SRAS Final Report:
The crocodile conundrum of Charotar: Understanding crocodile behaviours and their socioecological connections with humans

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Abstract

Interactions between humans and animals are escalating with increasing synurbisation of wild habitats, typically for agriculture, industry and the establishment of human settlements. The current framing of the resulting human–wildlife relationships is, however, biased towards conflict narratives, reinforcing the belief that coexistence necessarily results in physical interspecies conflict, largely ignoring the dynamic social and psychological dimensions of coexistence, which also include often-neglected aspects of mutual tolerance and occasionally positive relationships that develop between humans and nonhuman populations or individuals. While studying the impacts of conflict in such human and nonhuman communities are clearly important, equally critical are systematic studies on the ecology and behaviour of conflict-prone species to identify what facilitates such conflict, as well as promotes positive human–wildlife coexistence. This study investigated the behavioural ecology of mugger crocodiles (*Crocodylus palustris*) in the rapidly changing, human-dominated, landscapes of Gujarat state, with varying levels of conflict, together with the attitudes and perceptions of the local human communities towards muggers. Our study reveals the presence of certain human-sensitive behaviour in muggers that are displayed at significantly different levels across sites with varying levels of conflict, although other behaviours are similar in their occurrence. We also found that human attitudes play an important role in managing everyday interactions with crocodiles at these sites. Such human perspectives, in their turn, appear to be shaped by traditional – remarkably non-utilitarian – ecological knowledge, vernacular ethological accounts and past lifetime experiences. The local human and mugger communities have thus been able to create distinctive lifeworlds although such shared lives are not without their unique challenges.

Introduction

Conflict between humans and crocodilians has long been studied and documented, with the earliest reports from India stemming from the 8th century CE (Mahadevan, 2020). Human conflict with these reptiles is rapidly becoming a complex conservation issue worldwide, with an increasing number of incidents being reported every year. Crocodilians constitute one of the largest predators on the planet and they pose a serious threat to livestock and people across several human-dominated urban and rural landscapes (Bustard & Kar, 1983; Caldicott et al., 2005). Globally, most of the conflict cases and fatalities have been attributed to saltwater crocodiles, *Crocodylus porosus* (Patro & Padhi, 2019; Sideleau & Britton, 2013). Akin to the prevalent trends in human–wildlife conflict literature across taxa, studies on human–crocodile conflict have also mostly examined the ecological and social implications of such conflict (Fukuda et al., 2015; Shaney et al., 2019).

Nonetheless, very few studies have documented the impacts of interactions with humans on the behaviour of nonhuman populations or individuals, the ways in which negative interactions with wildlife influence the wellbeing of local human communities and how this, in turn, influences their perceptions towards the nonhumans with who they share their lives (see, for example, Jadhav & Barua, 2012).

It is, however, now well established that interactions between humans and nonhumans in their shared habitats are leading to the latter increasingly adapting to human-modified landscapes (Loveridge et al., 2010; Riley et al., 2010; Woodroffe et al., 2005). By the phrase ‘increasingly adapting’, we argue that

animal populations are capable of behaviourally adjusting to and surviving specific urbanising environments often during their lifetimes. This phenomenon, referred to as synanthropisation of nature (Luniak, 2004) has led ecologists, over the years, to document and report specific cases of nonhuman synurbisation under certain synanthropic conditions (Andrzejewski et al., 1978; Babińska-Werka et al., 1979). An illuminating study of such synurbisation is of ravens (*Corvus corvax*), one of the earliest known synanthropic avian species, which documents how the nesting patterns of some urbanised populations of this corvid have changed across Europe and certain parts of the United States of America over the years, including how the population densities of the species have increased in certain urban regions of Poland (Zawadzka & Zawadzki, 2014). Yet another study has explored the recent appearance of phenotypically flexible, behavioural strategies in a population of Asian elephants in southern India in response to the urbanisation of their habitats; these have included a preference for high-forage habitats, such as cropfields, but avoidance of human-dominated areas, the evolution of idiosyncratic, alternative foraging decisions by certain individual males (Srinivasaiah et al., 2012) and the emergence of a new social order – the all-male group, consisting of both young and older individuals – under conditions of increasing anthropogenic pressures in agricultural areas with high human activity (Srinivasaiah et al., 2019). Finally, a particularly thought-provoking study on bonnet macaques (*Macaca radiata*) from southern India has reported the evolution of a novel, multimodal communication system, wherein wild macaques direct an intentional food-requesting behaviour, which they appear to have learnt in recent years, only towards food-bearing tourists and never towards conspecific individuals within their troops (Deshpande et al., 2018).

Such cases of synurbisation beg the question of which species are synurbic and how the behavioural profiles of some of their populations are changing with increasing synurbisation and with the varying nature of their interactions with humans. In contrast to birds and mammals, we know comparatively little about large reptiles surviving in human-dominated landscapes and how they respond, behaviourally, to the environment and the humans around them. This could partly be because reptiles are one of the most underrepresented taxa in studies focusing on the anthropogenic impacts on the ecology, behaviour and conservation of nonhuman species (Gardner et al., 2007; Tingley et al., 2016). Furthermore, large reptiles, such as crocodilians, are significantly missing, even from the extensive reviews of anthropogenic effects on reptiles on the global scale, largely because of the differences in their biology and evolutionary history from that of other reptiles (Doherty et al., 2020; French et al., 2018). There have, therefore, been practically no serious studies that have examined the behaviour of crocodiles, living in human-dominated landscapes, especially with different levels of conflict, a research lacuna that prompted us to study mugger crocodiles in Gujarat state of western India.

