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Aversive Conditioning of Larger Estuarine Crocodiles (*Crocodylus porosus*) and the Remote Deployment of Transmitters

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Abstract.—**Aversive conditioning has been used with terrestrial predators to reduce conflict with humans by changing predator behavior or moving them away. Proving the effectiveness of this management tool for cryptic animals, however, can be challenging. In this study, we assessed the interaction between presence and sightability in Estuarine Crocodiles (*Crocodylus porosus*) after a period of aversive conditioning. Crocodiles > 2 m in length were subjected to aversive conditioning using two non-lethal beanbags fired from a 12-gauge shotgun. Traditional night-time surveys were conducted prior to and after aversive conditioning to determine any changes in crocodile sightability. To detect crocodiles underwater and their movement, we attached acoustic transmitters with a hand-held pole harpoon, which were monitored with an acoustic receiver array. This technique allowed for transmitter attachment without the need for capture. Immediately after aversive conditioning, there was a significant reduction in the sightability of larger Estuarine Crocodiles (> 2 m) using traditional spotlight survey, and a detectable change in the movement patterns of two of the three tagged individuals. The two tagged crocodiles resumed normal movement patterns soon after (42 h, 15 d) and no crocodiles left the area in response to the treatment. Aversive conditioning has limited use in moving crocodiles away from a discrete area; however, it did have a short-term impact on crocodile behavior and crocodiles became more challenging to detect by traditional spotlight survey. The reduced sightability may indicate an increased wariness of people, which in some circumstances may be an acceptable outcome for management.**

Key Words.—acoustic telemetry; aversive conditioning; *Crocodylus porosus*; non-lethal management; sightability; tag attachment.

Introduction

Human-wildlife conflict is driven by increasing populations of humans and wildlife, combined with habitat reduction and diminished resources (Athreya and Belsare 2007; Inskip and Zimmerman 2009). In the case of large terrestrial predators including big cats (lions, tigers, leopards; all *Panthera* sp.), Coyotes (*Canis latrans*), Wolves (*Canis lupus*), and bears (*Ursus* sp.), along with aquatic and semi-aquatic predators such as sharks (Carcharhiniforme) and crocodilians (Crocodilia), the threat they pose to public safety and livelihoods often leads to management actions involving removal of the animal (Mitchell et al. 2004; Fukuda et al. 2014; Bradley et al. 2015; Lewis et al. 2015; Krafte-Holland et al. 2018). Continued decline of these predators in many countries has stimulated investigations into alternative mitigation strategies which do not require removal, with the aim of achieving sustainable coexistence with humans (Woodroffe 2000; Mishra et al. 2003; Treves and Karanth 2003; Kabir et al. 2013).

One strategy is aversive conditioning, which typically involves creating a negative experience for an animal displaying unwanted behavior, with the aim of changing the behavior, or moving the animal away from an area (Brush 1971; Mason et al. 2001; Shivik et al. 2003; Beckman et al. 2004; Kidd-Weaver et al. 2022). Non-lethal aversive conditioning techniques, including the use of bean bag slugs, shock collars, and electrical fencing, have been used with varying levels of success to change the behavior of Black Bears (*Ursus americanus*; Mazur 2010), Wolves (Schultz et al. 2005), and foxes (*Vulpes* sp.; Cooper et al. 2005) in situations where they had become habituated to human activity and were coming into conflict with landowners. A recent study evaluated the efficacy of capture as a form of aversive conditioning in wild American Alligators (*Alligator mississippiensis*) in South Carolina, USA, and found that previously captured individuals were more likely to flee, and at a greater distance, in response to an approaching human (Kidd-Weaver et al. 2022). The Estuarine Crocodile (*Crocodylus porosus*) is the largest and most wide-ranging species of crocodilian in the world (Webb et al. 2010) and is responsible for many attacks on humans each year. In 2019, the species was responsible for 207 attacks on humans worldwide, of which 97 were fatal (CrocBITE. 2020. The worldwide crocodilian attack database. CrocBITE. Available from http://www.crocodile-attack.info [Accessed 1 May 2020]).

Across northern Australia, in particular the Northern Territory and Queensland, the population of Estuarine Crocodiles has recovered steadily since protection began (Fukuda et al. 2014; Taplin et al. 2020). This has coincided with a rapid increase in the human population and urban/rural development (Fukuda et al. 2014; Taplin et al. 2020). Consequently, there has been an increase in human-crocodile conflict in northern Australia with an increase in the number of non-fatal attacks over time (Fukuda et al. 2014; Brien et al. 2017).

The management of Estuarine Crocodiles in northern Australia has historically involved the removal of crocodiles ≥ 2 m long (or those otherwise deemed a threat to public safety) from in and around urban areas, combined with the Be CrocWise public education program (Fukuda et al. 2014; Brien et al. 2017). In Queensland, the Department of Environment and Science (DES) has been exploring alternative methods to help reduce the risk of crocodiles to public safety. One such method is the use of aversive conditioning to alter the behavior of crocodiles that have become habituated to people. Once a crocodile has been fed by a human, either directly or indirectly (e.g., fish scraps left at boat ramp), it can become less wary of humans and will associate a particular activity (e.g., fishing) and/or location (e.g., boat ramp) with food, posing a greater threat to public safety. The use of non-lethal rounds fired from a shotgun has been used on a few of what are considered problem crocodiles in remote areas of Queensland on occasion in recent years (DES, unpubl. data); however, the effect of this activity on the movement patterns and sightability of the animal in each case was unclear.

Despite its potential use as a management tool, only one study has previously examined the use of aversive conditioning in crocodilians (Kidd-Weaver et al. 2022). While the authors of this study recognized that capturing alligators was an effective method of aversive conditioning, however, it was also potentially costly, time intensive, and logistically difficult. In this study, we evaluated aversive conditioning using non-lethal shotgun ammunition (e.g., bean bags) to determine any effect on the movement patterns and behavior (using acoustic tags and standardized surveys) of Estuarine Crocodiles in response to human activity in the Norman River, Gulf of Carpentaria, Australia. We also describe a novel method for remotely attaching acoustic transmitters to free ranging crocodiles using a harpoon pole, negating the need to capture the animal. As this overall approach does not involve capture and handling, it potentially provides a comparatively safer and more efficient method of aversive conditioning.

