Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2012, **49,** 1046–1054 doi: 10.1111/j.1365-2664.2012.02189.x

Rigorous gharial population estimation in the Chambal: implications for conservation and management of a globally threatened crocodilian

Tarun Nair[1,2]*, John B. Thorbjarnarson[3†], Patrick Aust[4] and Jagdish Krishnaswamy[1,5]

[1]*Post-graduate Program in Wildlife Biology and Conservation, Wildlife Conservation Society—India Program, National Centre for Biological Sciences, Bangalore, 560065, India;* [2]*Centre for Wildlife Studies, Bangalore, 560070, India;* [3]*Wildlife Conservation Society, P.O. Box 357520, Gainsville, FL, 32635, USA;* [4]*Centre for Herpetology, Madras Crocodile Bank Trust, P.O. Box 4, Mamallapuram, Tamil Nadu, 603104, India; and* [5]*Centre for Biodiversity and Conservation, Ashoka Trust for Research in Ecology and the Environment (ATREE), Royal Enclave, Sriramapura, Jakkur Post, Bangalore, 560064, India*

Summary

1. India's Chambal River hosts the largest population of the critically endangered gharial. Boat-based daylight surveys to date only provide indices of relative abundance, without measures of survey bias or error. No attempt to quantify detection probabilities in these surveys has yet been made, and thus, absolute density estimates of this population remain unknown.

2. We surveyed 75 km of the River Chambal and photographed individual gharials for capture–recapture analysis. The total sampling effort yielded 400 captures. Population closure was supported ($z = -1{\cdot}48$, $P = 0{\cdot}069$), and closed-population models were used to estimate abundances.

3. Models were selected using the Akaike Information Criterion (AIC) index of model fit. The best model estimated 231 ± 32 adult, 83 ± 23 subadult and 89 ± 19 juvenile gharials (Mean ± SE), respectively, while the model-averaged estimate was 220 ± 28 adult, 76 ± 16 subadults and 93 ± 16 juvenile gharials, respectively.

4. The best model estimated absolute densities of 3·08 ± 0·43, 1·11 ± 0·3 and 1·19 ± 0·25 adult, subadult and juvenile gharials km^{-1}, respectively, while the model-averaged estimate was 2·93 ± 0·37, 1·01 ± 0·21 and 1·24 ± 0·21 adult, subadult and juvenile gharials km^{-1}, respectively, compared with relative densities of 0·94, 0·45 and 0·30 adult, subadult and juvenile gharials km^{-1}, respectively, from boat-based daylight surveys. On the basis of our best model, we suggest a detection probability based correction factor of 3·27, 2·47 and 3·97 to boat-based daylight survey estimates of adult, subadult and juvenile gharials, respectively.

5. *Synthesis and applications*. Used within the framework of capture–recapture analysis, photoidentification provides a reliable and noninvasive method of estimating population size and structure in crocodilians. We also opine that without determining the current status of gharials, highly intensive strategies, such as the egg-collection and rear-and-release programmes being implemented currently, initiated on the basis of underestimates of population sizes, are unwarranted and divert valuable conservation resources away from field-based protection measures, which are essential in the face of threats like hydrologic diversions, sand mining, fishing and bankside cultivation.

Key-words: abundance estimation, Chambal River, closed-population models, detection, *Gavialis gangeticus*, individual identification, noninvasive, photographic capture–recapture, program MARK

*Correspondence author. E-mail: tarunnair1982@gmail.com
†In memoriam.

Introduction

The Gharial *Gavialis gangeticus* Gmelin (1789) is endemic to the Indian subcontinent and historically occurred in the Indus, Ganges, Mahanadi, Brahmaputra and Irrawaddy River systems (Smith 1939). In the 1970s, the gharial population was estimated at <200 (Whitaker *et al.* 1974), following which a conservation initiative involving creation of protected areas and rear-and-release programmes was established. The subsequent recovery of the population was short-lived with the cessation of central government funding. By 2006, the gharial population reportedly experienced a 58% drop in numbers across its range; the total breeding population was estimated to be about 200 individuals, largely restricted to scattered locations in India and Nepal, and the global population, as a single unit, met the International Union for Conservation of Nature criteria for Critically Endangered (Choudhury *et al.* 2007). The Chambal River in India has the single largest contiguous population, reportedly between 48% and 85% of the global population (Choudhury *et al.* 2007; Hussain 2009). The gharial is threatened by river-bank land-use changes, reduction in river flows, modification of river morphology, loss of nesting and basking sites, increased mortality in fishing nets and egg-collection for consumption (Whitaker & Members of the GMTF 2007; Hussain 2009); and is especially at risk from flow regulation because it prefers fast-flowing river habitats, which are prime sites for dams (Dudgeon 2000).

Boat-based daylight gharial surveys, to date, only provide indices of relative abundance, without measures of survey bias or error. No attempt to quantify detection probabilities in these surveys has yet been made, and thus, absolute density estimates of this population remain unknown. Despite the release of over 5000 gharials into various Indian rivers over the past few decades, as part of the rear-and-release programmes, only about 200 breeding adults reportedly still survive (Choudhury *et al.* 2007), and this poses serious questions about age- and size-specific survival rates. These programmes lacked monitoring of survival and dispersal of released animals and hence the efficacy of this programme could not be evaluated. In this scenario, the estimation of absolute abundances can help assess the restocking programme, provide information on the current status of gharials and inform future conservation strategies.

The various survey techniques used to ascertain crocodilian populations world-wide, reviewed by Magnuson (1982) and Bayliss (1987), vary greatly in terms of applicability, cost-effectiveness, the species involved, and the socio–political and administrative environment. Conventional mark–recapture techniques, besides being affected by the above, also suffer from tag loss and unequal catchability (Bayliss 1987); altered natural behaviour (Gauthier-Clerc *et al.* 2004) and ethical and welfare issues arising from the application of tags or marks (Wilson & McMahon 2006).

