were 10.3% of total habitat area (approximately 4,230 km²).

The most common vegetation Association in which nests were found were the freshwater or hypo-saline habitats with tall, closed tussock grasslands dominated by *Oryza* species, typical of broad areas of the coastal floodplain environments north of 17° S (1,642 nests, 36.2 % of all nests; A and B in Fig. 2, Table 1). This

habitat represents 15.5% of the total area of the predicted habitats (6,374 of 41,152 km²). Open forests and woodlands with *Eucalypt*, *Melaleuca*, and *Pandanus* species were also common in the freshwater habitats in which nests were observed (C and D in Fig 2). The most common association in the saline habitats where nests were located was closed and open forests with *Rhizophora*, *Bruguiera*, and *Aegialitis* species (177 nests, 3.9% of all nests; Table 2). This habitat represents 2.3% of the total area of the predicted habitats (966 of 41,152 km²).

The harvest of the nests occurred between November and May (Fig. 3). Most nests were

TABLE 2. The number and percentage of the nests of Saltwater Crocodile (*Crocodylus porosus*) found in the saline water vegetation communities 2000–2011. The detailed description of each vegetation association is available in ESCAVI (2003) and DSEWPC (2012).

Vegetation Sub-Formation	Vegetation Association	Area (km ²)	% of total habitats predicted	Number of nests	% of total nests found
<i>Rhizophora</i> (mixed) mid closed forest/ <i>Bruguiera</i> low open forest/ <i>Aegialitis</i> (mixed) low open shrubland	<i>Rhizophora</i> spp, <i>Bruguiera</i> spp & <i>Xylocarpus mekongensis</i> mid closed forest with <i>Bruguiera parviflora</i> , <i>Ceriops tagal</i> & <i>Bruguiera</i> spp low open forest secondary tree layer and <i>Aegialitis annulata</i> & <i>Acanthus ilicifolius</i> low open shrubland.	966	2.3	177	3.9
<i>Avicennia</i> low open forest/ <i>Ceriops</i> low open forest/ <i>Avicennia</i> low open shrubland	<i>Avicennia marina</i> , <i>Ceriops tagal</i> , <i>Bruguiera</i> spp & <i>Rhizophora stylosa</i> low open forest with <i>Ceriops tagal</i> , <i>Avicennia marina</i> & <i>Osbornia octodonta</i> low open forest secondary tree layer and <i>Avicennia marina</i> , <i>Ceriops tagal</i> & <i>Aegialitis annulata</i> low open shrubland ground stratum.	730	1.8	130	2.9
<i>Ceriops</i> low closed forest/ <i>Ceriops</i> low open woodland/ <i>Ceriops</i> low sparse shrubland	<i>Ceriops tagal</i> , <i>Bruguiera</i> spp +/- <i>Excoecaria ovalis</i> low closed forest with <i>Ceriops tagal</i> +/- <i>Aegiceras corniculatum</i> &/or <i>Scyphiphora hydrophylacea</i> low open woodland and <i>Ceriops tagal</i> +/- <i>Aegialitis annulata</i> low sparse shrubland.	717	1.7	27	0.6
*Other	Various	1,817	4.4	225	5.0
Total		4,230	10.3	559	12.3*

*This vegetation class contained four Associations with the nest abundance ranging from 1 to 11, and 205 nests whose associations could not be determined.