Materials and Methods

Study area.—We conducted the study on the downstream tidal section of the Norman River (-17.634140°, 141.024481° to -17.738407°, 141.098328°), near Normanton in the south-eastern Gulf of Carpentaria, Australia (Fig. 1). Normanton is located 82 km upstream from the river mouth and supports a resident human population of 1,210 (2016 census), which increases during May-August as tourists, including many fishermen, converge on the town. The region experiences significant seasonal variation in temperatures and rainfall, with a distinct winter dry

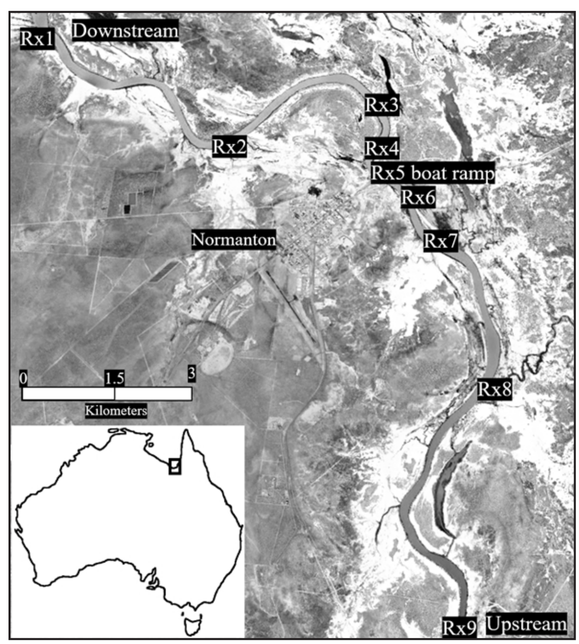

Figure 1. The study site was in a 20-km section of the Norman River, Gulf of Carpentaria, Australia. Nine acoustic receivers (Rx) were placed at various intervals up to 10 km downstream (Rx1: 10 km, Rx2: 5 km, Rx3: 1.5 km, Rx4: 0.5 km) and 10 km upstream (Rx6: 0.5 km, Rx7: 1.5 km, Rx8: 5 km, Rx9: 10 km) of the Normanton boat ramp (Rx 5).

(May-August: mean maximum temp: 27.5°–29.8° C, mean rainfall: 1.0–8.5 mm) and summer wet season (September-April: 29.9°–32.6° C; mean rainfall: 1.6–260.3 mm; www.bom.gov.au/climate/averages/tables/cw_029028.shtml). The Norman River and its tributaries flow through extensive alluvial plains and savannah woodlands, creating a shallow sediment-rich system surrounded by ephemeral creeks and lagoons along its length. We selected a 20-km section of the river for the study (10 km either side of the Normanton boat ramp). Within the study area, river width ranged from 82–169 m and river depth from 1.5–6 m at the midpoint of the tidal cycle at 2.0 m predicted tide height (https://www.ausmarinescience.com/tide-times/2018-queensland-tide-times/). Water temperature during the study ranged from 21.5° C to 32.9° C. The river supports a substantial population of Estuarine Crocodiles (range, < 0.6 m for hatchlings to 5 m total length, TL) that has recovered from an encounter rate of 0.22 non-hatchlings/km in 1985, 11 y after protection from decades of unregulated commercial hunting, up to 1.80/km in 2017 (Taplin et al. 2020). DES receives very few reports of problem crocodiles from this area; however, large individuals (> 3 m) are occasionally reported lingering near boat ramps and approaching boats, often feeding opportunistically on fish waste left by recreational and commercial fishers (DES, unpubl. data).

Acoustic tags and attachment.—We used acoustic transmitters (V9 69 kHz; Vemco Inc., Bedford, Nova Scotia, Canada) fitted with shark caps (Vemco Inc.) to track the movement patterns of crocodiles. These tags were preferred to satellite tags due to their smaller size and lower cost, while still enabling broad-scale movements up- and down-stream to be detected. We tethered each transmitter (26 mm long × 9 mm wide; weight, 6.0 g) to a stainless steel (316 medical grade) sub-dermal anchor (27 mm long × 7 mm wide) using a 50 mm length of nylon coated wire trace (27.2 kg, 0.66 mm diameter) secured together with two copper crimp sleeves (Fig. 2). To aid in visual identification of tagged crocodiles at night, we placed a 4-mm strip of SOLAS reflective tape (3M, Maplewood, Minnesota, USA) around the shark cap (Fig. 2). We implanted the subdermal anchor into the side of the muscular neck region of each crocodile using a hand-held harpoon pole, driven with force at a range of about 2 m from a boat. The pole consisted of a 3 m length of Rangoon cane fitted with a custom-made stainless steel deployment head (150 × 40 mm) that included a 35 mm circular stopping plate, which prevented the acoustic tag from penetrating through the skin further than 40 mm (Fig. 2). Once the dermal anchor was embedded under the skin with the pole, it slips off the pointed applicator end and rotates 90 degrees to lie horizontally with only the tether wire and transmitter protruding.

We only targeted crocodiles > 2.1 m (6 ft) in length, as this size class poses the highest risk to public safety (Brien et al. 2017). We initially located crocodiles at night with a handheld spotlight (Blitz 240–100 W halogen; LightForce, Hindmarsh, South Australia, Australia) and approached closely using an electric motor (Minn-Kota Riptide 55 lb Power Drive; Johnson Outdoors Inc., Racine, Wisconsin, USA) under low light (H7.2 Pro; LED Lenser, Solingen, Germany). To avoid inadvertently re-tagging a crocodile, we used a directional hydrophone (VR100 69 kHz MAP114; Vemco Inc.) when approaching each crocodile to detect transmissions and confirm it had not been tagged previously.

Captive trials.—We tested the attachment method prior to field deployment, using replica acoustic tags of the same size and weight. We attached replica tags to four captive crocodiles (TL, 2.2–3.6 m) at Melaleuca Crocodile Farm, Mareeba, Queensland (-16.934946°, 145.400620°) on 11 April 2018 prior to the study. Each crocodile was housed individually in an earthen pond enclosed with 1.6 m high chain link mesh fencing. We implanted replica tags into the side of the neck of each crocodile using the harpoon pole and monitored them