The use of natural markings to distinguish between individuals has been used for the identification of chimpanzees from facial characteristics (van Lawick-Goodall 1971); dolphins from dorsal fin cuts and nicks (Mazzoil *et al.* 2004); Nile crocodiles (Swanepoel 1996); African wild dogs from coat markings (Creel & Creel 1995); tigers from stripe patterns (Karanth 1995) and the use of pattern recognition software to identify cheetahs (Kelly 2001) and whale sharks (Arzoumanian, Holmberg & Norman 2005) from spot patterns. Individual identification, used within the framework of capture–recapture analysis, provides a statistical framework for estimating p (detection or capture probability) and quantities of biological interest such as population size (Nichols 1992).

Our objectives were to determine whether individual gharials were identifiable in the wild; and if individual identification could be used to estimate populations of wild crocodilians. Our approach fills an important gap in gharial monitoring and population estimation by combining photo-identification and capture–recapture techniques. This is the first such attempt for estimating crocodilian abundance in the wild. Our results shed new light on the gharials population status in the Chambal River and have major conservation implications in view of current management objectives and species recovery efforts.

Materials and methods

STUDY AREA

The 960-km long River Chambal originates in the northern slopes of the Vindhyan escarpment and its basin is characterized by an undulating floodplain, gullies and ravines (Gopal & Srivastava 2008). The Chambal is a typical anterior-drainage pattern river (Mani 1974) and joins River Yamuna to form a part of the greater Gangetic drainage system. The area lies within the semi-arid zone of north-western India (Hussain 1999) and the vegetation consists of ravine thorn forest (Champion & Seth 1968). Much of the landscape has been influenced by a long history of human occupation (Kaul 1962). Evergreen riparian vegetation is completely absent, with only sparse ground cover along the severely eroded riverbanks and adjacent ravine lands (Hussain 1999). Lying between 24°55′ to 26°50′N and 75°34′ to 79°18′E, the 600 km National Chambal Sanctuary (NCS), was established in 1978 to conserve the gharial and the unique Chambal ecosystem.

The study area (Fig. 1) comprises a 75-km stretch of River Chambal, within the NCS, between 26°32′22″N, 77°45′30″E and 26°48′37″N, 78°10′18″E (Daburpur Ghat & Sukhdyan Pura Ghat, Madhya Pradesh, India), and includes the river mainstream, mid-channel islands, sand-bars, rocky outcrops and adjacent banks. The study area exhibits straight and meandering channels with a sinuosity index (meander ratio) of 1·47 and passes through the flat terrain of the Malwa Plateau with an average gradient of 0·21 m km^{-1} (Jain, Pushpendra & Singh 2007).

In the dry season during the study (February to May 2010), river depth ranged from 0·02 to 18·6 m, while channel width ranged from 44 to 400 m. River discharge levels varied from 75

(February) to 23·9 (May) $m^3 s^{-1}$. The presence of rapids immediately upriver of the study area was a likely barrier to the movement of gharial during the dry season/low-flow conditions. For gharials, these conditions also resulted in the river being reduced to a series of functionally isolated pools with limited connectivity between them. Sand occupied 29·7% of the shoreline substratum, while gravel, clay–loam and sandstone–rock occupied 16·6%, 20·5% and 33·2% of this stretch, respectively. Anthropogenic influences observed during the study period were chiefly in the form of sand mining, bankside cultivation, domestic activities like bathing, defecation and water collection, gill net and hook-line fishing, livestock herding, grass-soaking, river crossing and temple fairs.

FIELD METHODS

The 75-km stretch was divided into 30 segments, each measuring 2·5 km, and a rowboat was used to cover the study area in a south-west to north-east (downstream) direction. Four sampling occasions were undertaken between February and May. Each segment was sampled once in February, March, April and May, that is, once in each sampling occasion. As virtually nothing is known about size-class-specific and seasonal home ranges of gharials, the basis for selecting segment lengths, conservatively, at 2·5 km were: (i) to allow segments to be grouped together in the future, in the light of new information on home-range sizes, (ii) to ensure that there were no 'holes' where an individual could have zero capture probability, that is, to cover potential spaces within the study area which may allow animals to escape detection and (iii) based on dry season (low-water level) conditions which restricted gharial movement along the length of the river. Boat survey and stationary bank observations at basking sites were used to collect data. The probability of basking gharial encounters was maximized by stationary bank counts at sites considered favourable based on the depth profile and basking site substrate. The segments were sampled during periods of maximum basking activity (between 1000 and 1700 h during winter; and between 0630–1030 h and 1500–1900 h during summer). At each of these basking sites, all basking individuals were photographed, their location and size-class noted and basking site characteristics measured.

Digiscoping was employed to observe, record and identify individual basking gharials. This was achieved using a 20–60 × 80 mm Spotting Scope (Bushnell Excursion FLP), coupled with a 6 megapixel digital camera (Casio EX-Z110, Casio, Tokyo, Japan) with 3× optical zoom. This was supported by a 9.1 megapixel digital camera with 20× optical zoom (Sony Cybershot DSC-HX1, Sony Corporation, Tokyo, Japan) and a 16 × 50 Porro-Prism Binoculars.

Other important considerations were to ensure that the sampling protocol met the basic assumptions of capture–recapture models. We used powerful optics to overcome any biases against animals in smaller size-classes, and hence, all individuals had an equal probability of being captured. Additionally, with little vegetation on the sand banks, there was no size-class-related visibility bias. Our study did not involve physical capture and restraint of gharial; and data collection through stationary bank observations were being carried out from concealed locations to minimize disturbance and observer influence. Therefore, capture did not affect subsequent recapture. Individual identification of gharial were made, primarily, by comparing natural permanent blotches and markings on the lateral scutes on the tail and by using additional cues like size classes, injuries and scars. These markings are not known to change and are individually unique. Marked animals were accorded no exclusive treatment, because captures and subsequent recaptures through photo-identification is a noninvasive technique. Hence, marked and unmarked individuals have the same probability of survival. As the timing of this study preceded the gharial hatching season, the likelihood of the demographic closure assumption being violated was low. Similarly, as the study coincided with the dry season (low-water level), the likelihood of animals moving in and out of the study area was low, supporting the assumption of geographic closure.