In this study, we report the behaviour of mugger crocodiles at two sites in central Gujarat, with varying levels of conflict. The sites that we selected for behavioural observations lay at two opposite ends of the continuum of human–crocodile interactions, ranging from the positive to the negative. The main objectives of this aspect of our study, therefore, was to (1) understand and describe the behaviour of mugger crocodiles in human-dominated landscapes with varying levels of conflict, and (2) identify the behaviours, if any, which differed across the sites. It was also important to examine whether the observed differences in mugger behaviours across the two sites, with varying levels of conflict, reflected and were commensurate with the attitudes and perspectives of the local human communities towards the crocodiles at these locations.

Methods

Study Area

This study was conducted at two locations – Charotar and Vadodara – in central Gujarat state of western India, a region not usually considered a pristine natural space (Figure 1). Surprisingly, however, central Gujarat is regarded as one of the state's greenest regions, although it includes several large urban centres and semi-urban areas with multiple linear intrusions, and has a human density of 580 individuals per square kilometre (Singh, 2013). The extensive human settlements and farmlands

of this area have historically coerced the wildlife populations of the region to share space with the local human communities, leading to the occasional development of unique human–nonhuman relationships across the study area. Charotar sits on the central plain of Gujarat, with its southern boundary attached to the Gulf of Khambhat. The word 'Charotar' roughly translates to 'a pot of gold', a possible reference to the fertility of the region. The area is primarily a plain, with loamy sand of alluvial origin, locally called 'Goradu soil' and which is known for significantly increasing soil fertility and crop productivity. Most of the land in the region has thus been converted to farmlands, with agriculture and dairy being the priority activities of the local people. Tobacco, paddy, pulses and wheat are the dominant crops here. The Mahi Irrigation Project irrigates large areas across this region and most of the waterbodies are, therefore, interlinked by an intensive irrigation network of lined and unlined canals (Vyas, 2013).

The Charotar region consists of parts of two districts, Anand and Kheda, and includes within it several villages, of which Petli (72.757°E, 22.598°N), located in Anand district, with a geographical area of approximately 534.18 ha and a population of approximately 4,319 people (Chandramouli, 2011) is notable. This region experiences a subtropical climate, with temperature ranging from 15° to 42°C, with a mean of 27°C. Rainfall typically occurs from mid-June to early October, with an annual mean of 811 mm and about 40 rainy days every year, on average (Priyan, 2015).

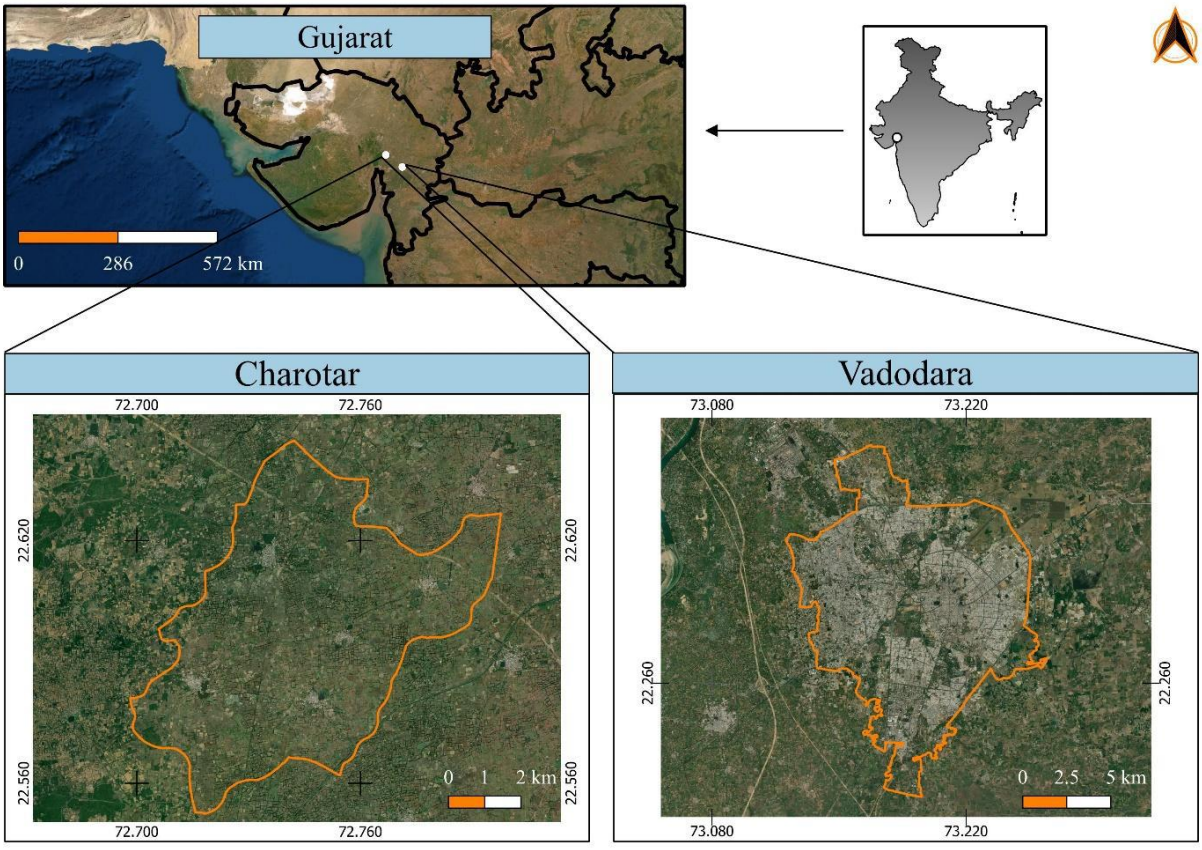


Figure 1. The study areas of Charotar and Vadodara in central Gujarat state, western India.