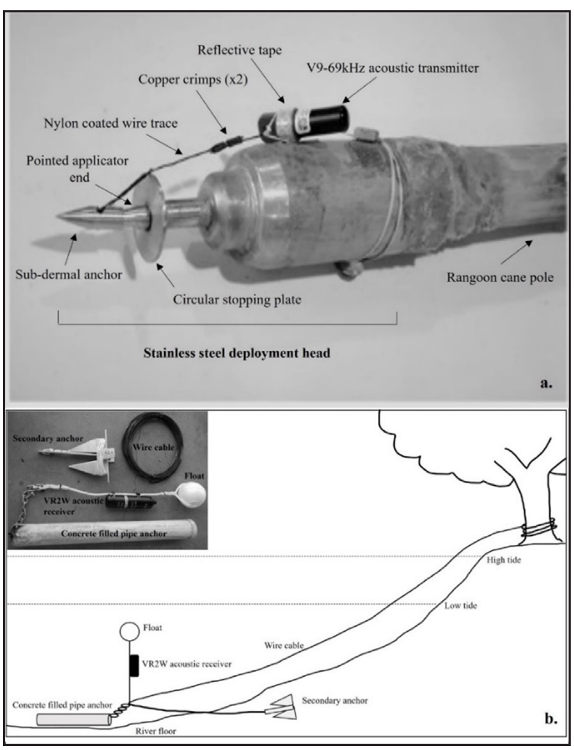

Figure 2. (a) Acoustic transmitter (V9-69 kHz) tethered with nylon coated wire trace and crimps to a sub-dermal anchor. The custom-made stainless steel deployment head consisted of a pointed applicator end, circular stopping plate, cap, which was fitted to a 3 m Rangoon pole. (b) VR2W acoustic receiver setup installed on the river floor, including two anchors, float, and tethered to a tree on the bank with stainless steel wire cable.

daily for 93 d for signs of infection or injury around the attachment site. Each crocodile was checked again after 302, 583, 702, and 1,274 d. We did not see any signs of infection or injury at any stage, with all four replica acoustic tags remaining in place for 302 d. After 583 d all tags had dislodged but the wire tethers and anchors remained in place, and after 700 d all wire tethers had corroded away with only the sub-dermal anchors remaining beneath the skin. Following the premature failure of one singly crimped tag, we decided that two crimps were required on each end of the tether wire for adequate attachment to the sonar tag.

Acoustic receiver array.—We detected tagged crocodiles moving up and down the river with an array of nine static underwater acoustic receivers (VR2W 69 kHz; Vemco Inc.). We installed receivers along a 20-km section of the Norman River, centered at the Normanton boat ramp. We installed one receiver (Rx5) at the boat ramp, and the remaining eight receivers at distances of approximately 0.5, 1.5, 5.0 and 10.0 km both upstream and downstream of the boat ramp (Fig. 1). We attached each VR2W receiver with five zip ties to about 1 m of rope, with a polyethylene float (230 mm diameter) on one end, and a length of galvanized chain (about 30 cm) and about 30 kg anchor constructed from concrete filled polyvinyl chloride (PVC) pipe (10 × 100 cm) on the other (Fig. 2). To tether the receiver setup to a large tree on the riverbank, we attached an additional boat anchor to the galvanized chain and a 25 m length of stainless-steel wire cable (6 mm; Fig. 2). The PVC pipe anchor laid horizontally on the river bottom, while the float held the receiver vertically in the water column (Fig. 2). We positioned receivers about 25 m out from the bank at depths of about 1–5 m. River depth was checked using vessel mounted depth sounder (Lowrance HDS 9) during receiver installation to ensure minimum coverage with water of about 1 m on the lowest possible tide (0.20 m). We checked all receivers midway through the study (74 d) to check anchor hardware, and at the end (148 d) when they were removed from the river to download acoustic data. We set pulse transmission rates for each acoustic tag at randomized intervals (60–90 sec; mean = 74 sec), which we deemed suitable based on previously published maximum rates of crocodile travel (about 3.5 km/h) and transmission rates for acoustic tags (Campbell et al. 2010, 2013, 2014).

Detection range.—The receivers require line of sight and the transmitter to be in the water to detect the acoustic transmissions effectively. Campbell et al. (2014) reported that Estuarine Crocodiles in the Port Musgrave system, carrying VR9 transmitters and detected by VR2W receivers were detected reliably at ranges of up to 200–300 m. Detection range for such systems is a complex phenomenon (Huveneers et al. 2016; Selby et al. 2016; Winter et al. 2021). We considered it important to characterize it to a first approximation given the width and depth of the Norman River, the potential influences of tide and salinity, and the necessary deployment of all but the central, closely spaced receivers at distances that did not allow simultaneous capture of movements on two or more receivers. The experiment did not rely on precise location of crocodiles but on their presence/absence within range of a receiver and on detecting movement sequences that might reflect them moving in or out of the acoustic array in response to aversive conditioning. The main requirement was to estimate the likelihood of detecting a crocodile passing a receiver in a river up to 170 m wide.

It was impractical to explore array performance across the full range of tides and environmental conditions encountered. We deployed a static receiver and transmitter (Rx/Tx) array at the conclusion of this study (6 December 2018) on a straight section of river close to the Normanton boat ramp to gain insight into the array performance. Using the same anchor system, we installed two receivers 1,000 m apart, giving clear lines of sight between all transmitter and receiver combinations and five acoustic tags set at 250 m intervals from 0–1,000 m. We recorded detections over 10 h to include most of a full tidal cycle.

The receiver at the 1,000 m position in the array failed part-way through this trial, so we applied the analysis only to counts detected at the 0 m receiver (R0). We accumulated counts from each transmitter in consecutive 10 min intervals and we plotted them against the Rx:Tx separation distance. We modeled counts using a Generalized Linear Model incorporating the variables Separation Distance (m), Mean Tide Height over the 10-min interval (from Karumba tide heights lagged by 5 h 20 min; https://www.ausmarinescience.com/tide-times/2018-queensland-tide-times/), hour-of-day (0900–1900), and tidal direction (coded -1, 0 and 1 for downstream, slack, and upstream flow, derived from the differences in predicted tidal heights over 10-min intervals).

Aversive conditioning.—We applied aversive conditioning with two consecutive 40 g Super-sock bean bag rounds (Combined Systems, Jamestown, Pennsylvania, USA; 25 m effective range; projectile velocity of 270–290 ft/sec) that we shot into the side of the tail or neck of each crocodile using a 12-gauge shotgun (Stoeger - Outback Tactical, E.R. Amantino, Veranópolis, Rio Grande do Sul, Brazil). Prior to the study, we tested 12-gauge rubber fin-stabilized slugs (model 2551; Combined Systems) with a manufacturer-stated effective range of 9 m (about 30 ft); however, we did not find that this ammunition had sufficient projectile weight (20 g) or effective range for the boat-based application. The rubber slugs rebounded off the body of the crocodiles during trials and were less effective at delivering an effective impact compared to the Super-sock bean bags.