INDIVIDUAL IDENTIFICATION

Individual identification of gharials were made, primarily, by comparing the shapes and positions of natural blotches and markings on the lateral scutes of the tail (Singh & Bustard 1976) and also by using additional cues like injuries and scars [Fig. 2; see Nair (2010) for more details]. Photographs lacking clarity were not used for identification.

All basking individuals were photographed, given a unique identity number and geo-tagged using a Global Positioning System (Garmin GPS 72, Garmin, Olathe, Kansas, USA). Gharial size-classes were determined by calibrating natural objects or landscape features beforehand, or by setting up measured reference markers at basking sites and then estimating gharial lengths from photographs using the software 'ImageJ' (available at http://rsb.info.nih.gov/ij; developed by Wayne Rasband; National Institutes of Health, Bethesda, MD, USA). Individuals <90 cm long were considered to be yearlings, those 90–180 cm as juveniles, those 180–300 cm as subadults and those >300 cm as adults.

ESTIMATING POPULATION SIZE

To estimate abundance using capture–recapture methods, a capture history matrix for each identified individual was constructed, in the standard 'X' matrix format (Otis *et al.* 1978) such that each entry takes the value '1' for being captured in that particular sampling occasion, or the value '0' for not being captured in the same sampling occasion. Thus, a capture history of 1001 means that a gharial was captured (photographed) on the first- and fourth-sampling occasions but not on the second and third occasions.

Capture–recapture data analysis and the estimation of abundance were carried out using program MARK (White & Burnham 1999), by modelling for variations in capture (p) and recapture (c) probabilities, using closed-population models. Analysis of the capture–recapture data in program CAPTURE (Otis *et al.* 1978; Rexstad & Burnham 1991) supported population closure ($z = -1{\cdot}48$, $P = 0{\cdot}069$). Finite mixture models (Pledger 2000), as incorporated in program MARK, employing two mixtures of P-values, were used to investigate the effects of individual heterogeneity, that is, individuals may have independent probabilities of being captured on account of their age, size, social status, etc. This is modelled by letting capture probabilities come from more than one capture probability distribution. There are three parameters with the two-distribution mixture model – the probability that a given capture probability will come from the first distribution (π), the mean capture probability of the first distribution and the mean capture probability of the second distribution (Pledger 2000).

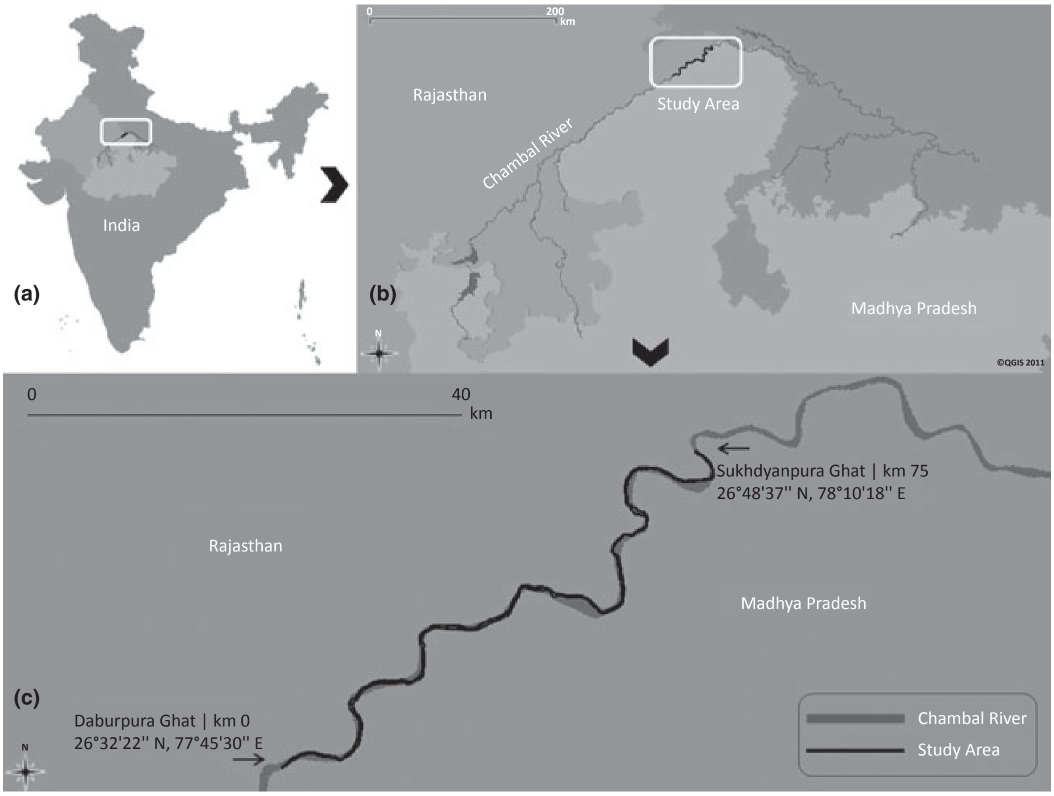

Fig. 1. (a, b) Location of the study area, in north-central India, along the Rajasthan – Madhya Pradesh border. (c) Enlarged map of the study area, showing the 75 km extent of the Chambal River.

Time was considered an important parameter because of the decreased intensity of basking, with the progress of the dry season, during the study (Nair 2010). Moreover, gharials are 'thermoconformers', avoiding extreme temperatures (Lang 1987a,b) and therefore, number of captures of basking animals are expected to vary from winter to summer. Individual heterogeneity (i.e. individuals have independent probabilities of capture) was also considered an important parameter because there are differences in accessibility to basking sites, because of social hierarchies; differences in individual responses to disturbances; and individual thermal behaviour is known to vary, influenced by a range of external (social mileau, climate, etc.) and internal (age, nutritional status, etc.) factors (Lang 1987a). Although size-related wariness is reported in crocodilians (Bayliss *et al*. 1986), we did not observe any obvious differences in wariness among individuals.

