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ARTICLE

Unveiling anti-predator responses of river lapwing, *Vanellus duvaucelii* (Lesson, 1826)

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Abstract

Anti-predator responses are not well explored in river lapwings; hence, in this investigation, we identified and quantified different anti-predator responses. The focal sampling method was used to estimate anti-predator responses. Crows and dogs were recognised as the most potential and abundant predators of river lapwings. However, kites, snakes, cows/buffaloes and foxes were identified as other predators. The vigilance rate was comparatively lower in larger flocks and at greater distances from predators. We documented that the river lapwing exhibited camouflage response (eggs and chick crypsis) to avoid nest predators. In a nutshell, alarm calls, mobbing, crouch run and swooping attack were the predominant anti-predator responses, whereas pecking attack and ungulate display were the least recorded anti-predator responses. Generalised linear mixed model (GLMM) analysis indicated that the river lapwing elicited more significant anti-predator responses at incubation as lapwings exhibited more investments in defending large-egg nests or clutches nearing hatch. Ground and perched predators were more responsive to predators due to the close proximity of nests; hence, river lapwings had to respond very quickly to these predators. The anti-predator responses of lapwings showed considerable individual variation, influenced by a combination of intrinsic (age and boldness) and extrinsic factors (predator type and nest visibility). River lapwings elicited maximum anti-predator responses against crows, dogs and herbivore (cows/buffaloes) predators. We conclude that river lapwings may demonstrate discrepancies in anti-predator defence, which may be consistent with numerous ideas drawn from the parental investment theory.

Keywords Alarm call · Camouflage response · Crow · Nest predation · Vigilance rate

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Introduction

The river lapwing, *Vanellus duvaucelii* (Lesson 1826) as the name implies, is mainly restricted to wide sandy riverbanks and islands (Ali and Ripley 1980; Duckworth et al. 1998; Mishra et al. 2021). Usually, they exhibit a clump distribution pattern (Mishra et al. 2018). As with most waders, they deposit three to four eggs during the breeding season, which runs from March to June (Ali 2002; Kumar et al. 2022). River lapwings have been placed on the worldwide near-threatened list due to threats and global population decreases (IUCN 2005). The population status of river lapwing is comparatively unwavering in the Gangetic landscape (Mishra et al. 2018). To elude predators, they build an open scrape nest in the ground that blends in with the surroundings (Baines 1990; Mishra et al. 2020; Kumar et al. 2022).

Breeding wader populations are decreasing due to habitat loss and ruin driven by agricultural practices including drainage and intensive grassland management (Shrubb 1990;

Wilson et al. 2004). Increased nest predation has been suggested as another potential contributing factor to the decline in wader populations (Chamberlain and Crick 2003; Claassen 2004; Milsom 2005). Predators of ground-nesting birds use a variety of cues to locate nests, including visual, olfactory and acoustic signals. However, we have little understanding of the exact mechanism of how predators find nests (Ibanez-Alamo et al. 2015). Farming exacerbation is perhaps associated with greater rates of predation on wader nests since uniform swards may reduce nest crypsis and taller swards may blight anti-predator vigilance (Whittingham and Evans 2004). Furthermore, owing to decreased population size, smaller breeding groups might not have as much armour against predators to defend their nests.

Since eggs are typically not a major part of a predator's diet, relationships between nest predators and prey are fascinating from an ecological perspective (Ibanez Alamo et al. 2015). Nest predation is the primary cause of nest failure; however, it can occur unintentionally during other foraging behaviours (Vickery et al. 1992). Predators can continue to provide pressure to prey nesting populations even when the number of nests does not determine the predator density (Angelstam 1986).

Avian and mammalian predators are the foremost threats to nests in riverine birds (Claassen 2004). The nests are also vanished due to flooding and hydropower dam releases (Claassen 2004; Claassen et al. 2017). In addition, locals' exploitation of this species through egg collection has put it in danger (Claassen et al. 2018). In addition, nests were also found to be disrupted owing to domestic animals and human disturbance (Claassen et al. 2017).