This unique landscape harbours one of the most exceptional populations of mugger crocodiles worldwide. Past surveys have revealed that about 250-300 adult muggers flourish amongst human habitations outside protected areas in the region and interact with humans daily (Patel et al., 2014; Vasava, 2016, 2019, 2020, 2021; Vasava et al., 2015). Interestingly, Charotar also has one of the

highest densities of sarus cranes (*Grus antigone*) and vultures in Gujarat (Kaur & Patel, 2022; Tatu et al., 2013, 2020).

Vadodara, located at 22.307°N and 73.181°E, is the tenth largest city in India, with an area of approximately 400 km2 and a population of approximately 3.5 million (Chandramouli, 2011). The city is located on the banks of the Vishwamitri, a seasonal river originating in the Pavagadh hills, about 50 km east of Vadodara. The river, which flows from east to west, surrounded by the two large perennial rivers of Mahi and Narmada, passes through the city and meets two of its tributaries, Dhadhar and Jambuva, before falling into the Arabian Sea at the Gulf of Khambhat. Vadodara experiences a dry and humid climate, with an annual rainfall of 930 mm, while its temperature ranges from 12° to 42°C, with a mean of 28°C (Shah et al., 2021). Due to irregular rainfall patterns, Vadodara city has witnessed multiple flooding events of the Vishwamitri river in the past (Ajinkya et al., 2015). In addition, as the river carves its way through the city, it becomes an open sewage system, carrying enormous amounts of industrial and domestic effluents. Most of the large sewage lines across the city are also designed to open into the river. Despite this intense pollution, nevertheless, the Vishwamitri supports a sizeable population of mugger crocodiles (Vyas, 2010a, 2012a, 2013, 2018). It is noteworthy that a study, reviewing global trends in human–crocodile conflict, reported that the reported cases of negative human–mugger crocodile interactions are predominantly from central Gujarat, especially Vadodara (Sideleau & Britton, 2013; Vyas & Stevenson, 2017a).

Study Species

Few animals inspire the sort of awe that crocodiles do or are as charismatic!

The mugger crocodile (Lesson, 1831) is a medium-sized crocodilian species, widely distributed in south Asia and Iran (Da Silva & Lenin, 2010). Being predators, crocodiles play critical ecological roles wherever they occur (Cavalier et al., 2021; Eversole et al., 2018; Pooley, 2016). Muggers typically prefer to live in freshwater habitats – ponds and rivers – but often inhabit human-made structures, like reservoirs, irrigation canals or artificial ponds (Whitaker, 1987; Whitaker & Andrews, 2003). During the 1960s, mugger populations declined markedly across the Indian subcontinent and were declared on the verge of extinction, primarily due to habitat loss, overfishing, and excessive hunting (FAO, 1974). A prohibition on hunting, creating protected areas and ex-situ conservation efforts for the species, all promoted by the government and other organisations, subsequently supported its recovery (Singh, 1999; Vyas, 2012) and led to its classification being moved down from ‘Endangered’ to ‘Vulnerable’ in the IUCN Red List (Choudhury & De Silva, 2013). The mugger crocodile is also included in the Schedule I, Part I species list of the Wildlife Protection Act 1972 of India (Wild Life (Protection) Act, 1972). According to the last large-scale population estimation of mugger crocodiles in 2009, there are around 2,500 to 3,000 individuals in India, currently distributed across ten states (Choudhury & De Silva, 2013).

Muggers are the only crocodilians found in Gujarat, with a widespread distribution and increasing population sizes. Long-term studies from central Gujarat suggest a steady increase in the local mugger populations; moreover, there have been several reports of newly discovered populations of muggers from the state, suggesting range extension of the species (Pandhi et al., 2022; Trivedi et al., 2022). In recent years, however, intensive land conversion, driven by increasing urbanisation and agricultural expansion, has escalated interactions between crocodiles and humans across India, including various parts of Gujarat (Pooley et al., 2021; Vyas, 2012). Both humans and muggers seem to be struggling over shared spaces, especially in urban and semi-urban regions; a prime example being Vadodara of central Gujarat, where 30-40 muggers are typically rescued, and multiple conflict cases are reported every year (Vyas & Stevenson, 2017).

Study Locations and Sites

There are about 25-30 villages in Charotar, where mugger crocodiles have been sighted in the past and of these, about 10 villages have substantial breeding populations of the species, as suggested by past surveys and reports (Patel et al., 2015; VNC, 2019, 2020, 2021). On the other hand, a 25-km stretch of the Vishwamitri river passes through Vadodara city, across which mugger crocodiles are distributed more or less comparably and in similar densities, barring a few exceptions (Vyas, 2010, 2018). The human densities at both places are more or less similar, with 482 people per sq. km. in Vadodara and 600 people per sq. km. in Anand (Charotar) (Chandramouli, 2011).

We visited the 10 villages in Charotar, mentioned above, and walked along randomly selected stretches of the Vishwamitri river in Vadodara to identify potential sites for our behavioural observations. We used the following criteria to choose our study sites: (1) similar population size and densities of muggers, (2) suitable visibility for behavioural observations, (3) at comparable distances from the nearest human settlements even though the dependency on waterbodies is rather different at both sites, and (4) especially for Charotar, a village where sewage water is being disposed into a pond and where crocodiles occur. Based on these criteria, Petli village (22.598°N, 72.757°E) in Charotar and a river segment near the Kalaghoda Circle (22.309°N, 73.190°E) of Vadodara were identified as suitable sites for our behavioural observations. On average, there were about 12-15 mugger crocodiles at both these sites at any point of time across the sampling period and both populations appeared to be open. The overall population of mugger crocodiles is also quite similar in both regions, with around 180 muggers in Vadodara and 216 muggers in Charotar based on recent census reports (Pagdand, 2019; Voluntary Nature Conservancy, 2021). Both sites had clear visibility, thus increasing the probability of observing crocodiles that were not submerged.