Models were selected using the Akaike Information Criterion (AIC) index of model fit. The model with the lowest Akaike Information Criterion corrected (AICc) score was considered the most parsimonious, thus minimizing estimate bias and optimizing precision (Burnham & Anderson 1998). When the AICc scores of the models were close, their Delta AICc (ΔAICc) values were used to evaluate the model fit. Models with ΔAICc < 2 were considered good models (see Table 2), because these models are best supported by the data, while models with ΔAICc between 3 and 7 have moderate support and those >7–10 are relatively poor (Anderson & Burnham 1999; Burnham & Anderson 2002). Estimates of the derived parameters (Burnham & Anderson 2004), from models with good and moderate support (ΔAICc < 7), were model averaged in program MARK, to produce an estimate which is conditional on the results from the above selected models.

Results

ABUNDANCE ESTIMATE

The total sampling effort yielded 400 captures (332 unique photographs; 159 only left flank, 134 only right flank and 39 both flanks). Only captures histories of 'left flank' and 'both flank' individuals were used in the analysis (Table 1). Photographs lacking clarity were not used for identification.

Abundance estimation was carried out using program MARK, using closed-population models and three groups (adults, subadults and juveniles). Models were selected using the AIC index of model fit (Table 2).

Table 1. Summary statistics for photographic capture–recapture data (left-side only + both sides) of 198 gharials (114 adults, 37 subadults and 47 juveniles) sampled in National Chambal Sanctuary during February–May 2010

	Sampling occasion			
	1	2	3	4
Animals caught at occasion	52	69	61	66
Newly caught at occasion	52	61	46	39
Recaught at occasion	0	8	15	27
Total caught at end of occasion	52	113	159	198

Fig. 2. Photoidentification of individual gharials by comparing the shapes and positions of natural blotches and markings on the lateral scutes of the tail.

Table 2. Model selection by program MARK for gharial capture–recapture data from the National Chambal Sanctuary during February–May 2010, using AICc, ΔAICc, AICc Weight, Model Likelihood and number of parameters (k)

Model	AICc	Δ AICc	AICc weight	Model likelihood	*k*
{pi(*g*), *p* (*g* + *t*) = *c* (*g* + *t*), *N*(*g*)}	−482·8165	0·0000	0·38051	1·0000	15
{pi(*g*), *p*a (*t*) = *c*a(*t*), *p*b (*t*) = *c*b(*t*), *N* (*g*)}	−482·6898	0·1267	0·35715	0·9386	14
{pi(*g*), *p*(.) = *c* (.), *N*(*g*)}	−481·3976	1·4189	0·18718	0·4919	4
{pi(*g*), *p*(*t*) = *c* (*t*), *N*(*g*)}	−478·5194	4·2971	0·04439	0·1166	7
{pi(*g*), *p*(*g*) = *c* (*g*), *N*(*g*)}	−477·5535	5·2630	0·02739	0·0720	6
{pi(*g*), *p*(*g* + *t*), *c*(*g* + *t*), *N*(*g*)}	−473·1566	9·6599	0·00304	0·0080	39
{pi(*g*), *p*a (*g* + *t*) = *c*a (*g* + *t*), *p*b (*g* + *t*) = *c*b (*g* + *t*), *N*(*g*)}	−468·8527	13·9638	0·00035	0·0010	30

Heterogeneity parameter, that is, probability of mixture (pi); varying across mixtures (*g*); varying over time (*t*); constant over time (.)
AIC, Akaike Information Criterion; AICc, Akaike Information Criterion corrected; AICc Weight is the relative likelihood of each model.

Capture probability (*p*) and recapture probability (*c*) were modelled as *p* = *c*, because the study design did not modify gharial behaviour across the four occasions, that is, no behavioural effects. Capture probability (*p*) and recapture probability (*c*) were modelled either as varying over time (*t*), constant over time (.), varying across mixtures (*g*), or varying across both mixtures and time (*g* + *t*). The heterogeneity parameter, that is, probability of mixture (pi) and population size (*N*), was modelled across mixtures (*g*) to compute independent estimates for adults, subadults and juveniles.

Models with good and moderate support (ΔAICc < 7) were model averaged, to produce an estimate (Table 3) which is conditional on the results of the selected models. Abundance estimates from the most parsimonious models (low ΔAICc) exert most influence to the final estimate. The standard error (SE $\hat{N}$) of the model-averaged estimate is a function of the SE $\hat{N}$ from each model and the extent of compatibility between model-specific estimates (Conn *et al.* 2006). The best model estimated 231 ± 32 adult, 83 ± 23 subadult and 89 ± 19 juvenile gharials respectively, while the model-averaged estimate was 220 ± 28 adult, 76 ± 16 subadult and 93 ± 16 juvenile gharials, respectively.

Table 3. Abundance estimates ($\hat{N}$) and standard errors (SE) for models with good and moderate support (ΔAICc < 7) and the model-averaged estimate, from gharial capture–recapture data from the National Chambal Sanctuary during February–May 2010

Model	Size-class	$\hat{N}$	SE $\hat{N}$
{pi(*g*), *p*(*g* + *t*) = *c*(*g* + *t*), *N*(*g*)}	Adult	231	32
	Subadult	83	23
	Juvenile	89	19
{pi(*g*), *p*a(*t*) = *c*a(*t*), *p*b(*t*) = *c*b(*t*), *N*(*g*)}	Adult	196	23
	Subadult	69	11
	Juvenile	94	15
{pi(*g*), *p*(.) = *c*(.), *N*(*g*)}	Adult	237	28
	Subadult	77	12
	Juvenile	97	14
{pi(*g*), *p*(*t*) = *c*(*t*), *N*(*g*)}	Adult	236	27
	Subadult	76	12
	Juvenile	97	14
{pi(*g*), *p*(*g*) = *c*(*g*), *N*(*g*)}	Adult	231	32
	Subadult	84	24
	Juvenile	96	21
Model-averaged estimate	Adult	220	28
	Subadult	76	16
	Juvenile	93	16

AICc, Akaike Information Criterion corrected.
All values rounded off to nearest integer.