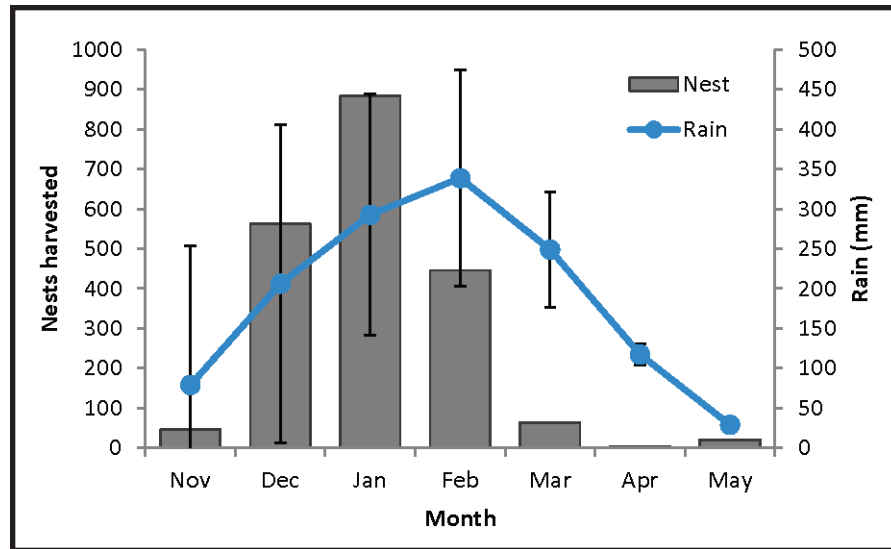


Figure 3. Nests of Saltwater Crocodile (*Crocodylus porosus*) harvested 2000–2011 and reported with the month of harvest and the average monthly rainfall for 2000–2011 at five weather stations in Northern Territory, Australia. Error bars on the average monthly rain are the standard error of the mean.

harvested between December and February (562 in December, 883 in January, and 446 in February). The average monthly rainfall was high (> 200 mm) December–March and highest in February (339 mm).

DISCUSSION

It should be noted that our nest records do not represent all the nesting habitats available in the study area. Search effort for nests was not standardized among the sites and observers. It is possible that anthropologic factors contributed to the heterogeneous distribution and abundance of the harvested nests (e.g., more nests were found around townships because of better accessibility, harvest targeted toward areas of highest return). Nevertheless, the nest records covered most of the coastal and sub-coastal regions of the Northern Territory (21 catchments), and their association with the vegetation communities in these catchments can be described with caution, accordingly. Despite some deficiencies in the design of this dataset for statistical purposes, these data represent the most comprehensive records of Saltwater Crocodile nesting sites.

Our results show that in overall terms, nest density of Saltwater Crocodiles was proportional to habitat availability, with 87.7% of nests found in freshwater or hypo-saline habitats, comprising 89.7% of the potential habitat area. The majority

of nests (68.7% overall) were located within vegetation Associations of the extensive riverine floodplains adjacent to the numerous rivers across the study area, with ground strata dominated by sedges and large perennial tussock grasses, representing 51.5% of the habitat area. Of the remaining nests, 19% were located in other freshwater habitats (i.e. Eucalypt woodlands and open forests), representing 38.2% of habitat area. These observations support previous studies (Webb et al 1977; Magnusson et al. 1978; Magnusson 1980) that Saltwater Crocodiles build their nests primarily in the freshwater habitats.

Even in the saline habitats where 12.3% of nests were found, it is likely that the water salinity at the nesting sites was more or less reduced because of the significant amount of floodwater and rainwater flushing into these habitats during the wet season, when nesting occurs. Similar observations of the freshwater input in the wet season, facilitating the survival of hatchlings in coastal wetlands have been reported for American Crocodiles, *Crocodylus acutus* (Mazzotti 1999), and Morelet's Crocodiles, *Crocodylus moreletii* (Platt et al. 2008).

Although the reasons why Saltwater Crocodiles select freshwater habitats for nesting are not readily clear, it has been suggested that freshwater habitats may impart a physiological advantage to hatchlings through increased

energetic efficiency of osmoregulatory processes (Grigg 1981; Mazzotti and Dunson 1989). Although Saltwater Crocodile hatchlings have highly developed physiological adaptations to hyper-saline conditions (Grigg et al. 1980; Grigg 1981; Taplin 1984, 1985), hatchlings physiologically require freshwater, especially in the following dry season when the freshwater input from rains cease and water salinity may dramatically rise in hypo-saline and saline habitats (Dunson 1970; Webb et al. 1977, 1983). Similar observations on hatchling adaptation to hyper-salinity and yet physiological preference for freshwater have been reported for American Crocodiles (Mazzotti et al. 1986; Mazzotti 1999; Platt et al. 2013). Webb et al. (1983) also suggested the importance of access to freshwater for adult females for internally developing eggs, particularly depositing shells. Given the physiological significance of freshwater for breeding females and hatchlings, it is unlikely that crocodiles select freshwater habitats solely on the basis that these habitats were more available in the species range.