We chose the tail and neck as target areas as they are strongly muscular and away from vital organs. We started aversive conditioning 20 September 2018 between 1900 and 0200, about 70 d after the attachment of acoustic transmitters. This was enough time to allow any potential negative effect of the tag attachment itself to dissipate and normal movement patterns to resume. All sub-adult and adult crocodiles (TL > 2.1 m) that we encountered within the study area (10 km either side of boat ramp) during this time were subject to aversive conditioning, which was undertaken from a boat (4.6 m) at low tide (≤ 1.20 m). Once we sighted a crocodile > 2.1 m, we approached it slowly to a range of 15–20 m before receiving two consecutive shots. For each animal that we approached, we used an underwater directional hydrophone (VR100 69 kHz) to try and identify tagged animals. Six crocodiles were subject to conditioning during the study, of which one was confirmed as a tagged animal with the directional hydrophone. The acoustic tags proved difficult to detect on approach, due to the infrequent ping schedules of tags (mean = 74 sec). We judged two crocodiles likely to have been tagged individuals based on their size (2.9 m and 3.5 m) and the known location and sizes of tagged animals in the vicinity based on VR2W receiver records.

Population surveys.—We undertook night-time boat surveys in the study area to determine the number of crocodiles present, their estimated size (total length: feet), location in the river (GPS coordinate), and approachability, which is measured as the distance in meters before a crocodile submerged in response to the approaching boat. We completed surveys in accordance with protocols described by Bayliss (1987) and Fukuda et al. (2013) in a 4.6 m aluminum boat using a 100W halogen hand-held spotlight at night. Surveys commenced from the Normanton boat ramp, heading 10 km downstream to the end of the receiver array, before returning and traveling 10 km upstream to the upper end of the receiver array. We did not approach crocodiles on return journeys. Once sighted, we approached crocodiles slowly at a constant speed of 10 km/h until the crocodile submerged. If a crocodile did not submerge within 10 m of the boat, we considered it to have shown no avoidance behavior. We conducted night-time spotlight surveys prior to aversive conditioning (10 July and 19 September), immediately after aversive conditioning (20 September), and again 50 d after aversive conditioning (12 November). We recorded the distance at which crocodiles submerged or demonstrated avoidance behavior (swam away, startled, moved up the bank) when approached by the boat for each crocodile we sighted.

Data analyses.—Receivers recorded and stored acoustic transmissions each time a tagged crocodile came within detection range. We downloaded data from the receivers midway through the project (24 September), and at the end of the study (5 December). We applied time corrections to account for temporal drift of the individual receivers (Vue 2.4.2 Software User Manual 2018). We analyzed movement patterns of tagged crocodiles pre- and post- aversive conditioning to quantify and assess any changes in movement patterns. We analyzed these movement patterns in R (R Development Core Team 2010) using the V-track package (Campbell et al. 2012) with additional R code written specifically for this study. We compared differences in the number and size classes of crocodiles detected and in the approachability of crocodiles in the target size range > 2.1 m between these three survey periods. Because of small sample sizes, we analyzed these data pre- and post-conditioning using a Kruskal-Wallis Test.

To determine the influence of tide, we overlaid individual crocodile movement patterns with Karumba tide station data, offset by 5.3 h to allow for the tidal lag between Karumba and Normanton. Only one crocodile (Tag 8499) was found to show frequent and likely tidally influenced movements. To examine the effect of tide on movement patterns, we scored each long travel event of 8499, defined as a movement of at least 3 km in one direction, as to whether it commenced on the first half of a rising tide, the second half of a rising tide, the first half of a falling tide or the second half of a falling tide. We analyzed the frequency of movement as a Contingency Table to determine the relationship between direction of movement and favorable tidal conditions. We used Pearson's Chi-squared Test with Yates' Continuity Correction to assess whether movements were independent of tidal flow.

Detection data analyzed from crocodiles showed that tags could be detected at distances of up to 1,000 m while the probability a sonar ping was detected declined in a roughly exponential fashion with distance. The calibration experiment showed that detection probability was more complex than this and that an unexpectedly high proportion of transmissions went undetected at separation distances over 500 m. We therefore compared Simple Poisson and Negative Binomial Generalized Linear Models with Zero-inflated Models incorporating Poisson and negative binomial distributed counts for the counts part of the mixed model (Appendices). The Poisson models were adequate to capture dispersion in the data, with the dispersion statistic for the best fit Poisson:Binomial model 0.85. Detection counts were

Table 1. Capture and detection data for nine Estuarine Crocodiles fitted with acoustic transmitters and tracked in the Norman River. The symbol + means the tag detached soon after deployment.

Tag No.	Total Length (m)	Date of last detection	Total days	Detections	Conditioned
8499	4.8	16 November 2018	127	32,332	Yes
8503	2.9	5 December 2018	146	11,890	Yes
8835	2.9	4 December 2018	145	43,850	Yes
8506	3.1	15 August 2018	34	3,334	No
8507	3.2	28 October 2018	108	17,591	No
8508	3.4	12 November 2018	123	11,244	No
8836	3.2	25 November 2018	136	50,709	No
8837+	3.8	24 September 2018	74	57,432	No
8838	3.1	25 August 2018	44	1,369	No

best fitted by a model incorporating Separation distance in the counts part of the ZIP model and Separation distance and Mean Tide Height in the binomial part. That is, the likelihood of excess zero-counts in a 10-min interval increased significantly with separation distance and with increasing tide height (Appendices; Table 1, Fig. 1, 2). The best-fit model for detection counts was taken to be the Poisson:Binomial fit with the lowest Akaike Information Criterion (AIC) value and the smallest number of predictors. We considered model averaging (Burnham and Anderson 2002) more complex than necessary for the first approximation to detection likelihood sought.

We estimated the likelihood that a tagged crocodile would be detected passing a receiver by using the Best-fit Model to predict expected counts over one-minute intervals as a crocodile traveled past a receiver at the maximum expected speed (3.5 km/h) on the opposite bank of the river (taken to be 170 m wide). We calculated separation distance using Euclidean geometry, and we estimated 95% confidence limits for predicted counts by bootstrapping estimates of the standard errors of regression parameters across the range of separation distances (0–1,000 m). Along with the Mean Tidal Height (1–2 m), we used these variables to predict the confidence limits around predicted counts. We adapted R code for this procedure from the code posted by Achim Zeileis 2008 (refer [R] Prediction intervals for zero inflated Poisson regression; ethz.ch). We tested the possibility (from model extrapolation) that detection might be compromised at tide heights close to 3 m using data from two crocodiles that spent considerable time in the central part of the array used for the main experiment, comprising receivers at -500 m, 0 m, and +500 m from the Normanton boat ramp.

Results

We attached acoustic tags to nine sub-adult and adult Estuarine Crocodiles (estimated total length = 2.9–4.8 m) in the Norman River from a boat at night (2000–0200) between 10 and 12 July 2018 (Table 1). We attached transmitters to crocodiles while they were swimming mid-stream (n = 4), resting in the shallows (n = 3), or actively stalking prey at the edge of the water edge (n = 2). Approach times, from when each crocodile was sighted to when it was tagged, varied from 2 min 29 s to 14 min 47 s depending on distance, tidal flow, and wind direction. We determined that tag 8837 detached shortly after deployment based on a strong and consistent correlation between detections and tidal pattern, which suggested it was sitting in a shallow section of river that was exposed on low tides, at which times no detections were received.

