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Individual differences in post-release behaviour and survival shape outcomes in a headstarting programme for the critically endangered gharial

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Abstract

Headstarting, or rear-and-release, is a widely used conservation intervention that assumes animals raised in captivity to a larger size have better survival than if left in the wild. It has been the main conservation intervention for the critically endangered gharial (*Gavialis gangeticus*) since the 1970s, yet most populations have not recovered. In Chitwan National Park, Nepal, recruitment of headstarted individuals into the adult population remains poorly understood, so we used VHF radio telemetry to monitor survival, dispersal, and residency of released gharial (n = 20).

Most individuals dispersed 20–60 km (mean=47km) downstream during an initial exploratory phase, after which some established residency. Individuals that established residency were significantly smaller, both overall and relative to age, than those that did not. Larger gharial showed no improved survival, and post-release mortality was high, with 25–50% dying within two years, mostly due to gill-net bycatch.

Our findings show telemetry is a useful tool for post-release monitoring, helping explain survival outcomes and evaluate release strategies. In Chitwan, reducing bycatch remains critical for population recovery. Releasing gharial upstream of suitable habitat, before the monsoon, and at smaller sizes may improve outcomes. More broadly, our results suggest the core assumption of headstarting—that bigger is better, regardless of captive rearing—should be critically evaluated across species and systems.

Introduction

A major problem in conservation biology is that once wildlife populations decline to very small sizes, a series of feedback loops known as the 'extinction vortex' can make a negative population trend difficult to reverse (Caughley, 1994; Fagan & Holmes, 2006; Gilpin & Soulé, 1986). In an attempt to counteract this issue, one popular conservation intervention is reinforcement: 'the intentional movement and release of an organism into an existing population of conspecifics' (IUCN/SSC, 2013). Reinforcement aims to enhance population viability, for example by increasing population size above a critically low threshold or restoring demographic structure (Bell et al., 2019; Oppel et al., 2021; Seddon, 2010). One widely used form of reinforcement is headstarting, used in birds (e.g. Ewing et al., 2025), turtles (e.g. Mullin et al., 2020; Starking-Szymanski et al., 2018), crocodylians (e.g. Elsey et al., 2001; Temsiripong et al., 2006), fish (e.g. Hunt & Jones, 2018; Simon, 2023) among other animals. Headstarting involves collecting eggs or hatchlings from the wild, and trying to give them a literal 'headstart' in life, by protecting the predation-vulnerable small size classes in captivity before releasing them into the wild (Burke, 2015). The presumed benefit of headstarting therefore relies on the assumption that bigger animals have higher survival than smaller ones, and consequently headstarted individuals have an increased chance of surviving to adulthood. Headstarting is popularly used for herpetofauna; however, evidence suggests outcomes are highly variable, with many programmes not leading to sustainable population recovery in the long term (Ballouard et al., 2010; Burke, 2015). Understanding of why headstarting programmes fail is vital to improve ongoing and future management, yet the underlying causes and mechanisms of failure often remain poorly understood (Bennett et al., 2017).

An essential component of any translocation, including headstarting, is post-release monitoring (IUCN/SSC, 2013; Sutherland et al., 2010). Without tailored and appropriate monitoring, it is not possible to understand which of a suite of possibilities has caused a programme to fail (Parker et al., 2013). Appropriate monitoring allows for adaptive management or informed cessation of the programme (Parker et al., 2013), whereas inadequate monitoring can lead to a programme being incorrectly classed as 'successful' (Fischer & Lindenmayer, 2000). Despite this, many programmes have failed to conduct adequate monitoring, although an increasing volume of reintroduction literature suggests

this is changing (Berger-Tal et al., 2020; Bubac et al., 2019; Griffith et al., 1989). Suitable monitoring enables headstarting programmes to pinpoint issues that can lead, or have led, to programme failure. Headstarting can fail due to many factors, including post-release mortality (Bubac et al., 2019), long-distance dispersal (Berger-Tal et al., 2020), and replacement rather than addition of individuals (Johnston et al., 2018; Radinger et al., 2023). Given the diversity of mechanisms that can underly failure across species and systems, post-release monitoring on a sample of marked individuals, with measures taken to avoid death and dispersal being confounded, should be core components of any headstarting programme (IUCN/SSC, 2013). Technologies such as telemetry offer the ability for detailed tracking of individual behaviour, providing insights into post-release adaptation. Behavioural patterns can reveal underlying processes such as learning, habitat selection, and the development of site fidelity, often before demographic outcomes become apparent (Bell, 2016; Berger-Tal & Saltz, 2014; Ranc et al., 2022).

Despite increasingly well-established post-release monitoring and behavioural frameworks, empirical data linking post-release movement, mortality, and recruitment outcomes remain limited for many species, particularly those subject to long-term headstarting programmes. The headstarting of the gharial (*Gavialis gangeticus*) in India and Nepal is one such instance. The gharial is a large crocodylian found only in South Asia, once widely distributed in the larger rivers of the Indus, Ganges and Brahmaputra basins, but extirpated from much of its range except a handful of small, isolated populations in the Ganges basin in India and Nepal (Ajji M. et al., 2025; Lang et al., 2019). Both the governments of Nepal and India set up headstarting programmes for gharial in response to declines, almost exclusively using eggs collected in the wild and reared to a larger size class in ex-situ facilities. By 2005, over 5000 gharial had been released in India (Whitaker, 2007), and by 2024 over 2000 gharial had been released in Nepal (DNPWC, 2025). Described in 1982 as “among the most successful conservation projects in the world”, it was evident by the early 2000s that headstarting efforts at this time had been contributing minimally to increasing wild adult populations in the majority of locations (Ballouard et al., 2010; Stevenson, 2015; Whitaker, 2007). There was, however, a lack of data to explain exactly why so few headstarted gharial were recruited into adult populations. Consequently, headstarting remains extensively used in both countries.

The headstarting programme of the Chitwan National Park in Nepal is a useful case study site for investigating causes of programme failure, and how to detect these. By 2021, 1369 gharial had been released in Chitwan, but the estimated adult population was just 28-43 (Griffith, 2022), suggested limited recruitment of headstarted individuals. A prevailing hypothesis was that individuals disperse downstream over a barrage on the India-Nepal border at the most downstream part of the river system, which prevents their movements back upstream (Ballouard et al., 2010; Maskey, 1989) but this hypothesis was based on limited observational evidence (Lang, 2016). Previous monitoring approaches, including population surveys and attempted resighting of marked individuals, have proved insufficient for determining survival and dispersal in this system (Ballouard et al., 2010; Maskey, 1989; Maskey & Percival, 1994). Radio telemetry provides a robust alternative, enabling direct tracking of individual fate, movement and behaviour. Telemetry methods have been developed and utilised very successfully by the Gharial Ecology Project in India (Lang & Whitaker, 2010), and are more broadly of great use for crocodilian biologists working with these amphibious, camouflaged, cryptic reptiles (Mascarenhas-Junior et al., 2023).

In this study, we used radio telemetry to conduct over two years of post-release monitoring of 20 gharial released from captivity into the Chitwan National Park in March 2019. We evaluated the effectiveness of radio-telemetry as a post-release monitoring technique, and used the resulting data to investigate patterns of fate, dispersal and movement. By analysing the relationship between size at release, and individual residency establishment and mortality patterns, we question the key assumption of headstarting, that 'bigger is better'.

Methods

Study site and conservation programme

The gharial population in Chitwan is currently found in the Narayani river, its major tributary the Rapti, and their tributary streams (Figure 1). These rivers form the western and northern borders of the Chitwan National Park in southern Nepal, and the gharial population is mostly restricted to the river sections within the National Park, or the adjacent buffer zone. This population is the largest remaining gharial population in Nepal (Acharya et al., 2017) and the most northerly and upstream part of the range of the gharial on the Gandak tributary of the Ganges river. A large barrage at the India-Nepal border (Figure 1) marks the end of Chitwan National Park protection, and after this the river flows into India (except a small meander back into Nepal a few kilometres below the dam).