Conversely, the vegetation communities Saltwater Crocodiles used for nesting were not proportional to the availability of habitats. Nesting habitat preference was highly skewed to *Oryza* tall tussock grassland (36.2% of nests), while this vegetation represented only 15.5% of the total habitat. The second most commonly used vegetation Association, *Melaleuca* open forest with sedge/tussock grass, dominated ground strata similar in composition to the *Oryza* floodplain tussock grasslands, which comprised 2.0% of the total habitat but contained 6.1 % of nests. These results would appear to indicate that the availability of suitable ground layer vegetative material for constructing a mound-like nest is a major determinant of nest site selection, as suggested by previous studies (Magnusson 1980; Webb et al. 1983). The availability of these freshwater vegetation communities also affects the abundance of non-hatchling (> 0.6 m total length) Saltwater Crocodiles at a catchment level across northern Australia (Fukuda et al. 2007). These particular vegetation communities may be used to map suitable nesting habitats and abundance of Saltwater Crocodiles for management and conservation purposes (Magnusson et al. 1978; Harvey and Hill 2003).

As well as the physiological requirements, the suitability of the vegetation for nesting may

explain why Saltwater Crocodiles did not commonly use the saline water vegetation. The pneumatophores of mangroves such as *Rhizophora*, *Bruguiera*, and *Aegialitis*, and sparse, short chenopod sub-shrubs and sedges associated with mangroves would make the construction of nests difficult in these vegetation communities (Magnusson 1980). Further, field observations suggest that nests located in mapped mangrove vegetation Associations often occur on the landward fringes of these saline habitats with Saltwater Couch (*Sporobolus virginicus*) and other salt tolerant grasses and sedges where the density of ground layer graminoids increases as a result of freshwater run-off and seepage from adjacent 'upland' vegetation Associations. This freshwater input results in an overall dilution of salt concentrations and the creation of a somewhat less saline microhabitat on the landward margins of the intertidal zone, likely to be physiologically more favorable habitat for Saltwater Crocodile nesting.

It should be noted that the occurrence of a significant number of Saltwater Crocodile nests in *Eucalyptus miniata*-dominated mid open forests, generally considered upland or terrestrial vegetation Associations, is explained by observations indicating wet season inundation adjacent to Saltwater Crocodile nests at the margins of these communities during monsoonal flooding events in the major drainage divisions of the study area. The actual area of suitable nesting habitat is limited to a very small proportion of this habitat adjacent to watercourses and floodplains that allow access for nesting individuals during the breeding season. Approximately 51% of these nest records (256 of 504 nests) were within 100 m of an adjacent wetland vegetation Association boundary and over 97% (491 of 504 nests) were located within the scale tolerance (1,000 m) of the vegetation mapping data used in this analysis. It could be expected that improvements in scale and refinement of vegetation Association mapping within the expected Saltwater Crocodile habitat range may result in a higher proportion of nests being located within wetland vegetation Associations and a reduction in possible commission errors resulting from the location of nests within mapped upland vegetation associations at the scale of vegetation mapping currently available.

In short, multiple factors appear to be involved

in the site selection for nesting by Saltwater Crocodiles: (1) freshwater habitat is proportionally more available than saline habitat and more commonly used; (2) predominantly non-saline (fresh and hypo-saline) water regimes have distinct physiological advantages over saline water regimes; and (3) the suitability of ground layer vegetation for constructing their mound-like nests is important. Despite some limitations in the interpretation of the data, our results indicate that the most commonly used nesting habitats can be characterized by prevailing non-saline water regimes at the time of nesting and freshwater vegetation Associations, with well-developed, graminoid dominated ground strata such as *Oryza* tall tussock grasslands with or without over-storey trees. These vegetation communities may be used to assess the suitability of nesting habitat for management and conservation purposes. These nesting habitats should have high conservation value and the monitoring of nests should continue. Management decisions for the species as a top predator in these wetland habitats should be based on evidence from such long-term monitoring programs.