Field Methods

Reconnaissance surveys were conducted in January 2022 and behavioural observations were carried out *ad libitum* at the two study sites to construct an ethogram of the behavioural states for individual crocodiles (Table 1). One of the most important behaviours for crocodiles – basking – was classified into three categories: Basking on Land, Partial Basking and Surface Basking, shown in Table 1.

The potential sites for behavioural observations in Charotar and Vadodara were identified in January 2022 and quantitative behavioural sampling conducted at these two study locations for 26 and 29 days respectively, between February and March 2022 (Table 2). Instantaneous group scans were carried out (Altmann, 1974), with a 30-min gap between successive scans, on all the visible individual crocodiles, in two phases over the day: (a) Phase 1 – 08:00 h to 14:00 h, and (b) Phase 2 – 16:00 h to 18:30 h; this resulted in approximately 400 h of total sampling effort, including a total of 760 behavioural scans, at the two locations (Table 2).

During each instantaneous group scan, lasting about 5 min, we categorised all the visible individual crocodiles into size classes and recorded their behavioural states (Table 1), distance from other conspecific individuals, all feeding details of the scanned individuals, whenever applicable and interactions with humans, whenever observed.

Observations, especially of the behavioural pairs of Basking on Land (BB) and Terrestrial Movement (TM), and of Surface Basking (SB) and Aquatic Movement (WM), were made with meticulous care as there could be a potential overlap between these respective pairs of behaviours. During the scans, therefore, individuals observed on the surface of the water, without any movement of their limbs or tail, were considered to be SB while individuals observed on land, without any movement at all, were considered to be BB.

Table 1. An ethogram of the mugger crocodiles, observed in Charotar and Vadodara, including only the behavioural states. Note that certain observed behavioural events may contribute to a particular behavioural state.

Code	Behaviour	Description
AG	Agonistic Interactions	Aggression directed by an individual towards another, involving charging, chasing, biting, tail slapping or aggressive grunting, with or without the target individual retreating or fleeing
BB	Basking on Land	Resting completely outside water (Plate I)
CR	Courtship	Following or approaching of one or more females by an individual male, involving the exposing of his head and tail, and quivering of the back
FD	Feeding	Biting, chewing or engulfing any food item
MT	Mating	Mounting of a female by an individual male
PB	Partial Basking	Resting, with approximately half of the body in water and the other half on land (Plate II)
SB	Surface Basking	Resting on the surface of water, without or with very little movement (Plate III)
TM	Terrestrial Movement	Any kind of locomotory movement on land
WM	Aquatic Movement	Any kind of movement in water, including swimming or direct approach towards or retreating from another individual
AV	Invisible	Submerging of an individual below the water surface and hence, not visible to an observer
IH	Interactions with Humans	One or more humans performing Domestic Activities in the presence of mugger crocodiles or interacting with them through Mugger-directed Behaviours (See text for details)

Table 2. Sampling effort and the number of individual crocodiles observed per scan during the quantitative behavioural observations at the two study locations.

Study Location	**Charotar**	**Vadodara**
Sampling Period	10 days, February 2022 16 days, March 2022	9 days, February 2022 20 days, March 2022
Hours of Observation	200	180
Number of Behavioural Scans	400	360
Mean (± SD) Number of Individuals Observed per Scan	10.8 (± 4.0)	15.4 (± 3.0)

All individuals were classified into three size classes: (a) LA – Large Adult, any individual larger than 2.1 m (7 ft) in length, (b) MA – Medium-sized Adult, individuals between 1 m (3ft) to 2.1 m (7ft) in length, and (c) J – Juveniles, individuals less than 1 m (3ft) in length.

Data for the distance of a scanned individual from conspecific individuals were collected as a categorical variable, with three categories: (a) A – in contact with another individual, (b) B – not in contact but within a distance of 2 m (6.5 ft) from another individual, and (c) C – all other individuals beyond 2 m (6.5 ft) of the scanned individual. Please note, however, that detailed analyses of the data on size class and distance from conspecific individuals are currently in progress and, therefore, not further referred to in this report.

Human activities and their interactions with muggers, if any, were observed during the instantaneous scans and classified into two categories: Mugger-related Interactions and Domestic Activities. The Mugger-related Interactions included directly watching muggers, approaching close to them, feeding them or taking their photographs. Domestic Activities included bathing, defecation, cattle herding, washing of clothes or utensils and the throwing of wet waste into the waterbody. The response of the crocodiles to human presence or activities, consisting of their moving away from or towards the humans, or the lack of any response thereof, were also recorded during the scans.

We made behavioural observations using Nikon binoculars (Prostaff 5 – 12x50, Japan) and recorded intra- and inter-specific interactions and feeding instances, using a Sony Handy Cam video recorder (HDRCX405 30x, China). The coordinates of the observation sites were collected using a GPS unit (Garmin eTrex 32x, Taiwan).

Data Analysis

The instantaneous group scans on both populations of mugger crocodiles were analysed to estimate the proportions of individuals that were involved in different behavioural states. The proportion of the study individuals in any given behavioural state (or activity) 'A' during the day was estimated as:

$$T_A = \sum \left(\frac{n_A}{N}\right)$$

where T_A was the proportion of individuals, of the total scanned individuals, in the behavioural state 'A' during a certain period of time, n_A the number of scanned individuals in the behavioural state 'A', and N the total number of individuals scanned during that period of time.

The proportion of individuals observed in the different behavioural states was typically averaged across the observation period to estimate the mean proportions of individuals engaged in particular behavioural states and their confidence intervals over this period.

We performed the G test of independence to compare the proportions of the individual study crocodiles engaged in different behavioural states over the defined observation period across the two sites as follows:

$$G = 2\sum_{i=1}^{n} site1_i \,.\ln\left(\frac{site1_i}{site2_i}\right)$$

where G is the test statistic, *n* the total sample size, *site*1 and *site*2 the two study locations being compared and *i* the cell value for the performance of a particular behavioural state at a particular site in the contingency table (Mangiafico, 2015; McDonald, 2009).