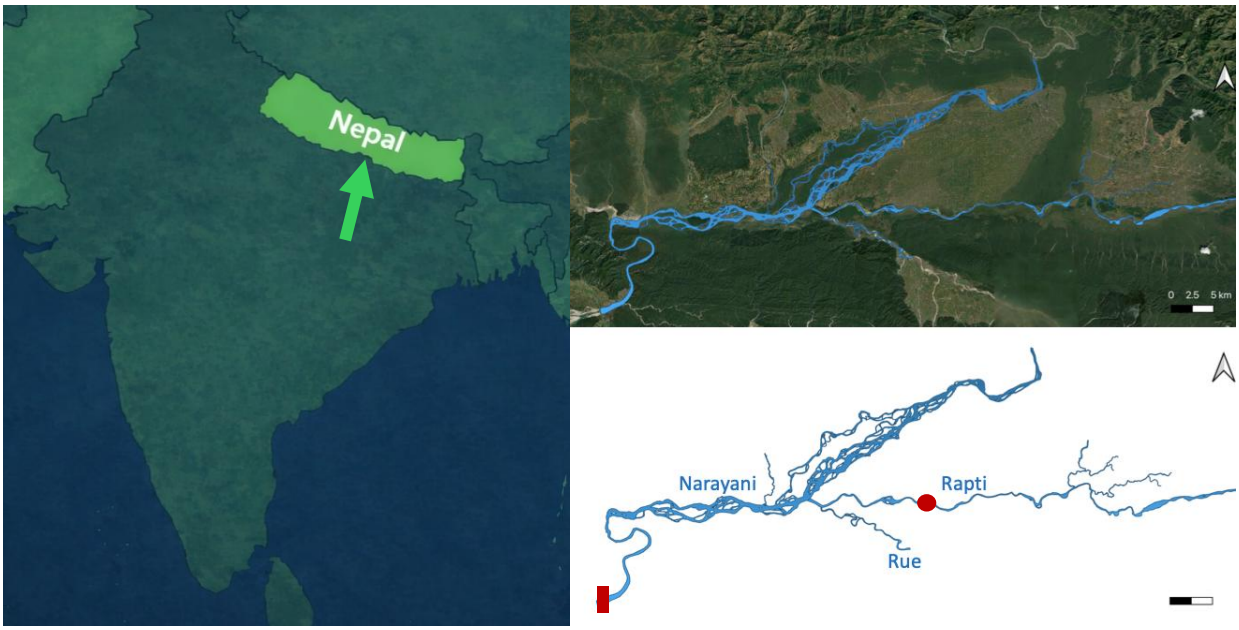


Figure 1: The location of the study site. Clockwise, from left: the location of Nepal in South Asia, with the central location of Chitwan indicated by the arrow; satellite imagery of Chitwan with the river system superimposed for clarity, forested areas south of or within the river are the Chitwan National Park; the river system with the major rivers labelled. The red dot indicates the location of Kasara, where the headstart release site is located, and the red rectangle indicates the location of the barrage on the Nepal-India border (at tip of green arrow, left panel).

The gharial headstarting programme is based at the Gharial Conservation Breeding Centre (GCBC), Kasara, within the Chitwan National Park, and is an initiative of the Department of National Parks and Wildlife Conservation (DNPWC), Government of Nepal. The centre and programme were started in 1978 in response to the collapse of the gharial population in Chitwan in the 1960s, leading to population counts of just 50-60 adult gharial and no immature gharial by the 1980s (Maskey, 1989). Eggs for the headstarting programme are collected from in-situ nest sites, and from 1980-2017 the majority of gharial nests found were brought into the centre. Gharial are hatched in artificial sandbanks and then reared in concrete pools. Gharial are released annually at an age of 5-7 years, usually in February and March. Gharial have primarily been released in the Rapti river at Kasara since 2004, which was the release site used in this study (Figure 1).

Tag attachment and release procedure

A cohort of 20 gharial was due for release in Chitwan in early March 2019. This was one fifth of a larger cohort of 100 gharial that were released in pre-monsoon 2019 (February-April). The gharial had hatched either in 2011 (n=11, 8 years old) or 2014 (n=9, 5 years old), and measured 170-197cm at release. This size would typically correspond to juveniles in the wild; however, their age is more consistent with subadult or adult classes, making classification into standard size–age categories difficult. We tagged these 20 gharial using VHF-transmitters (151 MHz; Advanced Telemetry Systems, USA) attached to the dorsal surface of the tail (Figure 2). For full details of tag attachment see Griffith (2022). In summary, the radio transmitter is attached using Kevlar fishing line attached to the epoxy casing of the transmitter. The line is then passed through holes drilled in the base of the tail scutes, underneath the dorsal skin below the transmitter, back through holes in the opposite tail scutes, and attached again to the opposite side of the radio transmitter. A numbered cattle tag was attached to the third single tail scute to assist in sighting released gharial (Figure 2). Morphometric measurements were collected (mass, snout-vent length, vent-tail length, total length, snout width, head length, head width, mid-body circumference and sex). All handling and transmitter attachment was conducted with permission from the Department of National Parks and Wildlife Conservation, under supervision of the Assistant

Conservation Officer in charge of the GCBC, and was approved through ethical review from the University of Oxford (APA/1/5/ZOO/NASPA/WildCRU/Gharial).

Gharial were released according to the standard release soft-release procedure of the GCBC, on 8-10 March 2019, at the annual release site in Kasara (Figure 1). A soft-release enclosure is annually constructed using a barrier made of elephant grass to enclose a section of both river and shore (gravel-sand bank). Gharial are able to force their way out of the enclosure and into the river beyond through the loosely packed grass barrier, and exit becomes increasingly easy in the weeks post-release, as the flow of the river causes the structure to become more permeable.



Figure 2: Top: a gharial at the Chitwan Gharial Conservation Breeding Centre prior to release into the wild, illustrating the attached VHF transmitter and cattle tag. The attachment of the transmitter allows for post-release monitoring, and the brightly coloured tag assists in sighting released animals. Bottom: a re-sighted tagged gharial (left/back) with an untagged headstart (right/front).

Post-release monitoring

The VHF-tagged gharial were manually tracked from release until the confirmed battery failure of the last radio transmitter, using an ATS R410 scanning receiver (Advanced Telemetry Systems, USA) and five element Yagi directional antenna. Tracking was carried out regularly, with the aim of locating each animal at least once per week, and those in more remote sites at least once per month. Full details of tracking protocol can be found in Griffith (2022), and was carried out concurrently with the tracking described in that study. In summary, gharial were tracked from listening posts on high ground every 2-3 km along the riverside, due to inaccessibility of much of the riverbank. According to strength and direction of the signal, gharial locations could be assigned to a particular stretch of river (0.5-3km). If the gharial could not be seen (due to being underwater or in an inaccessible area), its location was assigned to an empirically derived polygon representing the section of river from which the detected signal could originate. Each polygon was constructed using calibration data from fixed-position transmitters, boat-mounted transmitters, and visible tagged animals. Boat-based tracking took place sporadically, and gharial were assigned a specific GPS location using sighting and triangulation. The Wildlife Trusts of India, during their 02-12 March 2020 gharial survey on 278km of the Gandak River, tracked for the VHF numbers of all gharial missing from Nepal (WTI, 2020).