Natural selection on prey species is largely driven by predation, which has led to adaptations including anti-predator vocal signals that can warn off predators and encourage coordinated attacks (James et al. 2023). When the incubating parent detects an approaching predator, it must quickly decide how to react (Brynychova 2024). Generally, birds perform a variety of anti-predator behaviours that improve their chances of having a successful breeding season (Core 2005). The most frequent behaviours are nesting near species that act as protectors (Lima and Dill 1990), curtailing the number of eggs under augmented risk of nest predation (Eggers et al. 2006), altering their risk sensitivity in response to risk and re-nesting options (Schneider and Griesser 2015) and vigorously defending their nests through mobbing (Lima and Dill 1990; Core 2005).

Being ground-nesting waders, river lapwings fiercely battle predators that approach their nest sites in order to defend their nests. Since many predators can reach the nest of ground-nesting birds, parental defence behaviour such as chasing or enticing predators away from the nest is frequently essential to the nest's survival (Gochfeld 1984). Waders have developed several anti-predation strategies such as cryptic eggs and plumage, hiding nests in vegetation and using distraction displays to avoid predation (Hancock et al. 2023). Lapwings are well known for their range of anti-predator responses when reproducing in groups (Cramp and Simmons 1983). These responses embrace diving and striking at avian egg predators such as carrion crows, *Corvus corone*. They also generate a customised alarm call to notify about the type of predator and risk alert (Griesser 2008).

Furthermore, egg and nest crypsis is the central anti-predator nest defence mechanism used by many waders that nest on the ground (Lima and Dill 1990). An effective defence tactic against predators who hunt by sight is visual crypsis, which can significantly increase egg survival (Colwell et al. 2011; Skrade and Dinsmore 2013; Smith and Edwards 2018). Visual cues are often censorious during the day, with predators such as corvids depending on sight to detect the movement of adult birds or the presence of eggs and chicks in exposed areas (Santisteban et al. 2002). In addition, acoustic cues are also expected to be significant, especially at night; nevertheless, they have received only little attention with a focus on the sounds of chicks around hatching and during brooding (Kostoglou et al. 2020).

Anti-predator responses are still to be identified as well as quantified in river lapwings. Hence, the present field study was designed to estimate various anti-predator responses of river lapwings against different predators. Specifically, we investigated anti-predator response in relation to (1) stages of reproductive cycle, (2) predator location and (3) predator type. Such knowledge can help clarify the adaptive tactics used by river lapwings to improve their chances of surviving and reproducing in a variety of ecological settings. In this regard, we hypothesised that river lapwing would elicit different anti-predator responses against various predators particularly in the breeding season.

Methodology

Study area

We carried out multiple field surveys from March 2020 to July 2022 in the Gangetic landscape of district Raebareli (25° 49 and 26° 36 north latitude and 80° 41′ and 81° 34′ east longitude), Uttar Pradesh, India (Fig. 1). The average annual rainfall and temperature is about 1150 mm and 26 ℃ respectively in the district Raebareli. Several migratory birds may use the River Ganges as a wintering and staging area, while resident birds may use it as a nesting ground (Mishra et al. 2016). Moreover, 19 species of waders were recorded and identified (Mishra et al. 2016). River lapwing (*Vanellus duvaucelii*), Asian open bill (*Anastomus oscitans*), Cattle egret (*Ardea ibis*), Red-wattled lapwing (*Vanellus indicus*) and Common sandpiper (*Actitis hypoleucos*) were the most