Discussion

To obtain life-history parameters of animals and to be able to determine critical resource requirements, it is essential to monitor individuals for extended periods of time. Individuals use habitats differently (e.g. Peake 1997), employ different behavioural strategies (e.g. Rohner 1996) and have different reproductive success (Newton 1995); and therefore, individuals may have different conservation values (McGregor & Peake 1998). Knowledge of the life histories of individual animals used in a new generation of predictive models (Sutherland 1995) may prove vital to the conservation of those species that are especially vulnerable to human disturbance and for which predictive measures may be of more importance than reactive measures (McGregor & Peake 1998).

Information on gharial distribution and abundance, across its range, is either scant or completely lacking and thus are an impediment to effectively understand the conservation needs of the species. Additionally, as gharials, like other large crocodilians (Brandt 1991), are slow-growing and long-lived, long-term studies on various demographic parameters are lacking. Photographic identification of individual gharials offer several advantages employed within the sampling framework of capture–recapture for estimating detection probabilities and population size. It will also enable regular monitoring of their critically endangered populations. Photo-identification has the advantages of being a noninvasive technique, with fewer economic and logistic constraints of capture, handling, capture and postcapture stress, tracking, altered behaviour, and capable of providing large sample sizes.

Conventional crocodilian boat surveys, relying on daylight or eye-shine counts, have been shown to underestimate population sizes because of size-related wariness and visibility biases (Bayliss *et al.* 1986). This, together with the fact that captive-reared gharial have been released on an ongoing basis in many Indian rivers, has made it difficult to assess the true status of gharials based on existing population counts (Choudhury *et al.* 2007). Previous surveys (Hussain 1999) have erroneously assumed that 'during the census all gharials present were basking and that all the basking gharials were seen'. Consequently, protected–area managers have assumed that such survey figures are absolute estimates, and have resorted to restocking programmes to attain an arbitrary 'desired' population figure (Murthy 2004). In addition, boat-based daylight surveys and nest counts, both indices of relative abundance, indicated population increases of *c.* 8% for the period between 2007 and 2009 (R.K. Sharma, unpublished data; S.C. Bhadoria, N. Luikham & R.K. Sharma, unpublished data). However, this period witnessed a winter mass-mortality in 2007–2008, which claimed a significant proportion of adult and subadult gharials in the NCS (Whitaker, Basu & Huchzermeyer 2008), and yet, this decline and other gharial mortality events (R.S. Bhadauria, personal communication) remained undetected in these surveys. While relative density estimates have been used throughout the world to monitor trends in crocodilian populations (Bayliss 1987), they are often limited to the level of resolution they provide. Hence, we believe that absolute estimates at 3–5 year intervals, although time and resource intensive, have a crucial role in monitoring populations and informing conservation strategies, especially that of critically endangered species like the gharial.

Our study demonstrates the feasibility of combining photo-identification within the framework of capture–recapture analysis to estimate the abundance of crocodilians, in the wild. Although natural markings have been used to identify young individual gharials in captivity (Singh & Bustard 1976), this is the first attempt to do so in the wild. While Swanepoel (1996) used natural tail marks to individually identify Nile crocodiles in the wild, this method has never been adapted to estimate populations of crocodilians.

We estimated 231 ± 32 adult, 83 ± 23 subadult and 89 ± 19 juvenile gharials (best model) and 220 ± 28 adults, 76 ± 16 subadults and 93 ± 16 juveniles (model-averaged estimate), for our 75-km study area, while a 2009 survey based on boat-based daylight 'total' counts (S.C. Bhadoria, N. Luikham & R.K. Sharma, unpublished data), reported 102 adults, 49 subadults and 33 juveniles for a 109 km stretch of the NCS, within which our 75-km study area falls. Based on these values, we estimate absolute densities of adult, subadult and juvenile gharials at $3{\cdot}08 \pm 0{\cdot}43$, $1{\cdot}11 \pm 0{\cdot}3$ and $1{\cdot}19 \pm 0{\cdot}25$ per km, respectively (best model), and $2{\cdot}93 \pm 0{\cdot}37$, $1{\cdot}01 \pm 0{\cdot}21$ and $1{\cdot}24 \pm 0{\cdot}21$ per km, respectively (model-averaged estimate). On the other hand, Bhadoria, Luikham and Sharma estimate densities at 0·94, 0·45 and 0·30 adult, subadult and juvenile gharials per km, respectively. Although not accurate or precise, we suggest, on the basis of our best model, a detection probability based correction factor of 3·27, 2·47 and 3·97, to relative abundance estimates of adult, subadult and juvenile gharials, respectively, obtained from boat-based daylight surveys, until such time that better correction factors can be derived. Similarly, estimation of correction factors in other gharial habitats will enable a comparison between sites and a prioritization of conservation actions.