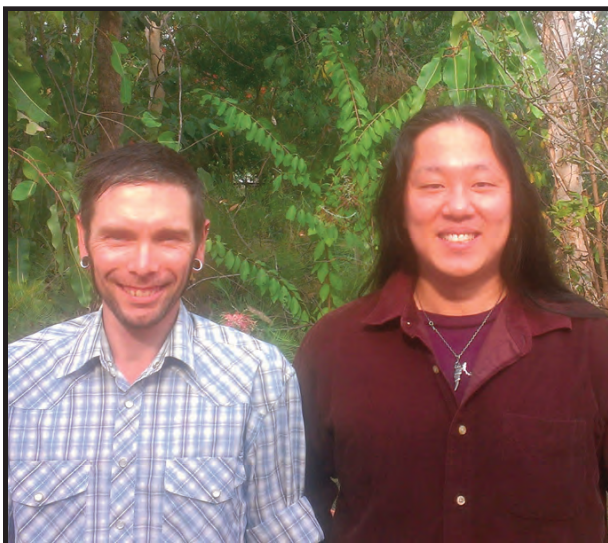
Acknowledgments.—This study was conducted as part of the crocodile management programs by the Northern Territory Department of Land Resource Management and the Parks and Wildlife Commission of the Northern Territory. This study used the historical data of crocodile nests that were harvested under permits required by the Parks and Wildlife Commission of the Northern Territory, in accordance to the Code of Practice on the Humane Treatment of Wild and Farmed Australian Crocodiles (NRMCC 2009). We thank the many staff in the agencies and industries of crocodile harvesting and farming for their cooperation in the management programs and data collection. Gordon Grigg, Glenn Edwards, Alaric Fisher, and Keith Saalfeld provided helpful comments on the earlier manuscript.

LITERATURE CITED

- Australian Nature Conservation Agency (ANCA). 1996. A Directory of Important Wetlands in Australia. 2nd Edition. ANCA, Canberra, Australia.
- Blackman, J.G., A.V. Spain, and L.A. Whitey. 1992. Provisional Handbook for the Classification and Field Assessment of Queensland Wetlands and Deepwater Habitats. Queensland Department of Environment and Heritage, Brisbane, Australia.
- Brazaitis, P., and M.E. Watanebe. 2011. Crocodilian behaviour: a window to dinosaur behaviour? *Historical Biology* 23:73–90.
- Brocklehurst, P.S., and D. Lynch. 2009. *Melaleuca* Survey of the Top End, Northern Territory. Technical Report No. 25/2009D. Land and Vegetation Branch, Land and Water Division, Northern Territory Department of Natural Resources, Environment, The Arts and Sport, Palmerston, Australia.
- Brocklehurst, P.S., and D. Van Kerckhof. 1994. *Melaleuca* Survey of the Northern Territory. Document 2. Methodology and Data-Base Description. Conservation Commission of the Northern Territory, Palmerston, Australia. 89 pp.
- Brocklehurst, P.S., D. Lewis, D. Lynch, and D. Napier. 2007. Northern Territory Guidelines and Field Methodology for Vegetation Survey and Mapping. Northern Territory Department of Land Resource Management, Darwin, Australia.
- Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe. 1979. Classification of Wetlands and Deepwater Habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., and Jamestown, North Dakota, USA.
- Department of Sustainability, Environment, Water, Population and Communities (DSEWPC). 2012. National Vegetation Information System (NVIS). Version 4.1. Australian Government Department of Sustainability, Environment, Water, Population and Communities, Canberra, Australia.
- Dunson, W.A. 1970. Some aspects of electrolyte and water balance in three estuarine reptiles, the Diamondback Terrapin, American and “Salt water” crocodiles. *Comparative Biochemical Physiology* 32:161–174.
- Executive Steering Committee for Australian Vegetation Information (ESCAVI). 2003. Australian Vegetation Attribute Manual: National Vegetation Information System, Version 6.0. Australian Government Department of the Environment and Heritage, Canberra, Australia.
- Fukuda, Y., G. Boggs, and P. Whitehead. 2004. GIS-based habitat suitability analysis of Saltwater Crocodiles (*Crocodylus porosus*) in