The performance of basking-related behaviours, terrestrial movement and inter-individual agonistic interactions by the study crocodiles were analysed independently, and a derivative of the non-parametric Mann-Whitney U test performed to test the differences in their performance across the two study locations (Ram et al., 2003).

One of the key assumptions of the Mann-Whitney U test is the independence of data. It is, however, hardly ever possible to meet this assumption in behavioural studies that are unable to monitor the behaviour of individually identified subjects and hence, run into the problem of pseudo-replication of data. Another issue that often emerges from certain behavioural data concerns the presence of a few extreme values or outliers. In our study, for example, on one particular day in Vadodara, a few behavioural scans recorded a rare event of 20+ muggers basking on land while some scans recorded no such basking at all. Ram et al. (2003) have thus suggested a novel statistical technique, the Pairs Test,

to address such issues that arise when comparing the behavioural performance of individuals within a particular population or across different populations of the same species.

The Pairs Test involves the execution of a random permutation procedure to generate a distribution, which is then used to assign a P-value to the observed test statistic. For this, we repeatedly calculated the Mann-Whitney U test statistic for two randomised arrays – corresponding to the number of observations in the two samples of the original data set – that were generated from the pooled original data set. We typically performed 10,000 such permutations to generate a random distribution of the U test statistic for each test and then plotted the original Mann-Whitney U test statistic on this distribution to determine its P-value.

Moreover, we examined the mean number of individual crocodiles performing certain behaviours – as, for example, the number of individuals basking on land – across the two locations by another procedure. We first calculated the mean number of individuals basking on land per scan, in this case, across both sites, taking care to include scans with no muggers exhibiting this behaviour, then bootstrapped these means with 10,000 iterations and finally plotted the median value of the simulated means, along with its 95% confidence interval. We examined the mean number of individuals displaying terrestrial movement and inter-individual agonistic interactions at the two locations, using this technique.

Results

A comparison of the study crocodiles of Charotar and Vadodara revealed that the proportion of individuals involved in different behavioural states (not including being Invisible) differed significantly between the two study locations (G test of independence, $G = 632.02$, $df = 9$, $P < 0.05$; Figure 2). However, it is noteworthy that in spite of the differences in the behavioural profiles at the two locations, the most prevalent behaviours displayed – Basking on Land, Partial Basking, Surface Basking and Aquatic Movement – were common across the two ecologically dissimilar sites. Moreover, basking-related behaviours were most common across all scans, indicating their importance in the everyday lives of the study crocodilian populations.

Although the importance of basking for crocodilian physiology is well established, as was also indicated by the predominance of basking-related behaviours of both our study populations, the type of basking displayed by individual crocodiles could be sensitive to local ecological conditions and thus vary across sites. Indeed, a comparison of the relative proportions of time spent in different basking-related activities – Basking on Land, Partial Basking and Surface Basking – varied significantly across Charotar and Vadodara ($G = 502.28$, $df = 2$, $P < 0.05$; Figure 3).

More specifically, we also found that, in Charotar, a significantly greater proportions of individuals were Basking on Land, as compared to those in Vadodara (Pairs Test, $n_{Charotar} = 400$, $n_{Vadodara} = 360$, $P < 0.0004$; Figure 3) while for the latter a relatively greater proportions of individuals were observed Partial Basking ($P < 0.0001$) or Surface Basking ($P < 0.0001$) than their counterparts in Charotar.

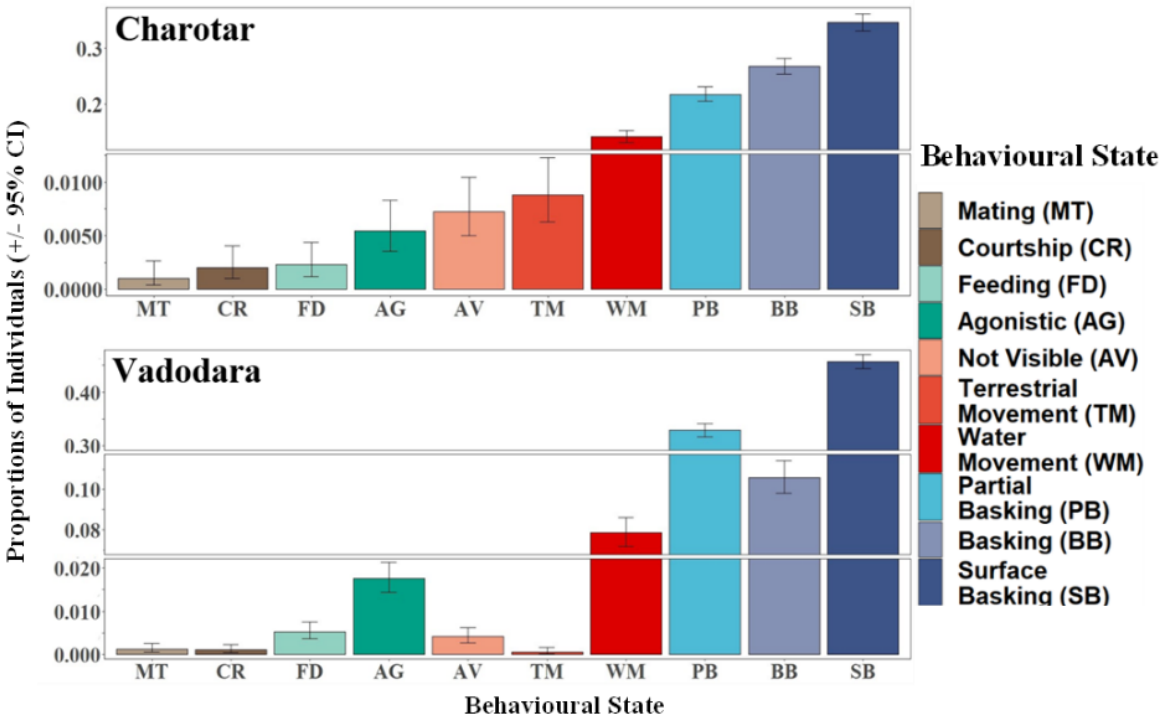


Figure 2. Comparison of time-activity budgets of the study muggers, inclusive of all size categories, in Charotar and Vadodara. The error bars represent 95% confidence intervals, calculated across all sampling days.