We monitored tagged crocodiles for a mean of 104 d (range, 34–146 d) and were detected on average 25,528 times (range, 1,369–57,432) up until the conclusion of the study (Table 1). We detected six crocodiles (8499, 8503, 8507, 8508, 8835, 8836) for almost the full duration of the study (108–146 d), and a further two (8506, 8838) only prior to aversive conditioning (34 and 44 d, respectively). We detected detached tag (8837) until 24 September 2018 (Table 1). We did not detect either 8506 nor 8838 moving past Rx1 or Rx10 and, hence, leaving the linear array.

All six larger crocodiles (> 2.1 m) that we sighted 19 September 2018 were subjected to aversive conditioning. All crocodiles responded to this treatment by startling, submerging, re-surfacing briefly (typically 80–120 m from boat), before submerging and moving away. Of the six tagged crocodiles present within the receiver array at this time, only three were likely subjected to conditioning (tags 8499, 8503, 8835). All but one receiver (Rx4: 500 m downstream) recorded acoustic detections until the conclusion of the study. Rx4 was lost sometime after 24 September (the latest data download) due to severe corrosion of the anchor hardware. It is unlikely based on our detection trial that any crocodiles would have been recorded on this receiver during the second half of the study that were

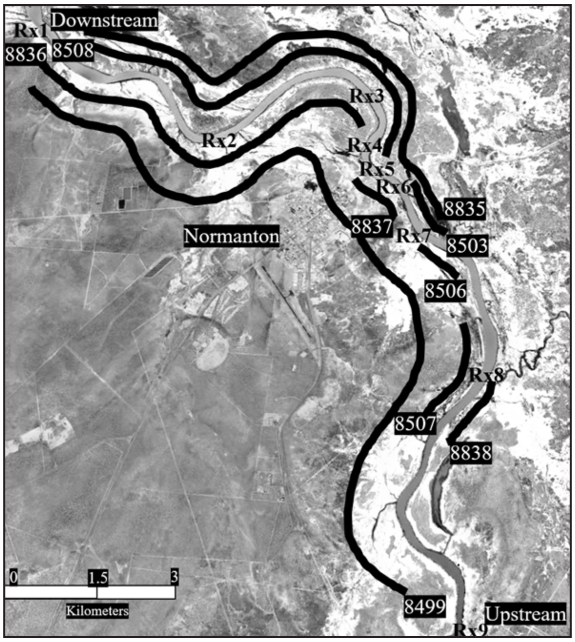

Figure 3. Extent of movement of eight tagged Estuarine Crocodiles (*Crocodylus porosus*) within a 20 km stretch of the Norman River, Gulf of Carpentaria, Australia, between 13 July and 5 December 2018. Tag 8837 likely detached shortly after deployment. Rx1-9 indicates receiver location along the river.

not also detected on one or both neighboring receivers (Rx5: 0 km and Rx3: 1.5 km downstream).

Movement patterns.—The tagged crocodiles movement patterns had significant overlap, with one large male (8499) regularly traversing or patrolling almost the entire 20 km length of river within the study area, and another 3.4 m individual (8508, likely male) moving back and forth along an approximately 9 km section (Fig. 3). The other six crocodiles occupied smaller stretches of the river (several km; Fig. 3). Shifts between consistent and intermittent detections of four crocodiles (8503, 8507, 8508, 8838, refer to Fig. 4) suggest these individuals may have moved in and out of side creeks or black spots within the receiver array during the study. Three crocodiles (8499, 8835, 8836) appeared to move out of the array with the onset of wet season rains and increasing day-time air temperatures in November and early December. Of the three tagged crocodiles subjected to aversive conditioning (8499, 8503, 8835), two were uncharacteristically absent for 42 h (8835) and 15 days (8503) immediately after aversive conditioning, before detections returned to their pre-conditioning patterns (Fig. 4). The large male (8499) demonstrated no discernible change in movement patterns, however, in response to aversive conditioning (Fig. 4).

Population surveys.—We sighted 40 crocodiles at an encounter rate of 2.0 non-hatchlings (NH) per km of river (NH/km) during the spotlight survey 19 September 2018 prior to aversive conditioning. They included eight individuals ≥ 2.1 m in length, 20% of the total. We sighted 24 crocodiles at an encounter rate of 1.20 NH/km immediately after aversive conditioning (20 September), none of which were ≥ 2.1 m (Fig. 5). At 50 d postconditioning (12 November), we sighted 39 crocodiles at an encounter rate of 1.95 NH/km, of which 18 (46.2%) were ≥ 2.1 m. While we sighted the large, tagged male (8499) on two occasions (out of a possible four) during spotlight surveys prior to conditioning, it was not sighted at all (out of a possible seven occasions) after conditioning.

Approachability and likelihood of detection.—There was no significant difference in mean approach distance for crocodiles ≥ 2.1 m prior to aversive conditioning (10 July: 22.1 ± 3.25 m; mean ± standard

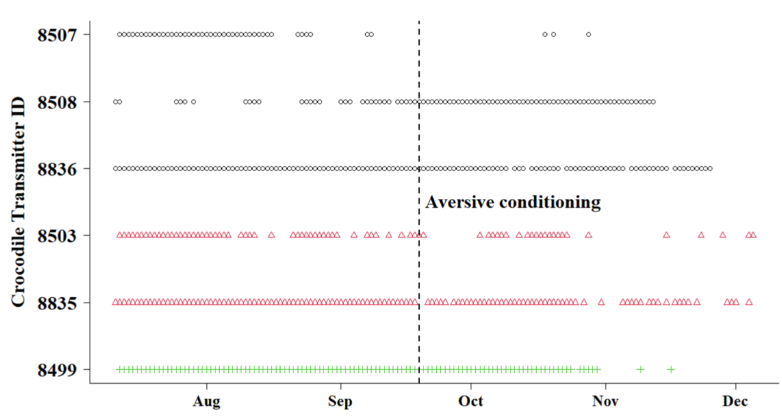

Figure 4. Number of days each tagged crocodile was detected during the study for crocodiles that were subject to aversive conditioning (red: likely female; green: male) and those that were not (black). Vertical dashed line indicates when aversive conditioning occurred (19–22 September 2018).