Morphometric indices

We derived two secondary measures from our morphometric data: relative size-at-age, and relative body condition. These measures were used to standardise individual variation in growth and condition relative to a reference population, allowing meaningful comparisons across individuals of different ages and sizes. As a reference dataset, we combined our focal dataset with measurements from an additional sample of individuals (n=28) of the same age range (5-8 years) recorded at the time of release from the GCBC between 2000 and 2021. To assess body condition, we first established the relationship between snout-vent length and body mass, using the reference dataset. We then calculated Le Cren's relative condition factor (K_n) as the ratio of an individual's observed mass to the mass predicted from this relationship (K_n= Mass / SVL^{slope}) (Balaguera-Reina et al., 2023; Cren, 1951). For relative size-at-age, we initially tried to model the age-length relationship for gharial in our reference dataset. However, we found no significant relationship between

age and length (Figure S1). Consequently, we define expected size as the mean total length of each year class. Relative size-at-age was calculated as the residual difference between an individual's observed length, and the corresponding age-specific mean.

Analysis of dispersal distance and settlement

We characterised and quantified post-release dispersal and time to settlement of the release gharial by comparing displacement from release site (km) with time since release (days). To convert raw detection data into dispersal distances, we firstly converted each raw detection into a point location by randomly sampling within the detection polygon (following Griffith 2022). We then estimated the distance between each relocation and the release site, following a least cost pathway constrained to the river channel using the R package gdistance (van Etten, 2017) following (Baker et al., 2019). To characterise variation in maximum dispersal among individuals, we calculated the maximum dispersal distance for each gharial as the greatest recorded distance from the release site across all detections. The distribution of maximum dispersal distances was assessed using histograms and kernel density estimation, and compared to a fitted normal distribution based on the observed mean and standard deviation. Skewness was quantified using moment-based skewness, and departure from normality was assessed using the Shapiro–Wilk test.

Juvenile and subadult wild gharial show limited movement, with a linear river home range of 15-20km (Gharial Ecology Project, pers. comm.). We classified gharial as either settled or not settled based on whether their dispersal distance reached an asymptote, indicating stabilisation within a home range. An asymptote was defined as the point at which dispersal distance no longer showed a consistent increasing trend and variation in distance between successive detections remained within 20 km over a period of at least 100 days. For individuals that died or were displaced due to external factors, this criterion was applied over the final two months of available tracking data. Gharial that settled in the river of release (Rapti), all of which settled before or during their first monsoon, were classed as residents, Rapti (RR). Gharial that settled in the downstream Narayani river, all of which settled after their first monsoon, were classed as residents, Narayani (RN). All gharial that did not establish residency, were classed as showing movement, continuous (MC). If gharial died or were lost before 200 days of redetection, they were classed as died/dispersed early (DE). To determine if the gharial that established residency (RR and RN), and did not (MC)

differed in size, condition and age at release, we conducted independent two-sample t-tests comparing the length, weight, relative size-at-age, Le Cren relative condition and age between gharial that did and did not establish residency. All analyses were conducted in the R statistical environment, version 4.4.1 (R Core Team, 2024).

Analysis of mortality

Gharial were assigned a status of alive, dead, missing (presumed dead), missing (presumed dispersed) and unknown at the end of the study. A gharial was classed as alive if it was seen at least once after the end of radio transmitter battery life. A gharial was classed as dead if the animal was found dead or its body parts were recovered. To understand all causes of mortality, all tagged gharial found dead underwent post-mortem inspection with veterinarians of the National Trust for Nature Conservation if there was sufficient non-skeletal material. Informal discussions were held with local communities to gather additional insights on cause of death. Gharial were presumed dead when we suddenly stopped detecting them following regular detection, and this period did not correlate with a time of flooding when a live or dead gharial could be moved swiftly downstream. Gharial were presumed dispersed (crossed the border into India) when we stopped detecting them after their displacement had been continually increasing and they had already moved further from the release site than the remaining distance to the border barrage. Gharial were classed as missing (unknown) when they disappeared without any strong evidence of how they might have died, or without the above correlations suggesting they may have dispersed.

To determine if gharial that died or were lost during the study, or that died or were lost within 200 days of release (group DE), differed in size, condition and age at release, we conducted two-sample t-tests comparing the length, weight, relative size-at-age, Le Cren relative condition and age between (a) gharial that were confirmed alive at the end of the study, and those that were dead or lost (b) gharial that had died or dispersed early (DE), and those that survived longer (RR, RN and MC). As a sensitivity analysis, tests were run twice, firstly with gharial of unknown fate excluded, secondly with these included as dead gharial. As there was no substantial difference, we report here the results with dead and lost gharial combined.

Results

Post-release monitoring and initial dispersal

Following release of 20 gharial on March 8-10 2019, individuals were tracked for up to approximately 850 days post-release (the end of tag battery life), or until death or loss of the individual (Table 1). Due to Covid-19 lockdowns, tracking of gharial on the Narayani river in 2020 was more sporadic, and ended after approximately 700 days.

All 20 released gharials initially moved downstream from the release site (Figure 5A, Figure 7). Mean maximum recorded downstream dispersal distance was 47 km (range = 2-112km; Table 1). Maximum downstream dispersal distance was approximately normally distributed with moderate positive skew (skewness = 0.4) with no evidence of deviation from normality (Shapiro–Wilk test: W = 0.98, p = 0.86). The long tail of the distribution suggests a small number of gharial may disperse longer distances (Figure 5A). Two gharial are suspected to have dispersed beyond the maximum recorded distance, but were not detected again so ultimate dispersal distance could not be confirmed (Table 1, O&S). Two individuals subsequently dispersed upstream, after reaching their maximum downstream dispersal distance, reaching 20km and 41km upstream of the release site (Table 1, M&R).

Gharial	Fate	Max dispersal (km) (-ve =upstream)	Final dispersal (km)	Days of Detection	Age	Length (cm)	Sex	Movement Group
A	Dead	32	16	674	8	173	F	RR
B	Missing	18	10	521	8	173	F	RR
C	Alive	10	4	766	5	175	F	RR
D	Alive	31	17	654	8	177	F	RR
E	Alive	84	84	703	5	173	F	RN
F	Alive	75	70	753	8	174	F	RN
G	Dead	41	37	339	5	175	F	RN
H	Dead	51	51	342	5	181	F	RN
I	Alive	62	57	756	5	182	M	RN
J	Alive	72	71	704	8	185	M	RN
K	Alive	83	59	754	8	183	F	MC

L	Alive	112	67	753	5	184	F	MC
M	Alive	29 (-20)	16	857	8	185	F	MC
N	Alive	58	58	754	8	191.5	F	MC
O	Missing (likely dispersed)	42	42	97	5	170.5	F	DE
P	Missing	22	20	118	8	176.5	M	DE
Q	Dead (unconfirmed)	0	0	58	8	178	F	DE
R	Dead	15 (-41)	41	205	5	182	F	DE
S	Missing (likely dispersed)	47	47	107	8	186	F	DE
T	Dead	57	57	239	5	197	F	DE

Table 1: The fate (alive or dead), age, sex and size (total length in metres=m) of the 20 juvenile gharial monitored in this study via radiotelemetry, post release at the Gharial Conservation Breeding Centre in Kasara, Chitwan National Park, March 2019