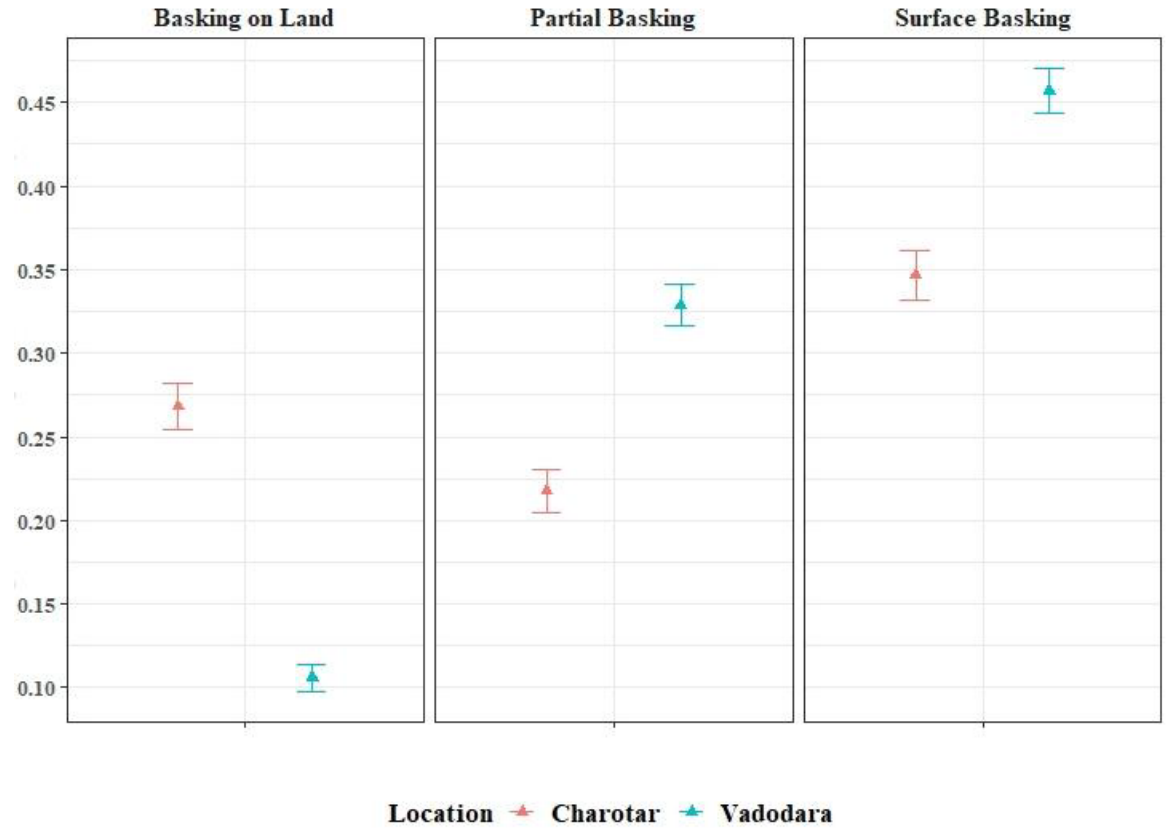


Figure 3. Proportions of individuals observed in basking-related behaviours in Charotar and Vadodara. The error bars represent 95% confidence intervals, calculated across all sampling days.

Using another measure to examine the possible dependence of basking by the study crocodiles on the local environment, we observed a relatively greater mean number of individuals basking on land per scan in Charotar, as opposed to those in Vadodara (Figure 4).

During our behavioural observations in Charotar, we recorded muggers basking on trees, roads, and human-made structures. On the other hand, in Vadodara, we recorded muggers basking on trees, garbage piles, car tyres, and riverbanks.

Although the proportions of individuals observed in other behavioural activities were less than that dedicated to basking in absolute terms at both Charotar and Vadodara, we, nonetheless, observed a statistically significant difference in the relative performance of several of these behaviours at the two study locations, largely contributed to by inter-individual Agonistic Interactions and Terrestrial Movement (G test of independence, G = 13.99, df = 4, P < 0.007; Figure 2).