- the Northern Territory. Pp. 470–474 *In* Crocodiles. Proceedings of the 17th Working Meeting of IUCN-SSC Crocodile Specialist Group. IUCN, Gland, Switzerland.
- Fukuda, Y., P. Whitehead, and G. Boggs. 2007. Broad scale environmental influences on the abundance of Saltwater Crocodiles, *Crocodylus porosus*, in Australia. *Wildlife Research* 34:167–176.
- Fukuda, Y., K. Saalfeld, B. Easton, G. Webb, C. Manolis, and M. Brien. 2012. Crocodile management and research in the Northern Territory of Australia, 2008–2011. Pp. 149–157 *In* Crocodiles. Proceedings of the 21st Working Meeting of IUCN-SSC Crocodile Specialist Group. IUCN, Gland, Switzerland.
- Fukuda, Y., G. Webb, C. Manolis, R. Delaney, M. Letnic, G. Lindner, and P. Whitehead. 2011. Recovery of Saltwater Crocodiles following unregulated hunting in tidal rivers of the Northern Territory, Australia. *Journal of Wildlife Management* 75:1253–1266.
- Geoscience Australia. 2004. Australian Surface Water Management Areas (ASWMA) 2000. Geoscience Australia, Canberra, Australia.
- Geoscience Australia. 2006. GEODATA TOPO 250K Series 3. Geoscience Australia, Canberra, Australia.
- Grigg, G.C. 1981. Plasma homeostasis and cloacal urine composition in *Crocodylus porosus* caught along a salinity gradient. *Journal of Comparative Physiology B* 144:261–270.
- Grigg, G.C., L.E. Taplin, P. Harlow, and J. Wright. 1980. Survival and growth of hatchling *Crocodylus porosus* in salt water without access to fresh drinking water. *Oecologia* 47:264–266.
- Grigg, G.C., L.A. Beard, T. Moulton, M.T. Queirolo Melo, and L.E. Taplin. 1998. Osmoregulation by the Broad-snouted Caiman, *Caiman latirostris*, in estuarine habitat in southern Brazil. *Journal of Comparative Physiology B* 168:445–452.
- Harvey, K.L., and G.J.E. Hill. 2003. Mapping the nesting habitat of Saltwater Crocodiles (*Crocodylus porosus*) in Melacca Swamp and the Adelaide River wetlands, Northern Territory: an approach using remote sensing and GIS. *Wildlife Research* 30:365–375.
- Hussain, S.A. 1999. Reproductive success, hatchling survival and rate of increase of Gharial *Gavialis gangeticus* in National Chambal Sanctuary, India. *Biological Conservation* 87:261–268.
- Lance, V.A. 1989. Reproductive cycle of the American Alligator. *American Zoologist* 29:999–1018.
- Leach, G.J., R. Delaney, and Y. Fukuda. 2009. Management Program for the Saltwater Crocodile in the Northern Territory of Australia, 2009–2014. Northern Territory Department of Natural Resources, Environment, The Arts and Sport, Darwin, Australia.
- Magnusson, W.E. 1980. Habitat required for nesting by *Crocodylus porosus* (Reptilia: Crocodylidae) in Northern Australia. *Australian Journal of Wildlife Research* 7:149–156.
- Magnusson, W.E., G.C. Grigg, and J.A. Taylor. 1978. An aerial survey of potential nesting areas of the Saltwater Crocodile, *Crocodylus porosus* Schneider, on the north coast of Arnhem Land, northern Australia. *Australian Journal of Wildlife Research* 5:401–415.
- Mazzotti, F.J. 1999. The American Crocodiles in Florida Bay. *Estuaries* 22:552–561.
- Mazzotti, F.J., and W.A. Dunson. 1989. Osmoregulation in crocodilians. *American Zoologist* 29:903–920.
- Mazzotti, F.J., B. Bohnsack, M.P. McMahon, and J.R. Wilcox. 1986. Field and laboratory observations on the effects of high temperature and salinity on hatchling *Crocodylus acutus*. *Herpetologica* 42:191–196.
- McDonald, R.C., R.F. Isbell, G. Speight, J. Walker, and M.S. Hopkins. 1990. Australian Soil and Land Survey Field Handbook. 2nd Edition. Inkata Press, Melbourne, Australia.
- National Committee on Soil and Terrain (NCST). 2009. Australian Soil and Land Survey Field Handbook. 3rd Edition. CSIRO, Collingwood, Victoria, Australia.
- Natural Resource Management Ministerial Council (NRMMC). 2009. Code of Practice on the Humane Treatment of Wild and Farmed Australian Crocodiles. Australian Government, Canberra, Australia.
- Platt, S.G., T.R. Rainwater, J.B. Thorbjarnarson., and S.T. McMurry. 2008. Reproductive dynamics of a tropical freshwater crocodilian: Morelet's Crocodile in northern Belize. *Journal of Zoology* 275:177–189.
- Platt, S.G., J.B. Thorbjarnarson., T.R. Rainwater, and D.R. Martin. 2013. Diet of the American Crocodile (*Crocodylus acutus*) population on Turneffe Atoll, Belize. *Journal of Herpetology* 47:1–10.