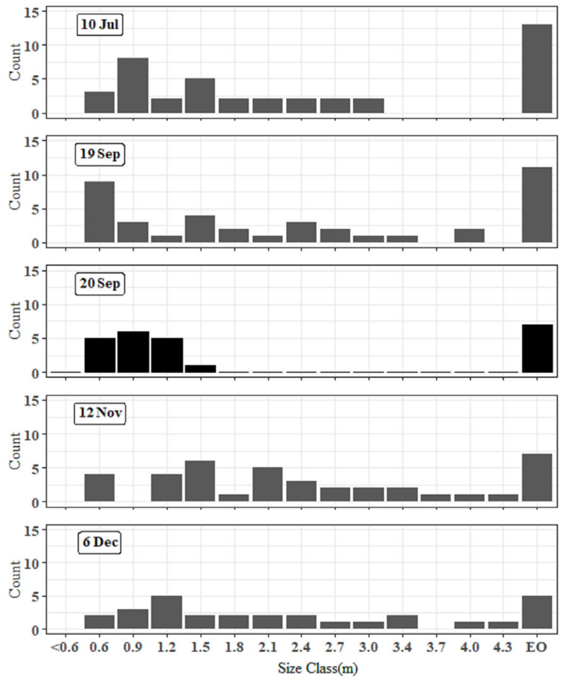

Figure 5. Size class distribution of crocodiles sighted on spotlight surveys in the Norman River, Gulf of Carpentaria, Australia, prior to aversive conditioning on 10 July and 19 September; immediately after aversive conditioning on 20 September, and in the aftermath of aversive conditioning on 12 November and 6 December.

error) or 50 d after (12 November: 21.2 ± 3.73 m) distance ($H = 0.179$, df = 1, $P = 0.673$). Because we did not observe any crocodiles ≥ 2.1 m immediately after conditioning, we could not compare approach distances. Plots of detections and estimated numbers of missed detections gave no indication that tide heights of 3 m or more resulted in markedly higher numbers of missed detections (Appendix; Fig. 3).

Discussion

The one-off use of beanbags fired from a 12-gauge shotgun as a form of aversive conditioning appeared to have some impact on crocodile behavior. While there was no change in the movement patterns of the large male post-conditioning, which continued patrolling up and down the river, the two other crocodiles were unusually absent for periods of 42 h and 15 d immediately post-conditioning before returning to the study area and resuming normal activity. This suggests that more sustained conditioning efforts may be required to have a greater impact on crocodile behavior.

The absence of crocodiles > 2.1 m during spotlight surveys immediately post-conditioning in this study suggests that aversive conditioning may, temporarily at least, make crocodiles more wary and less visible. This result is supported by anecdotal evidence from the Northern Territory, where rangers have in the past used non-lethal rounds on problem crocodiles just prior to annual Barramundi (*Lates calcarifer*) fishing competitions. It was believed anecdotally that these crocodiles did not leave the area, but instead became less visible (Garry Lindner, pers. comm.).

In our study, aversive conditioning was undertaken only once. After 50 d had elapsed, the number of larger crocodiles (> 2.1 m) sighted during night-time surveys in the study area was back to pre-conditioning levels. The success of aversive conditioning in other species such as bears (Mazur 2010), wolves (Schultz et al. 2005) and foxes (Cooper et al. 2005) has been dependent upon the type of method used, its frequency, duration, and the history and motivation of the individual to remain in the area (e.g., access to food). The impact of repeated and sustained aversive conditioning on Estuarine Crocodiles is largely unknown, and based on the results of this study, warrants further investigation. The limited evidence available from studies of other species and observations of what are considered problem crocodiles in Queensland, however, suggests that the ongoing presence of an artificial food source may reduce its effectiveness significantly.

Estuarine Crocodiles in northern Australia generally become a problem because of feeding by people, either directly or indirectly (e.g., when fish frames are left on the ground at boat ramps or on riverbanks). In these situations, the lure of a consistent and easy source of food may inhibit even a temporary response to aversive conditioning. The negative impact of an artificial food source on crocodilian behavior is widely acknowledged and may limit the effectiveness of aversive conditioning (Kidd-Weaver et al. 2022). For example, a large Estuarine Crocodile (TL = 4.8 m) in the Proserpine River (north of Mackay) was subjected to aversive conditioning by DES in February 2020, using the same non-lethal projectile method described here. The crocodile was targeted for management purposes having been fed by local people for over a year. The crocodile was shot in the head and neck on 12 occasions from 10 m over three consecutive nights (DES, unpubl. data). Each time the crocodile would startle, move to the middle of the river, submerge, and make its way back to the original location while underwater. The crocodile remained in the area (about 50 m) the entire time and the exercise was deemed unsuccessful. To test whether aversive conditioning could be effective in situations such as these, the stimulus (i.e., food source) likely needs to be removed and conditioning undertaken more frequently and over a longer period.

During the study we did not detect any of the three tagged crocodiles leaving the study area after undergoing aversive conditioning, which was not unexpected. Estuarine Crocodiles, particularly males, spend large amounts of energy and can suffer serious injury and sometimes death in the acquisition and maintenance of a territory (Lang 1987; Campbell et al. 2013). The regularity in time and space of the patrolling behavior of crocodile 8499 is more likely attributable to maintenance of territorial dominance than to pursuit of feeding opportunities or active searching for mates. Satellite telemetry studies have found that if a male with an established home range is relocated, it will often return quite rapidly, and over long distances, back to its place of capture (Read et al. 2007; Fukuda et al. 2019). While aversive conditioning was only conducted as a one-off event in this study, we speculate it is unlikely to result in a large resident crocodile vacating an area. To our knowledge, our study is the first to employ a method for remotely attaching transmitters to crocodiles. The advantage of this method is that it is rapid and avoids the need for manual capture and restraint, thus minimizing stress to the animal. This method was developed and adapted from existing methods commonly used to attach tracking tags to whales (Szesciorka et al. 2016). It is envisaged that this method could be used to attach other types of tracking devices to crocodilians as devices become smaller and lower in cost.

The movement patterns of the eight crocodiles in our study largely overlapped, with two larger (likely male) crocodiles (3.4 m, 4.8 m) making longer distance movements than the other six that remained in smaller sections of the river. While the study was limited to only a few months, these patterns were consistent with what has been previously reported for adult Estuarine Crocodiles in tracking studies (Kay 2004; Brien et al. 2008; Campbell et al. 2013). We recorded three crocodiles leaving the survey area late in the study. All three of these movements coincided closely with the first significant rains of the season and an increase in daytime temperatures. This result supports previous findings (Campbell et al. 2013; Baker et al. 2019), which suggested that some of these movements may be associated with crocodiles moving from non-breeding sites to breeding sites.