Adults (>300 cm), subadults (180–300 cm) and juveniles (90–180 cm) were determined on the basis of size, because demographic and reproductive variables in crocodilians are dependent on size rather than age (Nichols 1987). Yearlings (<90 cm) were not considered in this study because logistical and optical constraints impeded our ability to consistently obtain clear photographs. In robust and stable populations, between 30% and 50% of adult females are considered mature breeding animals (Gharial Species Recovery Plan, unpublished data; J. Lang, personal communication) and 14% of adults are considered mature breeding males (Hussain 1999). The high proportion of adults, as estimated in this study, was previously reported in the 2009 survey for gharial in the NCS (S.C. Bhadoria, N. Luikham & R.K. Sharma, unpublished data). Generally, in crocodile populations, depleted populations have population structures heavily biased towards juveniles, with few adults, and as they recover, this shifts to populations heavily biased towards adults and subadults, with low numbers of juveniles (Webb *et al.* 2000; Fukuda *et al.* 2011). These changes in population size structures are usually thought to reflect density-dependent changes in survivorship, which involve complex interactions between predation, cannibalism, social exclusion, and increased rates of both emigration and mortality (Messel *et al.* 1981; Webb & Manolis 1992; Fukuda *et al.* 2011). Among gharials, smaller size-classes are more susceptible to drowning in fishing nets (Sharma & Basu 2004) and also prone to being washed out into unsuitable habitats during flooding events because of the sudden discharge of impounded water (Choudhury *et al.* 2007), resulting in their decreased survival and recruitment. Additionally, juvenile and subadult size-classes have been accorded an upper size limit (180 and 300 cm respectively) and on reaching this, move onto the subsequent class, whereas the adult size-class does not have an upper limit and therefore, individuals in this class accumulate over time. These could be among the factors shaping the observed population structure. This size-class distribution (adults > juveniles > subadults) was previously reported in 2009 in the NCS (S.C. Bhadoria, N. Luikham & R.K. Sharma, unpublished data). However, a different size-class distribution (juveniles > subadults > adults) observed from 1988 to 1992 has been attributed to gharial reintroductions (Hussain 1999) at the height of the rear-and-release programme [juveniles/subadults/adults; 421 : 129 : 100 (1988), 522 : 221 : 97 (1990) and 469 : 296 : 109 (1992), respectively] (Hussain 1999).

One issue that needs to be addressed is the fact that only one side of the gharial is visible at any one time and that unless both sides are photographed, an individual's identity remains unknown when presented with only the unrecorded side. However, this can be dealt with by identifying basking sites in advance and positioning oneself before these animals emerge to bask. Thereafter, the sequence of events that accompany most basking episodes provide a way to address the issue. Gharials emerge head first onto basking sites, providing an opportunity to 'capture' one side and then re-orient themselves so as to face the river. This allows for the other side to be captured too. Other factors that could complicate the implementation of this technique are poor weather conditions, animals lying at odd angles or congregating in a way such that individuals are blocking the observers' view of other individuals, or disturbances that drive basking gharials into the water.

Almost all available population literature on gharials offer only the first level of resolution (relative abundance estimates), which help determine whether these populations are stable, increasing or decreasing (Webb & Smith 1987). However, we believe that our study is a transition to the second level of resolution, which quantifies the basic population parameters of population size, population age and sex structure, rates of reproduction, rates of survival and rates of immigration and emigration (Webb & Smith 1987). We also believe that this level of resolution is necessary in the current scenario – to assess the restocking programme, provide information on the current status of gharials and inform future conservation strategies, such as the recent Government of India initiative (Nair 2011). Multiseason capture–recapture data would additionally enable the estimation of various demographic parameters, vital rates and state variables (e.g. Karanth *et al.* 2006). We also believe that our approach could be further developed to include the spatial component of such data by using spatially explicit capture–recapture models (Borchers & Efford 2008).

Gharial conservation over the last three decades has centred around strategies like egg-collection and rear-and-release programmes, whose theoretical basis as a conservation tool is based largely on the assumption that natural breeding is incapable of sustaining wild populations and that captive-reared individuals have a better chance of survival and recruitment. Such measures, touted as a panacea to gharial conservation challenges, often attract favourable media attention and hence are popular management interventions. While these strategies hope to address hatchling and juvenile mortality, they do not address current threats to gharials that are primarily related to habitat loss, fishing-related mortality and disturbances from activities such as hydrologic diversions, sand mining, gill net and dynamite fishing and riverside cultivation. Our results demonstrate that present-day population assessments do not provide an accurate account of the gharials population status, and we, therefore, contend that highly intensive strategies like egg-collection and rear-and-release programmes, on the basis of underestimates of population sizes are unwarranted and divert valuable conservation resources away from field-based protection measures, which are essential in the face of the aforementioned threats. Further, the observed population structure (biased towards adults with low numbers of juveniles) indicates a recovering population (Webb *et al.* 2000; Fukuda *et al.* 2011), which also suggests that artificial supplementation is unnecessary for the Chambal population. Moreover, gharial reintroductions are poorly monitored, have low success rates (Ballouard *et al.* 2010) and have never re-established viable breeding populations in areas where they were locally extirpated, for all the currently recognized breeding sites had surviving populations when the restocking programmes were initiated (Choudhury *et al.* 2007). Future conservation and management efforts should be based on periodic and rigorous monitoring of demographic and reproductive parameters of gharial populations, and we suggest a reassessment of all reintroduction and restocking programmes.

Acknowledgements

This study was funded by the Department of Science and Technology, Government of India. We thank National Centre for Biological Sciences, Tata Institute of Fundamental Research, Wildlife Conservation Society-India and Centre for Wildlife Studies for academic and logistic support. We thank the Rajasthan, Madhya Pradesh and Uttar Pradesh Forest Departments for research permissions. H.S. Pabla (IFS), S.C. Badoria, R. K. Sharma, Vijay Singh Tomar, Jyothi, Daulat Ram, Tejpal and Ramveer (all MPFD), Rajeev Tomar, Rakesh Vyas, Rakesh Singh, Ram Awatar, Kaptan Singh, Jagdish, Rajveer and Shyam Singh for field and logistical support; Romulus Whitaker, Jeffery Lang, Ajith Kumar, Devcharan Jathanna, Nachiket Kelkar, Varun Goswami, Umesh Srinivasan, Nishant M. S. and Barry Noon for all the discussions and critical inputs at different stages of the study; Krishnapriya Tamma for generously lending her camera and Madhukar Rao, for demonstrating the fundamentals of digiscoping.

References

Anderson, D. & Burnham, K. (1999) General strategies for the analysis of ringing data. *Bird Study*, **46**(Suppl. 1), S261–S270.