- Sattler, P.S., and R.D. Williams. 1999. The Conservation Status of Queensland's Bioregional ecosystems. Environmental Protection Agency, Brisbane, Australia.
- Taplin, L.E. 1984. Homeostasis of plasma electrolytes, water and salinity pools in the Estuarine Crocodile, *Crocodylus porosus*, from fresh, saline and hypersaline waters. *Oecologia* 63:63–70.
- Taplin, L.E. 1985. Sodium and water budgets of the fasted Estuarine Crocodile, *Crocodylus porosus*, in sea water. *Journal of Comparative Physiology B* 155:501–513.
- Taplin, L.E., and G.C. Grigg. 1981. Salt glands in the tongue of the Estuarine Crocodile *Crocodylus porosus*. *Science* 212:1045–1047.
- Wang, J.J., X.B. Wu, D.W. Tian, J.L. Zhu, R.P. Wang, and C.L. Wang. 2011. Nest-site use by the Chinese Alligator (*Alligator sinensis*) in the Gaojingmiao breeding farm, Anhui, China. *Asian Herpetological Research* 2:36–41.
- Webb, G.J.W. 1991. The influence of season on Australian crocodiles. Pp. 125–131 *In* Monsoonal Australia: Landscape, Ecology and Man in the Northern Lowlands. Ridpath, M.G., C.D. Hayers, and M.J.D. Williams. (Eds.). AABalkema, Rotterdam, Netherlands.
- Webb, G.J.W., and S.C. Manolis. 1989. Crocodiles of Australia. Reed, Sydney, Australia.
- Webb, G.J.W., S.C. Manolis, and M.L. Brien. 2010. Crocodile Specialist Group Action Plan Saltwater Crocodile *Crocodylus porosus*. IUCN-SSC, Gland, Switzerland.
- Webb, G.J.W., H. Messel, and W.E. Magnusson. 1977. The nesting biology of *Crocodylus porosus* in Arnhem Land, northern Australia. *Copeia* 1977:238–249.
- Webb, G.J.W., P.J. Whitehead, and G. Letts. 1984. A Proposal for the Transfer of the Australian Population of *Crocodylus porosus* Schneider (1801), from Appendix I to Appendix II of C.I.T.E.S. Conservation Commission of the Northern Territory technical report. Northern Territory Government, Darwin, Australia.
- Webb, G.J.W., G.C. Sack, R. Buckworth, and S.C. Manolis. 1983. An examination of *Crocodylus porosus* nests in two northern Australian freshwater swamps, with an analysis of embryo mortality. *Australian Wildlife Research* 10:571–607.
- Webb, G.J.W., A.R.C. Britton, S.C. Manolis, B. Ottley, and S. Stirrat. 2000. The recovery of *Crocodylus porosus* in the Northern Territory of Australia: 1971–1998. Pp. 195–234 *In* Crocodiles. Proceedings of the 15th Working Meeting of IUCN-SSC Crocodile Specialist Group. IUCN, Gland, Switzerland.
- Wildlife Management International. 2007. Monitoring Saltwater Crocodile (*Crocodylus porosus*) Nests in the Northern Territory: Trends in Melacca Swamp over 28 Years (1980–2007). Wildlife Management International, Darwin, Australia.
- Wilson, B.A., P.S. Brocklehurst, M.J., Clark, and K.J.M., Dickinson. 1990. Vegetation Survey of the Northern Territory. Conservation Commission of the Northern Territory, Technical Report No. 49, Australia.



YUSUKE FUKUDA (right) is a Wildlife Scientist for the Northern Territory Department of Land Resource Management, Australia. He specializes in the population ecology of wild crocodiles in Australia. He is a member of the IUCN-SSC Crocodile Specialist Group since 2009. He received his B.Sc (Hons I) with double majors in Ecology and Environmental Biology, and Geographic Information from Charles Darwin University (2005). He was awarded the Chancellor's Medal by Charles Darwin University in 2005.

NICHOLAS CUFF (left) is a Vegetation Scientist for the Northern Territory Department of Land Resource Management, Australia. He specializes in field botany and vegetation community ecology and has worked extensively throughout northern Australian ecosystems. He received his B.Sc (Hons) with double majors in Botany and Zoology from James Cook University (1998). (Photographed by Kylie Cuff).