We used acoustic telemetry because it was cost-effective, transmitters were small enough to enable remote deployment, and a receiver array could be structured to monitor broad scale movements. The narrow linear system proved effective in detecting changes in location or activity patterns which may have been linked to aversive conditioning. The calibration component of our study demonstrates the complexity of using acoustic telemetry in complex estuarine/ tidal environments (Fisk 2014; Huveneers et al. 2016; Selby et al. 2016; Loher et al. 2017; Winter et al. 2021) and highlighted that the extrapolation of the model from the calibration array to tide heights over 2 m underestimated actual detection probability. The early loss of detections from transmitters 8506 and 8838 may be attributable to tag failure, detachment, or because the crocodile moved into a detection blackspot that was not covered by the acoustic receivers (i.e., into a mainstream location between well-separated receivers or into side-creeks, lagoons, or billabongs adjacent to the river).

Management implications.—It is a common perception in northern Australia that larger crocodiles that were present when commercial hunting was occurring were more wary of people and less likely to attack (Webb and Messel 1979; DES, unpubl. obs.), and that aversive conditioning using real or dummy projectiles is a simple and effective management tool. This study suggests that while aversive conditioning using projectiles may be effective in changing crocodile behavior and increasing wariness, further work is required on the potential effects of frequency and duration of conditioning treatments, presence of an artificial food source, location (urban, rural), crocodile size, and time of day (day, night). To improve on the current study, we recommend the use of smaller satellite or GPS tags with longer battery life (e.g., solar rechargeable) attached using the remote deployment method described here, combined with traditional spotlight and daytime surveys conducted over a longer timeframe.

The only other study to evaluate the effects of aversive conditioning involved the capture of alligators (Kidd-Weaver et al. 2022). While this method was effective in increasing wariness, the authors acknowledged that this approach was also costly, time intensive, and logistically difficult for most organizations to employ. The method of aversive conditioning described here is potentially more cost-effective and efficient, repeatable on the same individuals at a greater distance, and safer for people and crocodiles as it does not involve the capture of individuals.

While it is unlikely that crocodiles will leave an area in response to aversive conditioning (by firing projectiles), reinforcing the natural avoidance behaviors of an individual may be a preferred management option under some circumstances. For example, areas to use aversive conditioning may be in national parks and wildlife reserves where the priority is the preservation of natural resources, but where conflict can still arise between crocodiles and people. As the impact on crocodile behavior, and the likelihood of attack (on humans) from aversive conditioning is still not well understood, care should be taken if considering the technique for use in areas of high human populations, as problem crocodiles will likely be more difficult to capture and remove when posing a risk to public safety. Future trials should be focused in areas with low human populations in the first instance (e.g., national parks).

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Simon Booth completed BLArch at the University of Melbourne, Australia, in 2011 before moving into environmental sciences completing his Masters of Environmental Management at Charles Darwin University, Darwin, Australia, in 2020 of which this work was a component. From 2011 to 2013, Simon coordinated Black-footed Rock Wallaby (*Petrogale lateralis*) re-introduction and research projects. Since 2016 he has worked for the Queensland Government undertaking wildlife monitoring and management. His research focus has been to improve methods of crocodile capture and management including behavioral modification, drone capture, sonar detection, crocodile genetics, and population modeling. In 2022 he was invited to join the International Union for the Conservation of Nature Species Survival Commission - Crocodile Specialist Group and is looking forward to taking a more regional focus to crocodile management and research into the future. (Photographed by Phillipa Booth).

Laurence Taplin is a Crocodile Biologist who studied at the University of Melbourne, James Cook University, Townsville, and Sydney University, all in Australia. His early work on crocodilians focused on osmoregulation. In the 1980s Laurence conducted the first large scale surveys of estuarine crocodiles in Queensland. He has been collaborating with the Queensland Department of Environment and Science in recent years, contributing to their crocodile research and management program. (Photographed by Hellena Hanssen).

Matthew Brien completed his B.Sc. at the University of Wollongong, Australia, his Honours degree in crocodile home range and movement patterns at the University of Queensland, St Lucia, Australia, in 2004, and his Ph.D. on juvenile crocodilian behavior at Charles Darwin University, Brinkin, Australia, in 2015. He spent 3 y (2005–2008) working for the University of Florida, Gainesville, USA, as a Wildlife Biologist working with crocodilians and invasive Burmese Pythons (*Python bivittatus*) in south Florida. Matthew returned to Australia in 2009 and was the Research Coordinator for Wildlife Management International in Darwin (2009–2013), where he undertook research and consultancy. He is currently (2013 to present) working as the Program Coordinator for the Department of Environment and Science in Queensland, where he is focused on applied research and monitoring involving crocodiles, cassowaries, and flying foxes. He is also the current Reginal Chair for Australia and Oceania of the Crocodile Specialist Group (CSG) a part of the International Union for the Conservation of Nature, Species Survival Commission (IUCN SSC). (Photographed by Jemeema Brien).

Hamish Campbell is an Associate Professor and Senior Research Fellow at the Research Institute for the Environment and Livelihoods (RIEL) and is the Leader of the Movement and Landscape Ecology Laboratory at Charles Darwin University (CDU), Brinkin, Australia. He is the Chair of the Environment Discipline for the College of Engineering, IT, and Environment at CDU. Hamish is interested in studying the spatiotemporal relationship between animals and their environment. In particular, what drives animals to move, how do they respond to environmental heterogeneity, and why they select certain areas over others. His current projects study the movement and migration of birds, reptiles, mammals, and fish across northern Australia. (Photographed by Hamish Campbell).

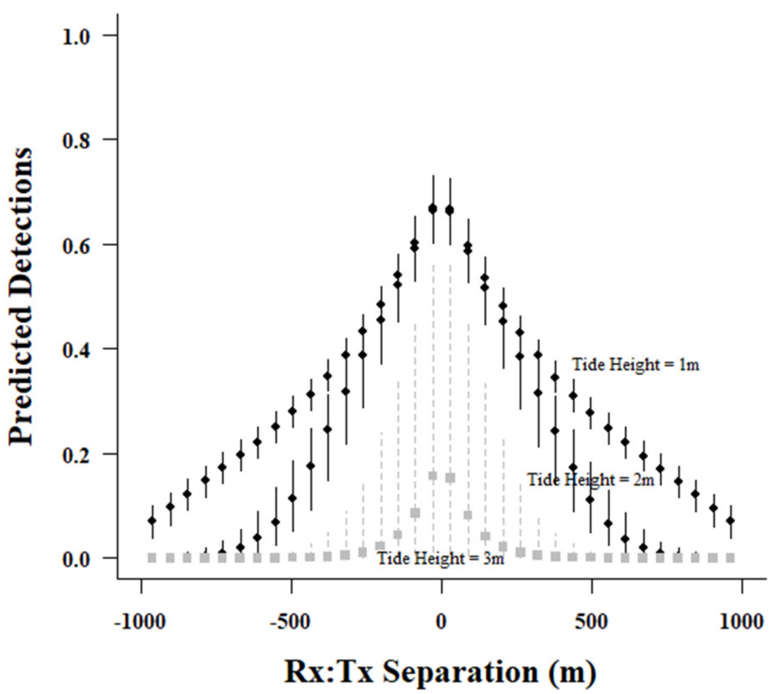
Keith Christian is a Physiological Ecologist with particular interests in reptiles and amphibians. He has lived and worked in North America, the Galapagos Islands, Puerto Rico, and has been in the Northern Territory since 1987. Research interests include temperature and water balance, metabolism, digestive physiology, and the use of weaver ants as biological control agents on tropical tree crops. He is currently studying the physiological and genetic diversity of *Gehyra* geckos in northern Australia, physiological plasticity of organisms in the seasonal tropics, and the microbiota on the skin of amphibians and reptiles. (Photographed by Julianne Osborne of Charles Darwin University Media).