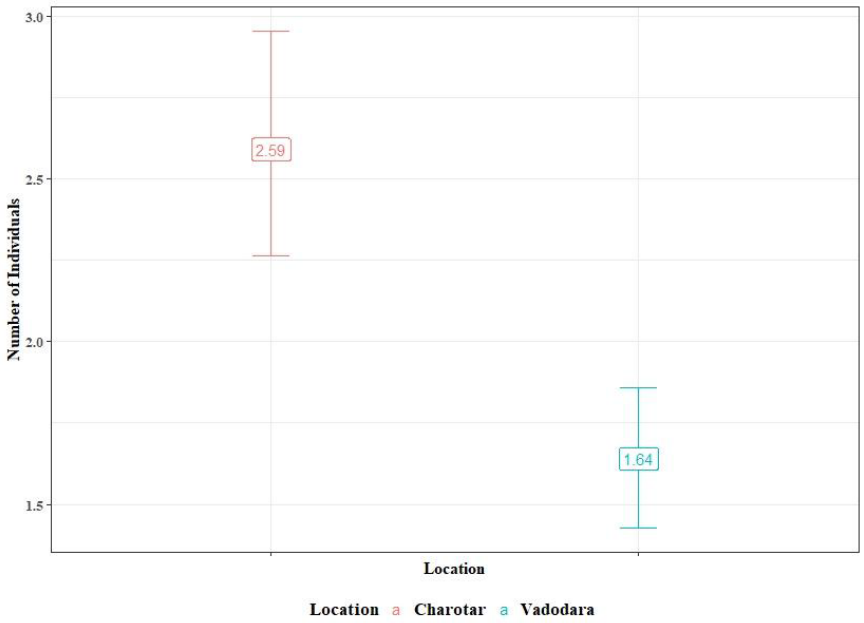


Figure 4. Mean number of crocodiles basking on land per instantaneous scan in Charotar and Vadodara. The boxed numbers are the median values of 10,000 means, simulated by bootstrapping, at each location while the error bars represent 95% confidence intervals.

An analysis of the proportions of individual muggers of Charotar and Vadodara observed in Terrestrial Movement revealed a significantly greater display of this behaviour in the former location (Pairs Test, $n_{Charotar}$= 400, $n_{Vadodara}$ = 360, P < 0.0001; Figure 5a). In striking contrast, the proportions of individuals observed in inter-individual Agonistic Interactions was significantly higher in Vadodara (Pairs Test; $nCharotar$= 400, $nVadodara$ = 360; P < 0.0001; Figure 5b).

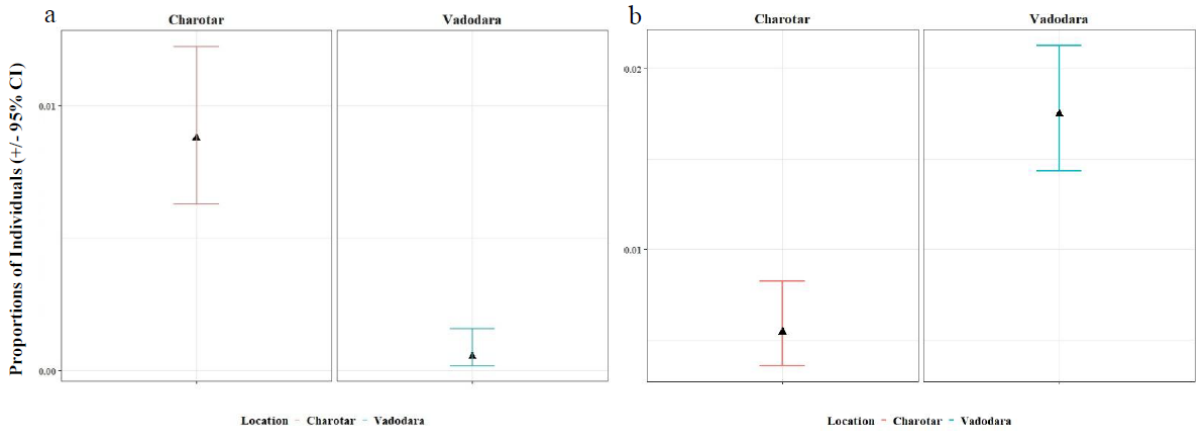


Figure 5. Proportions of individual crocodiles observed in Terrestrial Movement (a) and Agonistic Interactions (b) in Charotar and Vadodara. The error bars represent 95% confidence intervals, calculated across all sampling days.

Human activities, including both Mugger-related Interactions and Domestic Activities were recorded at a relatively higher frequency in Charotar, with human presence being observed in 288 of the 400 scans (72%) conducted. In Vadodara, however, only 8 of the 360 scans (2.2%) documented the presence of humans. It is also noteworthy that, in Charotar, 141 of the 288 scans with human presence (49%) consisted of Mugger-related Interactions while the remaining 51% of the scans revealed human Domestic Activities. In contrast, Domestic Activities of humans, consisting of the throwing of wet waste into the river, was observed in three of the eight scans (37.5%); Mugger-related Interactions, consisting of feeding the crocodiles with animal waste, in two scans (25%) and the simple presence of humans in the remaining three of the eight scans, conducted in Vadodara.

The focal muggers responded by moving away from all Mugger-related Interactions but displayed no response during Domestic Activities in Charotar. On the other hand, the crocodiles moved towards the waste thrown into the water during Mugger-related Interactions or Domestic Activities but did not respond in any way to the simple presence of humans in Vadodara.

Discussion

The behavioural ecology of wildlife populations, especially in human-influenced landscapes, is increasingly being modulated by changes in their immediate surroundings, due to urbanisation or agricultural expansion. It can, therefore, be assumed that the behavioural repertoire of crocodilians must be changing too in response to anthropogenic pressures but their repertoires being relatively small, it is often quite problematic to study their behaviour.

Most species of crocodiles are found in the tropics, with a few exceptions, such as alligators and gharials, which also occur at high latitudes (Thorbjarnarson & Wang, 2010). Elevation and temperature are critically important factors for their survival and functioning, as the metabolic processes of crocodilians are typically temperature-sensitive (Grigg, 2015; Seebacher et al., 1999).

Most work on crocodiles comes from captive populations, focusing on the temperature regulation of their bodily processes (Downs et al., 2008; Lang, 1987). Even though it has been established that crocodilians are quite efficient at regulating and maintaining their body temperature through physiological and biochemical adaptations, behavioural adaptations too appear to play a very significant role in this regard.