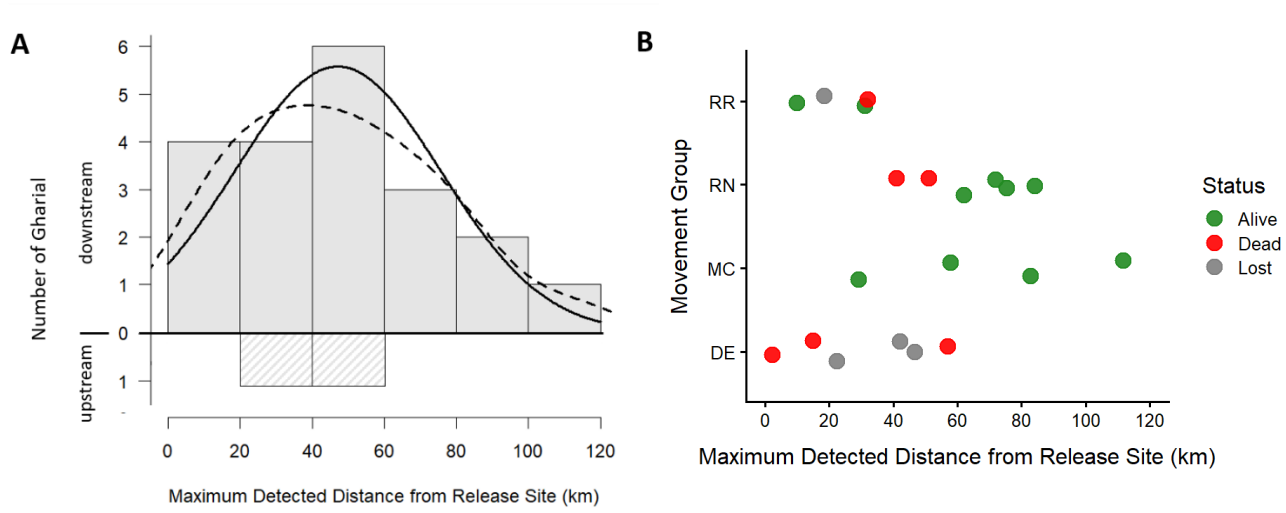


Figure 5: (A) Distribution of maximum dispersal distance for all gharials, defined as the furthest recorded detection of each individual from the release site. All individuals initially dispersed downstream (upper y-axis, solid bars); two later moved upstream after reaching their maximum downstream distance (lower y-axis, striped bars). For downstream dispersal distances, the solid line shows the normal distribution and the dotted line the observed distribution (empirical kernel density). (B) Maximum recorded downstream dispersal distance of each gharial, coloured by fate at the end of the monitoring period (alive, dead, lost) and grouped by movement category (Resident Rapti RR, Resident Narayani RN, Moving Continuously MC, Died/Dispersed Early DE)

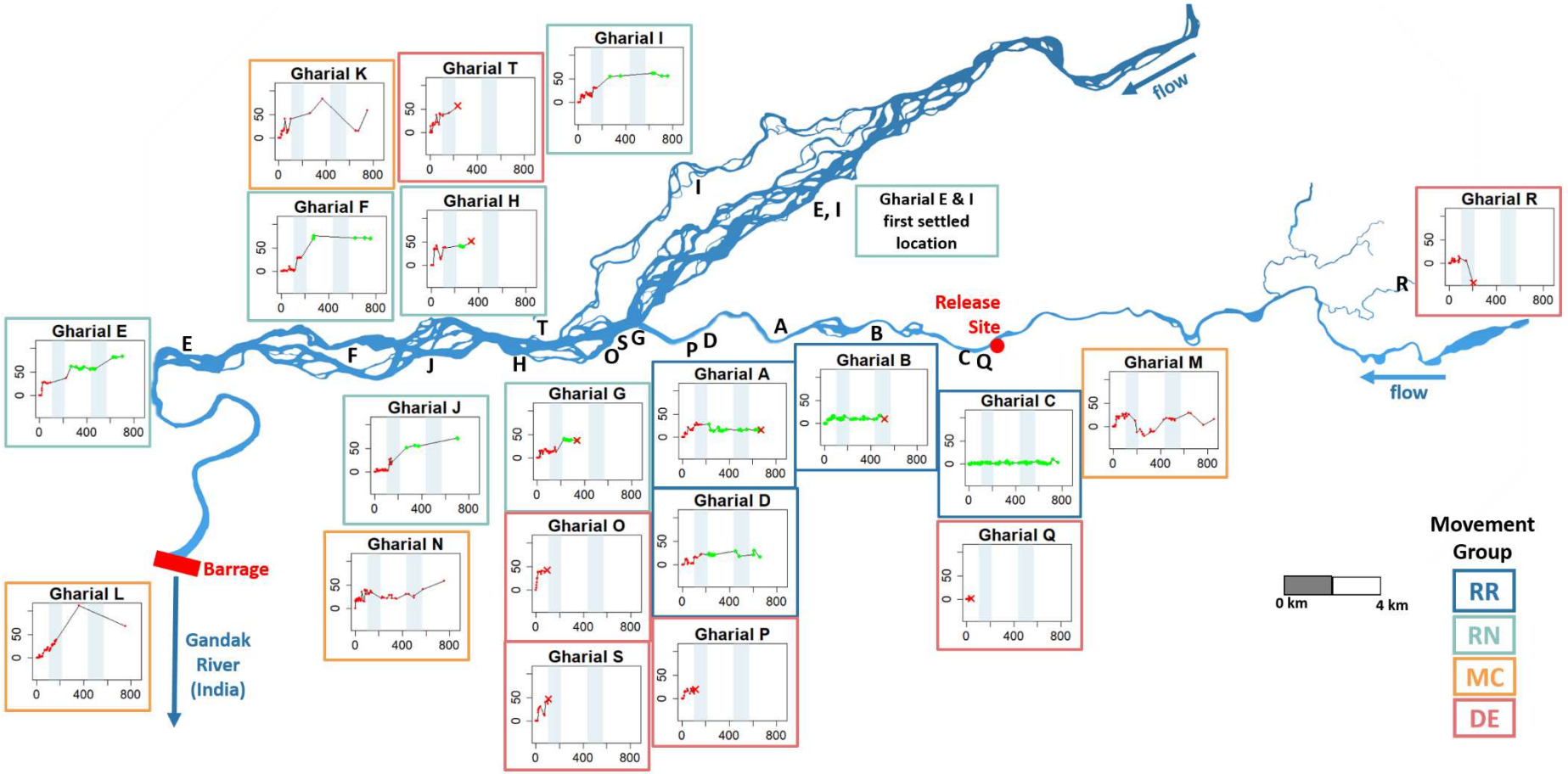


Figure 6: Movement trajectories of 20 radio-tagged gharial in the Rapti River (tributary, right) and Narayani River (main river, left) bordering Chitwan National Park. Each panel shows the full post-release movement record of an individual, with days since release on the x-axis and distance from the release site (km) on the y-axis. Individuals are coloured by movement group, representing distinct post-release movement strategies: Rapti residents (RR, blue) established residency in the Rapti River before or shortly after the first monsoon; Narayani residents (RN, green) established residency in the Narayani River after the first monsoon; moving continuously (MC, orange) did not establish residency during the monitoring period; and died/dispersed early (DE, red) died or disappeared before a movement strategy could be established. Panels are positioned approximately above or below the river location where individuals established residency indicated by the letter on the riverside (RR and RN), reached their maximum recorded distance from the release site with no letter (MC), or were last detected/found dead indicated by letter (DE).

Gharial post-release behaviour

Although all gharial initially dispersed downstream, most exhibited highly variable dispersal distances for the first 180 days after release (Figure 6, Figure S1; red dots before and during first blue band), corresponding to their first pre-monsoon and monsoon seasons following release. After this variable period, individuals could be categorised into one of four movement groupings (Figure 6, Figure S1). Resident Rapti gharial (RR) established residency in the river of release, the Rapti (n=4), Resident Narayani gharial (RN) established residency in the downstream Narayani river (n=6), moving continuously gharial (MC) continued to range over a large stretch of river without establishing residency (n=4); and died/dispersed early gharial (DE) died or disappeared before a longer-term movement pattern could be assigned (n=6). Two resident gharial switched residency locations during their second monsoon, as the sandbank habitat they had settled in were completed eroded by monsoon floods (Figure 6, Gharials E and I).