Arzoumanian, Z., Holmberg, J. & Norman, B. (2005) An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. *Journal of Applied Ecology*, **42**, 999–1011.

Ballouard, J.M., Priol, P., Oison, J., Ciliberti, A. & Cadi, A. (2010) Does reintroduction stabilize the population of the critically endangered gharial (*Gavialis gangeticus, Gavialidae*) in Chitwan National Park, Nepal? *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 756–761.

Bayliss, P. (1987) Survey methods and monitoring within crocodile management programmes. *Wildlife Management: Crocodiles and Alligators* (eds G.J.W. Webb, S.C. Manolis & P.J. Whitehead), pp. 157–175. Surrey Beatty & Sons Pty Limited, Chipping Norton, Australia.

Bayliss, P., Webb, G.J., Whitehead, P.J., Dempsey, K. & Smith, A. (1986) Estimating the abundance of saltwater crocodiles, *Crocodylus porosus* Schneider, in tidal wetlands of the northern territory – a mark-recapture experiment to correct spotlight counts to absolute numbers, and the calibration of helicopter and spotlight counts. *Australian Wildlife Research*, **13**, 309–320.

Borchers, D.L. & Efford, M.G. (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, **64**, 377–385.

Brandt, L.A. (1991) Long-term changes in a population of *Alligator mississippiensis* in South Carolina. *Journal of Herpetology*, **25**, 419–424.

Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: A Practical Information Theoretic Approach*. Springer, New York, 353 pp.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York.

Burnham, K.P. & Anderson, D.R. (2004) Model selection: understanding AIC and multimodel inference, with contrasts to BIC. *Sociological Methods & Research*, **33**, 261–304.

Champion, H.G. & Seth, S.K. (1968) *A Revised Survey of the Forest Types of India*. Manager of Publication, Delhi, pp. 404.

Choudhury, B.C., Singh, L.A.K., Rao, R.J., Basu, D., Sharma, R.K., Hussain, S.A., Andrews, H.V., Whitaker, N., Whitaker, R., Lenin, J., Maskey, T., Cadi, A., Rashid, S.M.A., Choudhury, A.A., Dahal, B., Ko, U.W.K., Thorbjarnarson, J. & Ross, J.P. (2007) *Gavialis gangeticus*. IUCN 2009. IUCN Red List of Threatened Species. Version 2009.2. www.iucnredlist.org. Downloaded on 22 November 2009.

Conn, P.B., Arthur, A.D., Bailey, L.L. & Singleton, G.R. (2006) Estimating the abundance of mouse populations of known size: promises and pitfalls of new methods. *Ecological Applications*, **16**, 829–837.

Creel, S. & Creel, N.M. (1995) Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, **51**, 1325–1339.

Dudgeon, D. (2000) Large-scale hydrological changes in tropical Asia: prospects for riverine biodiversity. *BioScience*, **50**, 793–806.

Fukuda, Y., Webb, G.J.W., Manolis, C., Delaney, R., Letnic, M., Lindner, G. & Whitehead, P. (2011) Recovery of saltwater crocodiles following unregulated hunting in tidal rivers of the Northern Territory, Australia. *The Journal of Wildlife Management*, **75**, 1253–1266.

Gauthier-Clerc, M., Gendner, J.P., Ribic, C.A., Fraser, W.R., Woehler, E.J., Descamps, S., Gilly, C., Le Bohec, C. & Le Maho, Y. (2004) Long-term effects of flipper bands on penguins. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, S423–S426.

Gopal, L. & Srivastava, V.C. (2008) *History of Agriculture in India (up to c. 1200 A.D.). History of Science, Philosophy and Culture in Indian Civilization*. Project of History of Indian Science, Philosophy and Culture. Centre for Studies in Civilizations, New Delhi, India.

Hussain, S.A. (1999) Reproductive success, hatchling survival and rate of increase of gharial *Gavialis gangeticus* in National Chambal Sanctuary, India. *Biological Conservation*, **87**, 261–268.

Hussain, S.A. (2009) Basking site and water depth selection by gharial *Gavialis gangeticus* Gmelin 1789 (Crocodylia, Reptilia) in National Chambal Sanctuary, India and its implication for river conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **19**, 127–133.

Jain, S.K., Pushpendra, K.A. & Singh, V.P. (2007) *Hydrology and Water Resources of India*. Water Science and Technology Library, Tributaries of Yamuna River, Volume 57. Springer Verlag, Dordrecht.

Karanth, K.U. (1995) Estimating Tiger *Panthera tigris* populations from camera-trap data using capture–recapture models. *Biological Conservation*, **71**, 333–338.

Karanth, K.U., Nichols, J.D., Kumar, N.S. & Hines, J.E. (2006) Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology*, **87**, 2925–2937.

Kaul, O.N. (1962) Management of Chambal ravines in Rajasthan. *Indian Forester*, **88**, 725–730.

Kelly, M.J. (2001) Computer-aided photograph matching in studies using individual identification: an example from Serengeti cheetahs. *Journal of Mammalogy*, **82**, 440–449.

Lang, J.W. (1987a) Crocodilian behaviour: implications for management. *Wildlife Management: Crocodiles and Alligators* (eds G.J.W. Webb, S.C. Manolis & P.J. Whitehead), pp. 273–294. Surrey Beatty & Sons Pty Limited, Chipping Norton, Australia.

Lang, J.W. (1987b) Crocodile thermal selection. *Wildlife Management: Crocodiles and Alligators* (eds G.J.W. Webb, S.C. Manolis & P.J. Whitehead), pp. 301–317. Surrey Beatty & Sons Pty Limited, Chipping Norton, Australia.

van Lawick-Goodall, J. (1971) *In the Shadow of Man*. Collins, Glasgow.

Magnuson, W.E. (1982) *IUCN-SSC* techniques for surveying crocodilians. *Crocodiles: Proceedings of the 5th Working Meeting of the Crocodile Specialist Group*, pp. 389–403. Gainesville, Florida, USA, 12–16 August 1980. IUCN, Gland.