Basking is, in fact, one of the most important behaviours in crocodilians and it significantly impacts their physiology, particularly by regulating their body temperature (Grigg, 2015; Seebacher et al., 1999; Smith, 1975, 1979; Terpin et al., 1979). The amount of time spent by individuals in basking typically depends on factors, such as body size, season and the ambient body temperature. Smaller individuals, such as juveniles or subadults, have shorter basking bouts but at relatively high frequencies whereas large individuals have more extended basking bouts but at lower frequencies (Grigg et al., 1998). Basking behaviour also tends to change significantly with seasonal climatic variations (Seebacher & Grigg, 1997).

Seasonal changes in crocodilian behavioural profiles with changing climatic conditions are crucial for survival, to the extent that even choosing a summer behavioural pattern in winter could be highly lethal for crocodiles (Seebacher et al., 1999). Several studies have thus observed seasonal changes in basking activity in Australian freshwater crocodiles (*Crocodylus johnstoni*) and *C. porosus*, due to factors, such as changes in atmospheric temperature and other microclimatic variations (Downs et al., 2008; Seebacher & Grigg, 1997). For our own study, however, we have presented single-season data from two nearby sites with similar climatic conditions and thus believe that the major differences that we have observed in basking behaviour in our study crocodiles were not significantly influenced by climatic factors.

We observed a sharp distinction in the basking patterns of mugger crocodiles in Charotar and Vadodara, with the former having a greater proportion of individuals basking on land and with relatively higher numbers of individuals basking on land per scan. Unable to bask conveniently on land, possibly due to certain anthropogenic factors, as discussed below, the crocodiles in Vadodara spent more time engaging in partial or surface basking.

The availability of sites to bask could be a significant factor influencing the basking behaviour of crocodiles. Unlike many crocodilian species, muggers are habitat generalists and have been observed basking on various substrates (Venugopal & Deviprasad, 2003). During our behavioural observations, we recorded muggers basking on trees, garbage piles, car tyres and of course, on riverbanks. We therefore propose, based on our observations and knowledge of mugger crocodile biology and in spite of our need for substantial, quantified evidence on basking site availability at our field sites, that the study crocodiles were generalists to the extent that the potential absence of traditional basking sites did not seem to pose a major constraint to their basking, particularly in Vadodara.

Although the riverbanks were available for basking to the crocodile population in the Vishwamitri river at Vadodara and there were no significant human activities near our study group, very few individuals – except a few large ones – came out of the water to bask on land. In striking contrast, the number of interactions with humans was far greater in Charotar and yet, we observed a significantly greater proportion of individuals outside water at Petli.

Moreover, we argue here that this difference in the behavioural repertoire of the crocodiles at the two locations could possibly be in response to the nature and quality of interactions with humans rather than the number of interactions they typically experience. Multiple studies have reported behavioural changes in response to humans in urban regions although the impact of quality of interactions has been largely ignored even in such studies (Beale & Monaghan, 2004; Miranda, 2017; Morelli et al., 2018).

In Vadodara and Charotar, muggers have been living in human-dominated landscapes for a very long time and there is a rich history of interspecies interactions that pervades this region. Muggers have undoubtedly been a very significant part of peoples' lives in the past as evidenced from the centuries-old wall paintings and sculpture of mugger crocodiles that we found in Charotar and Vadodara (Y. C. Joshi & A. Sinha, pers. obs.). There remains, however, a striking difference in the quality of interactions that the crocodiles appear to have historically experienced with humans across regions, with high numbers of negative interactions recorded in Vadodara for many years now (Patel et al., 2014; Vyas & Stevenson, 2017a).

We must, nevertheless, point out a few other differences between the two study locations that we observed during this project. For example, we observed a significantly higher involvement of the study crocodiles in inter-individual agonistic interactions in Vadodara. Agonistic behaviours in crocodiles, including aggressive physical contact, vocal threats, submission or retreats, are typically very important in establishing a dominance hierarchy within groups of crocodiles. Not surprisingly, therefore, crocodiles can often be very aggressive towards one another and this can even disrupt their normal behavioural patterns and temperature regulatory behaviours. Unlike mammals, however, levels of aggression in most reptile groups decrease with density, possibly due to an increase in positive social interactions (Brattstrom, 1974; Mayer et al., 2020).

Agonistic interactions in free-ranging nonhuman populations and individuals have often been linked to human-origin food and provisioning by humans (Asquith, 1989; Hodgson et al., 2004; McKinney, 2011; Ram et al., 2003) and such responses could have significant implications for the health and wellbeing of all individuals involved, often in the long-term, as well as for the human–animal relationships that emerge subsequently (Barua et al., 2021; Newsome & Rodger, 2008; Ramakrishna et al., in press).

It is also possibly noteworthy that, in Charotar, the several instances of muggers feeding, which we observed during our study, involved individuals consuming fish, except in one instance, when an individual had killed an egret. In stark contrast, we did not make a single observation of muggers feeding on fish or hunting for them in Vadodara. These crocodiles were observed to primarily feed on domestic animal carcasses and waste, dumped into the river from the bridges. 'Waste' typically includes wet waste, such as bones or rotten/leftover meat from small households as well as from hotels and restaurants. Moreover, we saw a few instances – and this needs to be substantiated further –local people providing the muggers with food in Vadodara, a process that was not opportunistic feeding, as there appeared to be a definite routine, involving the feeding of muggers on a particular day of the week and at specific times. Furthermore, interestingly, a few individual muggers were even conditioned and quickly learned to respond to distinct human sounds by emerging from the river for food.

We thus conclude that the proportion of individuals basking outside water significantly differed between Charotar and Vadodara, with more mugger individuals basking on land in Charotar. Moreover, we also observed differences in the use of waterbodies by both humans and muggers at our two study locations, with the local people being much more dependent on the use of ponds in Charotar. Accordingly, human interactions with muggers were also far more frequent there than that observed in Vadodara. In spite of this, however, a relatively greater number of muggers emerged from the water and spent higher proportions of their time basking on land in Charotar.

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