Gharial that established residency (RR and RN) were significantly smaller than those that did not establish residency (MC), including having shorter total length ($t(6.31) = 3.85$, $p = 0.008$), lighter mass ($t(4.79) = 2.92$, $p = 0.035$), and lower relative size-at-age ($t(3.98) = 3.40$, $p = 0.028$) (Figure 7). On average, RR and RN gharial were 9 cm shorter (176.8 cm vs 185.9 cm) and 2.4 kg lighter (14.5 kg vs 16.9 kg) than MC gharial, and exhibited lower relative size-at-age (−0.51 vs 0.71). No significant difference in body condition was detected between the groups ($t(5.66) = 1.78$, $p = 0.13$). Age was not associated with movement group ($t(5.87) = 0.83$, $p = 0.44$), with both hatching cohorts evenly distributed across movement outcomes and trait ranges (Figure S3).

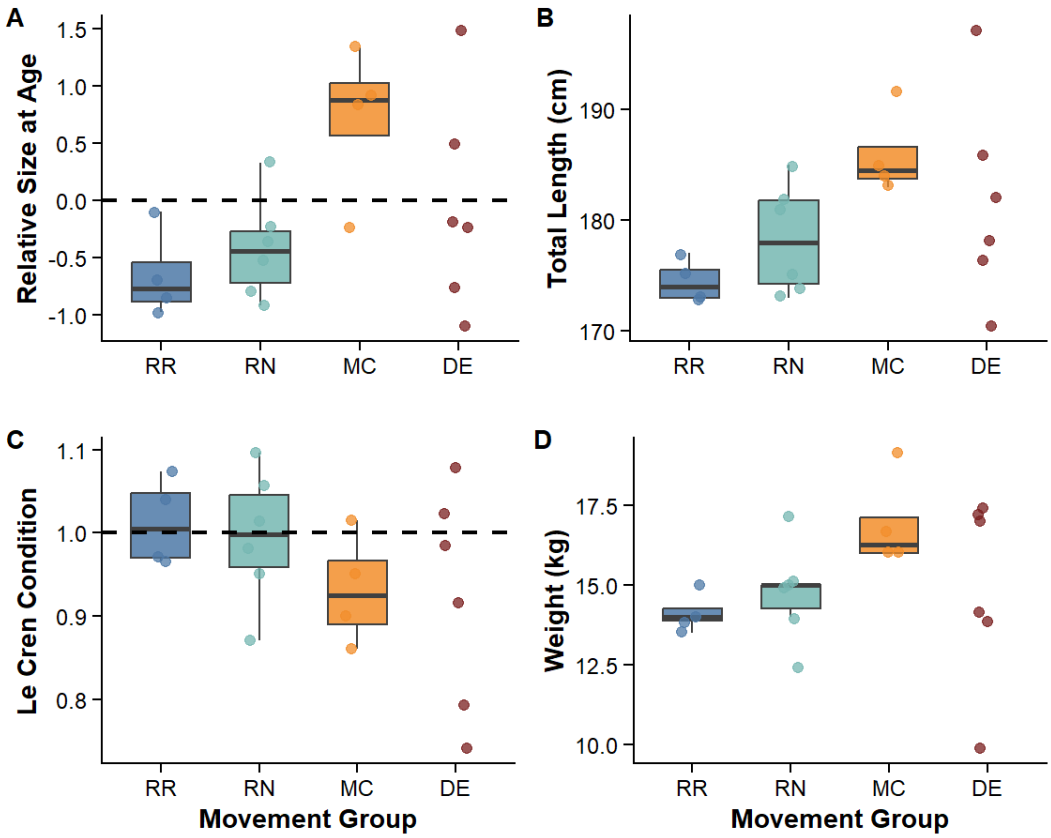


Figure 7: All panels (A-D) show movement group on the x-axis: RR = Resident, Rapti; RN = Resident, Narayani; MC = Moving Continuously; DE = Dead/Disappeared Early. Boxplots show median (line), interquartile range (box), and non-outlier values (whiskers). DE gharial do not have a box plot, as they span the range of values and died/disappeared before groups were established. (A) relative size-at-age, an adjusted measure of whether individuals are longer or shorter than expected based on a reference dataset. (B) total length. (C) Le Cren condition, indicating whether individuals are lighter or heavier than expected for their length based on the reference dataset. (D) body weight.

Gharial mortality and non-detection

Of the 20 gharial released in 2019, 10 were confirmed to be alive at the end of the monitoring period (Figure 8). Five gharial were confirmed dead, all of which had strong evidence they had been killed by human activities. One additional gharial was classed as dead as it was lost from a closely monitored stream adjacent to the Gharial Conservation Breeding Centre, where it was seen daily before suddenly disappearing, most likely the result of a terrestrial predation, possibly a tiger. Two gharial are suspected to have dispersed to India, where their fate is unknown as they were not detected in the March 2020 Gandak survey (Figure 8, 'dispersed?'). Both individuals were last detected while

continuing to move downstream and had already travelled farther from the release site than the remaining distance to the India–Nepal border barrage. The two individuals classified as 'dead?' (Figure 8) had been regularly redetected before suddenly disappearing, suggesting abrupt removal from the system and probable mortality.

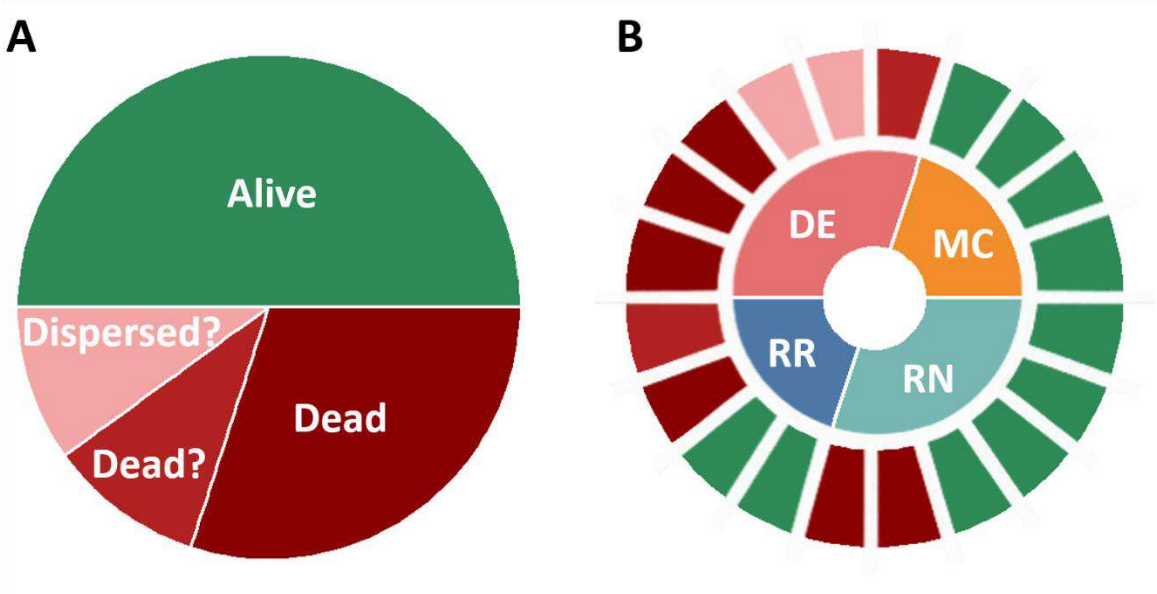


Figure 8: (A) the fate of a cohort of 20 VHF-tagged released from the Gharial Conservation Breeding Centre in Kasara, March 2019, based on their status at last detection: alive, dead, missing presumed dispersed ("dispersed?") and missing presumed dead ("dead?"). (B) Fate of each individual gharial. The outer ring shows final fate, coloured as in panel A. The inner ring indicates assigned Movement Group (RR = Resident, Rapti; RN = Resident, Narayani; MC = Moving Continuously; DE = Dead/Disappeared Early).