Mani, M.S. (1974) *Ecology and Biogeography of India*. The Hague, W. Junk.

Mazzoil, M., McCulloch, S.D., Defran, R.H. & Murdoch, M.E. (2004) Use of digital photography and analysis of dorsal fins for photo-identification of bottlenose dolphins. *Aquatic Mammals*, **30**, 209–219.

McGregor, P. & Peake, T. (1998) The role of individual identification in conservation biology. *Behavioral Ecology and Conservation Biology* (ed. T.M. Caro), pp. 31–35. Oxford University Press, New York.

Messel, H., Vorlicek, G.C., Wells, G.A. & Green, W.J. (1981) *Monograph 1. Surveys of the Tidal Systems in the Northern Territory of Australia and Their Crocodile Populations. The Blyth-Cadell River Systems Study and the Status of Crocodylus porosus* Populations in the Tidal Waterways of Northern Australia. Pergamon Press, Sydney, Australia.

Murthy, R.S. (2004) *Management Plan of National Chambal Sanctuary, Morena (M.P.) 2003–2004 to 2013–2014*. Forest Department, Government of Madhya Pradesh, Bhopal, India.

Nair, T. (2010) *Ecological and Anthropogenic Covariates Influencing Gharial Gavialis gangeticus* Distribution and Habitat Use in Chambal River, India. M Sc Thesis, National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore, India.

Nair, T. (2011) India to launch a brave new initiative to save the critically endangered gharial. *SPECIES – Magazine of the Species Survival Commission*, **53**, 21.

Newton, I. (1995) The contribution of some recent research on birds to ecological understanding. *Journal of Animal Ecology*, **64**, 675–696.

Nichols, J.D. (1987) Population models and crocodile management. *Wildlife Management: Crocodiles and Alligators* (eds G.J.W. Webb, S.C. Manolis & P.J. Whitehead), pp. 273–294. Surrey Beatty & Sons Pty Limited, Chipping Norton, Australia.

Nichols, J.D. (1992) Capture–recapture models: using marked animals to study population dynamics. *BioScience*, **42**, 94–102.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical-inference from capture data on closed animal populations. *Wildlife Monographs*, **62**, 7–135.

Peake, T.M. (1997) *Variation in the Vocal Behaviour of the Corncrake Crex crex*: Potential for Conservation. PhD thesis, University of Nottingham, Nottingham, UK.

Pledger, S. (2000) Unified maximum likelihood estimates for closed models using mixtures. *Biometrics*, **56**, 434–442.

Rasband, W.S. (2007) *ImageJ*. National Institutes of Health, Bethesda, MD. Available at http://rsb.info.nih.gov/ij/.

Rexstad, E.A. & Burnham, K.P. (1991) *Users Guide for Interactive Program CAPTURE*. Colorado Cooperative Wildlife Research Unit, Colorado State University, Colorado, USA.

Rohner, C. (1996) The numerical response of great horned owls to the snowshoe hare cycle, consequences of non-territorial "floaters" on demography. *Journal of Animal Ecology*, **65**, 359–370.

Sharma, R. & Basu, D. (2004) Recent reversals in the population trends in the population of Gharial in the National Chambal Sanctuary in North India; implications and a suggested strategy for the conservation of one of the world's most endangered crocodilians. In: *Crocodiles. Proceedings of the 17th Working Meeting of the Crocodile Specialist Group, IUCN – The World Conservation Union*, pp. 180–186. Gland, Switzerland and Cambridge, UK.

Singh, L.A.K. & Bustard, H.R. (1976) A method to identify individual young gharial (*Gavialis Gangeticus*). *British Journal of Herpetology*, **5**, 669–671.

Smith, M.A. (1939) *The Fauna of British India Including Ceylon and Burma, Reptilia and Amphibia. Vol.I Loricata, Testudines*. Indian Reprints. Vol. Edition 1974. Todays and Tomorrow's printers and publisher, New Delhi.

Sutherland, W.J. (1995) *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford.

Swanepoel, D.G.L. (1996) Identification of the Nile Crocodile *Crocodylus niloticus* by the use of natural tail marks. *Koedoe*, **39**, 113–115.

Webb, G.J.W. & Manolis, S.C. (1992) Monitoring saltwater crocodiles (*Crocodylus porosus*) in the Northern Territory of Australia. *Wildlife 2001: Populations* (eds D.R. McCullough & R.H. Barrett), pp. 404–418. Elsevier Applied Science, New York City, New York, USA.

Webb, G.J.W. & Smith, A.M.A. (1987) Life history parameters, population dynamics and the management of crocodilians. *Wildlife Management: Crocodiles and Alligators* (eds. G.J.W. Webb, S.C. Manolis & P.J. Whitehead), pp. 199–210. Surrey Beatty & Sons Pty Limited, Chipping Norton, Australia.

Webb, G.J.W., Britton, A.R.C., Manolis, S.C., Ottley, B. & Stirrat, S. (2000) The recovery of *Crocodylus porosus* in the Northern Territory of Australia: 1971–1998. *Crocodiles. Proceedings of the 15th Working Meeting of the IUCN-SSC Crocodile Specialist Group*, pp. 195–234. IUCN, Gland, Switzerland.

Whitaker, R., Basu, D.J. & Huchzermeyer, F. (2008) Update on gharial mass mortality in National Chambal Sanctuary. *Crocodile Specialist Group Newsletter*, **27**, 4–8.

Whitaker, R. & Members of the GMTF (2007) The Gharial: going extinct again. *Iguana*, **14**, 24–33.

Whitaker, R., Rajamani, V., Basu, D. & Balakrishnan, V. (1974) Preliminary survey of the Gharial, Gavialis gangeticus. Madras Snake Park Trust Report, pp. 16.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–138.

Wilson, R.P. & McMahon, C.R. (2006) Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment*, **4**, 147–154.

Received 17 March 2012; accepted 16 July 2012
Handling Editor: Andy Royle