Appendices

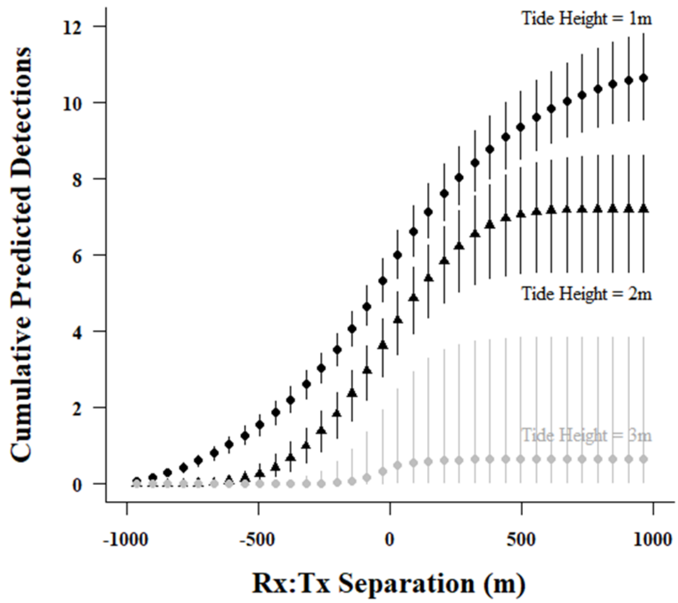
Appendix Table. Parameters for the best-fit ZIP model.

	Estimate	SE	Z	P
Count model				
β_1	1.96	0.045	43.94	< 0.001
β_2	-0.0019	0.00015	-12.86	< 0.001
Zero-inflation model				
λ_1	-16.53	3.034	-5.45	< 0.001
λ_2	0.011	0.0018	5.86	< 0.001
λ_3	5.81	1.333	4.36	< 0.001

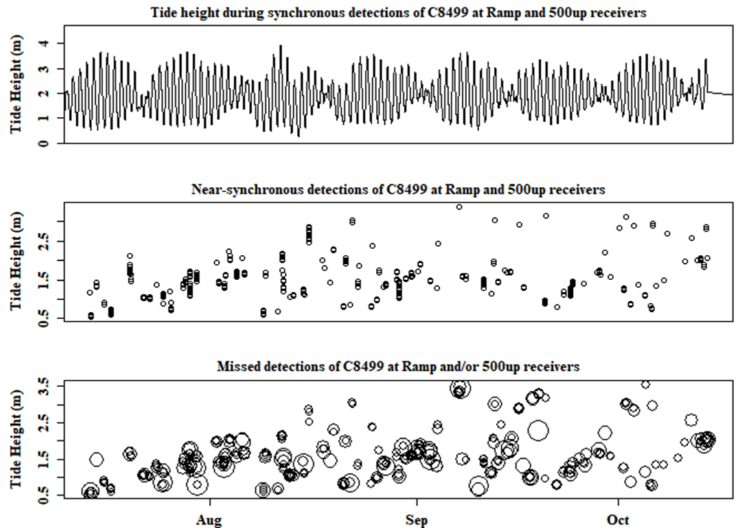
Counts detected at each receiver in the calibration array were tallied over 10-min intervals. Detection probability declined non-linearly with distance but was poorly fitted by an exponential curve, principally because as Rx : Tx separation distance went beyond 500 m, the number of 10-min intervals in which no counts were detected increased greatly. Testing of the data against a range of Poisson and negative binomial distributions showed the data were best fitted using a zero-inflated Poisson model. The likelihood that a crocodile would be detected passing a receiver while on the opposite bank of the river at its widest point (Appendix Fig. 1) was estimated as set out in Materials and Methods and used to determine the cumulative number of detections as an animal transited from 1 km downstream to 1 km upstream of a receiver (Appendix Fig. 2).



Appendix Figure 1. Likelihood that a crocodile would be detected as a function of Rx : Tx separation distance and tide height. Plots for 1 m and 2 m tide heights lie within the range of tide heights encountered in the calibration experiment. Points for 3 m tides are an extrapolation and included only to illustrate that, should the modeled relationship hold for higher tides, which can reach 4.5 m at Karumba, the likelihood of detection might fall to very low levels.



Appendix Figure 2. Predicted cumulative detections of a crocodile passing a single receiver at 3.5 km/h as a function of Rx : Tx separation distance and tide height. The 3 m tide estimates are an extrapolation. The bootstrapped 95% confidence limits indicate that a crocodile would almost certainly be detected at tide heights of 1–2 m. The possibility (from model extrapolation) that detection might be compromised at tide heights close to 3 m was tested using data from two crocodiles that spent considerable time in the central part of the array used for the main experiment comprising receivers at -500 m, 0 m, and +500 m from the Normanton boat ramp. Plots of detections and estimated numbers of missed detections gave no indication that tide heights of 3 m or more resulted in markedly higher numbers of missed detections (Appendix Fig. 3 illustrates this for one of the two animals). This suggests that the extrapolation of the model from the calibration array to tide heights over 2 m underestimated actual detection probability.



Appendix Figure 3. Near-synchronous and estimated missed detections of crocodile 8,499 in the three-receiver array around Normanton boat ramp over the period of the main experiment. Predicted tidal heights at Normanton are in the first panel. Near-synchronous detections occur when a tagged crocodile is within range of two receivers. Missed detections occur when a crocodile is known from near-synchronous detections to be within range of two receivers but at least one of them fails to detect transmissions. Missed detections in the third panel are shown with symbols proportional in area to the square root of the number of missed detections. There is no indication that the number of missed detections increased markedly on tides over 2 m.