Traits measured at release were not associated with subsequent fate. No significant differences were found between alive or dead gharial, including for body condition ($t(15.29) = 0.08$, $p = 0.93$), relative size-at-age ($t(18.00) = 0.98$, $p = 0.34$), and age ($t(17.99) = 0.43$, $p = 0.67$). Gharial that died or were lost early (DE) spanned a similar range of morphological measures as other movement groups (Figure 7, DE). DE gharial did not significantly differ from other gharial in condition ($t(6.33) = 1.03$, $p = 0.34$), relative size-at-age ($t(7.88) = 0.26$, $p = 0.80$), length ($t(6.84) = 0.56$, $p = 0.59$), or weight ($t(6.46) = 0.21$, $p = 0.84$).

Discussion

Summary

We used radio-telemetry to investigate dispersal, survival and post-release behaviour of headstarted gharial released in Chitwan, to provide insights into why this long-running programme has led to limited population recovery. Contrary to the underlying premise of many headstarting measures that 'bigger is better', we found smaller gharial were more likely to establish residency within the target habitat, whilst mortality was associated with neither size nor condition at release. Together, these findings challenge the assumption that rearing gharial to larger sizes prior to release improves post-release outcomes, and raises concerns about the potential phenotypic costs of prolonged captivity. Additionally, we found post-release mortality was high, with 25-50% dying within 2 years of release, primarily due to bycatch-related mortality. Almost all gharial intially moved 10-112km downstream of the release site, with most individuals dispersing a maximum of 20–60 km, and a few likely moving considerably further. Overall, our results suggest that headstarting has had relatively limited success in Chitwan due to ongoing high mortality, compounded by post-release downstream dispersal. These constraints could be mitigated in future through in-situ conservation actions, complemented by evidence-based adaptations to headstarting protocols.

Radio-telemetry as an effective methodology for gharial post-release monitoring

Radio-telemetry provided critical insights into the post-release fate, mortality, and dispersal of headstarted gharial that could not have been obtained through conventional monitoring alone. Tags enabled the detection of otherwise hidden carcasses, and the inference of probable mortalities from missing gharial, allowing more accurate estimation of mortality rates and causes than reporting of carcasses and population surveys alone. Radio telemetry also provides robust data on individual-level dispersal trajectories, residency establishment, and behavioural variation among released gharial. Thsee findings support broader recommendations that movement data provide an informative and practical tool for evaluating reintroduction outcomes (Berger-Tal & Saltz, 2014). Such data can inform structured decision-making approaches (Pritchard et al., 2022) and adaptive management frameworks to close the research-implementation gap (Dubois et al., 2020). Our results suggest the use of post-release telemetry should be a priority for all gharial headstarting

programmes, as both mortality and dispersal tendencies will be influenced by local environmental conditions and release decisions. This recommendation also extends to reinforcement and reintroduction efforts for other crocodylian species, where tracking technologies are increasingly used but not consistently reported (Mascarenhas-Junior et al., 2023). Transparent reporting of telemetry utility, and post-release outcomes, remains essential for improving conservation effectiveness, consistent with recommendations across a range of translocated taxa (Doogan et al., 2023; Stahl et al., 2023; Stone et al., 2024).

High observed post-release mortality for headstarted gharial of all sizes

Post-release mortality was higher than expected, contrasting with nearly 100% annual survival in similarly sized wild gharial in the Chambal River (Gharial Ecology Project, pers. comm.), and similarly low mortality in other crocodylian species at sizes >150cm (Briggs-Gonzalez et al., 2017; Wilkinson et al., 2016). Headstarting is only effective if individuals have a higher probability of recruitment than their wild counterparts. The high post-release mortality observed in our study, particularly in combination with high captive mortality in the past (Griffith, 2022), raises concerns that historically headstarted gharial in Chitwan may not have achieved the survival advantage over wild inviduals that headstarting is intended to provide. Neither smaller size, nor lower relative condition, was associated with higher mortality either shortly after release (Figure 6), or during the entire study period (Figure S3). As rearing individuals in captivity to larger sizes to reduce size-dependent mortality does not appear to improve survival, this calls into question the premise of many headstarting programmes, that individuals raised to larger sizes in captivity will have lower mortality.

The main identified cause of gharial mortality was direct killing by humans, either incidentally through drowning after gill-net entanglement, or from intentional killing. Intentionally killed gharial likely also came into contact with people during fishing activities. VHF telemetry was critical for recovering bycatch gharial - only three of the dead gharial would have been recovered if they were not tagged. The lack of telemetry in the past may have led to the impact of this threat being underestimated. Furthermore, the loss of two other tagged gharial in areas with high fishing pressure, suggest the impact may be even greater. Bycatch-related mortality is a major issue for gharial in much of their remaining range (Lang et al., 2019), as well as other sympatric freshwater megafauna (Behera et al., 2013). Bycatch-related mortality was identified as one key factor leading to the decline of

gharial in Nepal as early as the 1980s (Maskey, 1989), and the introduction of monofilament gill nets (1950s-1960s) corresponds to declines in gharial across South Asia (Radhalekshmy & Gopalan Nayar, 1973). Failure to address persistent drivers of decline is a common limitation of conservation translocations (Berger-Tal et al., 2020; Bubac et al., 2019; Fischer & Lindenmayer, 2000; Jule et al., 2008). Although gill-net fisheries are illegal in Chitwan, they remain widely used, primarily at night.

Larger body size is unlikely to reduce entanglement risk, and we speculate that releasing gharial at larger sizes (>100cm) may increase, rather than reduce, bycatch mortality. This is because headstarted gharial are first caught in nets at a large size, when they are already difficult for fishers to handle. In contrast, wild-hatched gharial are first caught at small sizes and may be more easily released, potentially giving them a change to learn avoidance behaviours. Releasing headstarted gharial at substantially smaller sizes should therefore be investigated, and mortality compared across a broader range of size classes than were available for release in this study.

Downstream dispersal and establishment of residency

Gharial in our study dispersed a mean maximum distance of 50km (10-120km), with multiple gharial then moving back towards the release site before settling. Gharial that ultimately established residency in either the Rapti or Narayani spanned a broad range of initial dispersal distances (Figure 5, RR and RN), indiciating that longer intial exploratory movements do not necessarily preclude successful estbalishemnt of residency.

Although based on a small sample size (n=20), these movements suggest that release sites less than 50km above a dam or protected area edge are likely to be unsuitable, as individuals are likely to leave during exploratory movements, or be lost at downstream barriers. In our study, gharial that reached the larger, downstream Narayani by the start of monsoon flooding dispersed further. Prior to 2004, gharial releases in Chitwan occurred in the Narayani river, and apparent survival was as low as 2% (Ballouard et al., 2010). Although most of the VHF tagged gharial dispersed less than 120km downstream, two untagged gharial from the 2020 release cohort travelled over 1000 km to West Bengal, and both faced poor outcomes, with one dying after stressful human encounters, and another removed to captivity (Khadka, 2020; WTI, 2020). These cases underscore that dispersal to areas outside targeted release zones is often a conservation failure, consistent with broader evidence that

unexpected coexistence challenges will arise when large carnivores disperse outside of the release area (Osborne & Seddon, 2012). Our results suggest that, unlike when the release site was in the Narayani river (Acharya et al., 2017; Ballouard et al., 2010; Maskey, 1989), at the current release site on the Rapti, dispersal over the barrage into the Gandak river in India is no longer the major limiting factor in Chitwan. The comparative success of the headstarting programme at the current Rapti release site highlights the importance of selecting suitable release locations in similar headstarting programmes.

The predominately downstream movements of gharial post-release lasted approximately 180 days, with six of the apparent mortalities occurred during this initial period. We defined residency in gharial as occupancy within <20km of linear river after initial dispersal. Gharial which established residency in the Rapti river settled early in the first monsoon, whereas gharial that established residency in the larger Narayani river, only did so after the end of the first monsoon. Four gharial did not appear to establish residency throughout the monitoring period, suggesting they had not acclimated to the wild (Bell, 2016; Berger-Tal & Saltz, 2014). These observed patterns in establishing residency among our released gharial correspond well with three behaviouaral phases typically observed in translocated animals: exploration, establishment and settlement (Figure 9; Panel A).

The exploratory phase is characterised by high movement rates and distances (Hempel et al., 2020; Osborne & Seddon, 2012), as individuals explore unfamiliar surroundings and begin forming spatial memory (Berger-Tal & Saltz, 2014; Ranc et al., 2022), indicated in gharial by initial high frequency downstream movements. This exploratory behaviour is often coincident with elevated mortality, termed the acclimation period (Figure 9) (Bell, 2016; Berger-Tal et al., 2020b; Hamilton et al., 2010; Hester et al., 2008) which we observed with the initially high rates of dead and lost gharial (Figure 6, DE). Following exploration, individuals then enter an establishment phase, where dispersal distance stabilises but movement remains frequent, before reaching a settlement phase in which translocated individuals establish residency patterns reflecting those of residents of the same demographic class (Bell, 2016; Hester et al., 2008; Moehrenschlager & Macdonald, 2003; Sievert et al., 2022). This transition may be underpinned by spatial memory development, as individuals increasingly revisit previously encountered locations, leading to the emergence of stable home ranges (Ranc et al., 2022). The longer time taken to establish residency in the Narayani, relative to the Rapti, likely reflects greater seasonal variability in

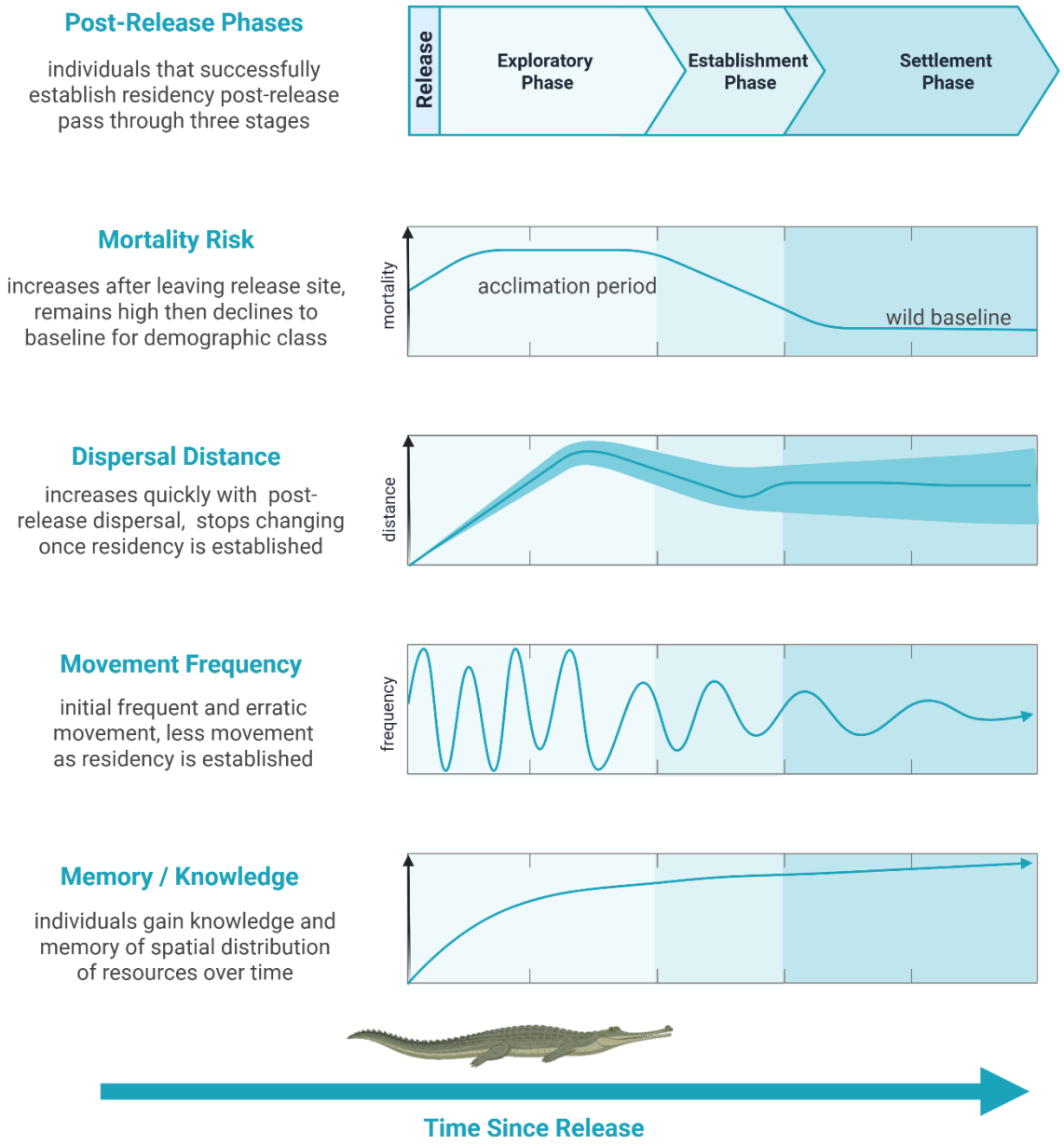


Figure 9*:* Post-release behavioural modification phases typically observed in translocated wildlife, which correspond to the behavioural phases observed by most gharial in this study. Phases, concepts and terminology are drawn from Bell, 2016; Berger-Tal et al., 2020; Berger-Tal & Saltz, 2014; Hamilton et al., 2010; Hester et al., 2008; Moehrenschlager & Macdonald, 2003; Osborne & Seddon, 2012; Ranc et al., 2022. Figure made with Biorender.

the Narayani, where monsoon flooding inundates basking habitat and alters river structure. The exploration phase would therefore necessarily be longer, as the spatial structure of exploitable resources continuously shifts (Berger-Tal & Saltz, 2014). Overall, these phases

554 represent a shift from exploration to exploitation of resources, and this shift – termed post-
555 release behavioural modification – has been suggested as indicative of successful post
556 release adaptation (Bell, 2016; Berger-Tal & Saltz, 2014). Where gharial have sufficient
557 resources, are able to adapt to exploit them, and anthropogenic threats are low, they
558 should survive and establish residency, indicating successful headstarting.

559 **Implications for pre- and post-release headstarting management**

560 Reinforcement in gharial, as in other species, seeks to supplement the resident
561 population at a specific site. Consequently, in our study, the gharial that survived and
562 established residency within the Chitwan National Park can be viewed as headstarting
563 successes. Dispersal distances and establishment of residency are likely to reflect individual
564 responses to environmental, and intra- and inter-specific cues, with movement balancing
565 attractive features (e.g. suitable habitat or conspecific groups) and repelling factors (e.g.
566 area of high disturbance of threat, such as fishing activity or sand mining) (Berger-Tal &
567 Blumstein, 2025). Previous work in Chitwan found recaptured gharial had shown little to no
568 growth, and a loss of condition, in the first two-years post-release (Khadka et al., 2022),
569 indicating challenges in resource acquisition post-release. This is potentially linked to finding
570 and catching live prey for the first time. As ectotherms, gharial have higher resource
571 requirements in warmer seasons (Barham et al., 2024; Lang, 1987), and releasing gharial just
572 as the weather is warming up (Feb-Mar) is likely to add additional pressure on individuals to
573 find resources. This challenge may be compounded in the gharial who have the largest size-
574 at-age, which suggests they have grown faster in captivity, as animals with faster growth
575 require more resources (Brown et al., 2004).

576 Patterns of dispersal in our study suggest river characteristics and release timing are
577 also important. Individuals entering the larger Narayani River dispersed farther than those
578 remaining within the Rapti, particularly during the first monsoon season. Lower dispersal
579 may therefore be expected in smaller rivers and during periods of lower discharge.
580 Conspecifics may also be important as a repelling or attracting factor, depending on social
581 context. Crocodylians are intelligent and exhibit diverse systems of conspecific interactions
582 (Brien et al., 2013; Garrick & Lang, 1977; Reber et al., 2021), while gharial are notably social,
583 displaying complex behavioural interactions (Ajji M. & Lang, 2025) . We observed gharial
584 that established residency (RR and RN) did so in larger groups of conspecifics, and all gharial
585 initially moved downstream until they reached an area with aggregatings of gharial.

Attention to social learning and developmental plasticity should be incorporated into headstarting research in gharials and other crocodilians, with studies of avian translocation success providing a useful model (Aplin et al., 2025; Miller et al., 2024). Taken together, releasing gharial in sites sufficiently upstream of suitable habitat, in smaller rivers, during the early winter, and considering the presence of conspecifics, are likely to improve headstarting success.

Finally, the most successful individual headstarts in our study were significantly smaller, especially relative to their age at release. This suggests faster growth in captivity, and/or larger size, does not confer post-release advantages. The release of substantially smaller and younger gharial should also be investigated, which may also reduce the negative impacts of longer times in captivity. The lack of a relationship between size and age in 5-8 year old gharial released from the GCBC (Figure S2), despite the gharial being far from mature sizes, indicates the captive conditions are leading to highly constrained growth. Additionally, individuals that successfully established residency were those with the smallest size-at-age, suggesting that faster relative growth under captive conditions does not translate into improved performance post-release. This pattern indicates individuals that perform comparatively poorly under captive conditions may be more able to adapt to natural environments. The impact of captivity on phenotypic traits has been highlighted as a concern for reintroduction programmes, including through different or relaxed selection, stress, artificial social environments, and a lack of appropriate learned responses to threats (Bell, 2016; Crates et al., 2023).

Studies on captive alligators found a strong negative relationship between levels of stress hormones and body mass (Elsey et al., 1990; Turton et al., 1997). Therefore, differences in size at release may reflect differences in chronic stress in captivity. Chronic stress in other species has been linked to higher dispersal rates and exploratory behaviour (Dickens et al., 2010; Korte et al., 2005). Alternatively, captivity may favour behavioural or physiological traits that are maladaptive in the wild due to differing selection pressures. Additional individual observations, such as a gharial released from captivity at 10.7 years old who was recaptured at adult-size and tracked using telemetry, did not breed over three years of monitoring, despite exceeding the size of other breeding females, suggest potential long-term effects of captivity on headstarted gharial(Griffith, 2022). These findings highlight

the importance of understanding and minimising the phenotypic costs of captivity as part of adaptive management in gharial headstarting programmes.

Headstarting as a tool for education and awareness

This study focused solely on the contribution of headstarting to population recovery in Chitwan, and we recognize that there are alternative conservation incentives for headstarting programmes, including education, awareness building, and improving understanding of gharial biology. Where the evidence suggests headstarting is not contributing to population recovery, but has separate conservation benefits, such programmes should investigate alternative options including short-term headstarting (holding gharial for months rather than years), limiting egg or hatchling collection to a much smaller number of gharial, and focusing on the headstarting of captive-bred gharial. Changes such as these will also result in greatly reduced costs for headstarting programmes, which can then be redistributed for other aspects of gharial conservation.

Management Recommendations

1. **Implement post-release monitoring using telemetry.** Post-release monitoring is essential for evaluating headstarting outcomes in gharial, and other species. Radio-telemetry provides a suitable methodology for this, providing informative data that cannot be obtained with population surveys alone, including indivudual fate, causes of moratality, dispersal trajectories, and residency establishment.

2. **In-situ threats should be removed if headstarting is to succeed.** The primary cause of gharial mortality in Chitwan is human-related killing, mainly illegal fisheries bycatch. Conservation programmes must first address root threats, like bycatch, to ensure effectiveness. Headstarting may inadvertently worsen bycatch issues by increasing gharial size at first entanglement.

3. **Release sites should be carefully selected to minimise downstream loss,** at least 60 km, ideally over 100 km, upstream of river barriers. In Chitwan, shifting the release site further upstream on the Rapti River could improve retention within the National Park. Similar dispersal challenges likely exist in other sites, including Bardiya, Corbett,

and Katerniaghat, and this should be investigated. Release sites should be on smaller tributaries rather than large rivers to limit downstream movement.

4. **Release season and social context require further investigation.** Early winter releases may provide longer acclimation periods for gharial before the first monsoon, to learn to acquire resources during a period where there is minimal physiological demand. This would also avoid releases during high river discharge seasons, when downstream movements appear more likely. Residency establishment patterns should be investigated, and their relationships to environmental and social factors.

5. **Bigger is not necessarily better, and longer time in captivity may be negative.** Age and size of gharial at release should be investigated for each system, without the assumption that 'bigger is better'**.** The phenotypic impacts of captivity on gharial should be investigated, including comparing pre-release condition to post-release survival and behaviour. Shorter times in captivity, in semi-natural conditions including learning behaviours such as catching live food, should be trialled.

6. **Retain educational benefits whilst reducing conservation costs.** Some headstarting facilities play important roles in public education and awareness of gharial conservation, including the GCBC in Chitwan. Alternative strategies to facilitate these benefits, whilst reducing the costs of such facilities could be implemented, for example, through **r**earing gharial for much shorter periods of time, rearing a much-reduced number of gharial, or shifting to have interpretation and education centres rather than rearing centres.

7. **Adopt adaptive management as a core framework.** Adaptive management is widely seen as one of the best available frameworks for structured decision making to underpin effective reintroduction management (Keith et al., 2011; Nichols & Armstrong, 2012), allowing managers to account for high levels of uncertainty (Gillson et al., 2019). We recommend gharial headstarting programmes adopt an adaptive management approach, using data on pre-release phenotypes and post-

680 release survival and behaviour to continually improve approaches (Crates et al.,
681 2023; McCarthy et al., 2012).
682

683 **Conclusion**

684 Headstarting programmes are predicated on the idea that raising individuals to
685 larger sizes increases their probability of surviving to become adults. Our results do not
686 provide support for this assumption in gharial, at least for the size range of the released
687 cohort studied here. Mortality of headstarted gharial remained high, even in size classes
688 that would be expected to have low natural mortality in wild populations, and survival was
689 not associated with body size or condition at release. Instead, smaller individuals were
690 more likely to establish residency in the target habitat. We therefore suggest that the
691 release of substantially smaller size classes should be investigated, alongside targeted
692 telemetry-based monitoring to evaluate post-release survival, dispersal, and behaviour.
693 Changes in release site and season that may reduce downstream dispersal should also be
694 explored within an adaptive management framework. We recommend that all headstarting
695 programmes operate in an adaptive management framework that is regularly re-evaluated
696 based on available evidence.
697 Our results suggest the principal barrier to successful population recovery in Chitwan
698 is ongoing anthropogenic mortality, in particular illegal fisheries bycatch. As with many
699 conservation translocations, reinforcing populations without adequately addressing the
700 original causes of population declines cannot achieve sustainable population recovery. In-
701 situ conservation efforts are therefore essential, and for gharial this should include habitat
702 protection, protection of nesting sites in situ, and working with fishing communities to
703 reduce bycatch.
704 More broadly, our study demonstrates the value of radio-telemetry for evaluating
705 headstarting outcomes and informing evidence-based management. We found no evidence
706 that longer periods in captivity, or larger release sizes, improved post-release survival or
707 behaviour, and our results suggest they may even be detrimental. These findings highlight
708 the importance of evaluating individual post-release outcomes and challenge conservation
709 practitioners to question, for each species and release context, the common assumption
710 that ‘bigger is better’. We encourage all headstarting programmes to undertake rigorous

evaluations of their effectiveness and to embed adaptive management and post-release monitoring as core components of programme design.

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