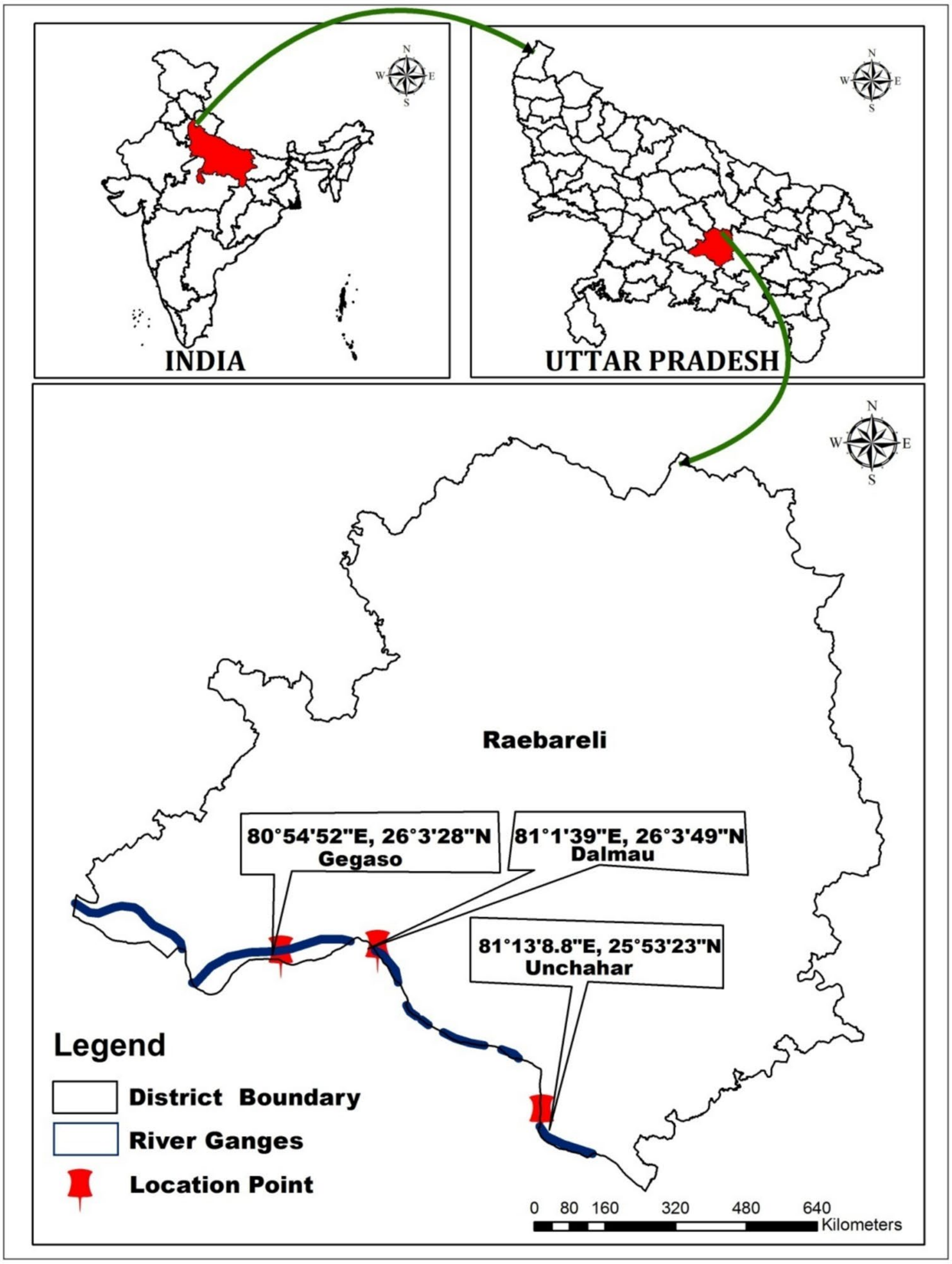

Fig. 1 GIS map of study area where anti-predator responses of river lapwing were recorded

common resident species, while European white stork (*Ciconia ciconia*) and White necked stork (*Ciconia episcopus*) were the most common migratory species along the Ganges' banks in Raebareli district (Mishra et al. 2016, Kumar et al. 2017). Due to frequent sighting and easy accessibility, we have selected these study sites for the estimation of anti-predator responses against various predators in river lapwings. River lapwings found their habitat on sandbars and fluvial islands with sparse to moderate amounts of vegetation and seasonal emergent plants. Hence, we took into account four different types of habitats: (1) open unvegetated river bank (OURB), (2) open unvegetated island (OURI), (3) vegetated river bank (VRB) and (4) crop fields (CF).

Focal observations

At first, systematic observations of the nesting area of river lapwing have been made to identify different predators of river lapwing. Based on our observations and literature cited (Claassen et al. 2018; Mishra et al. 2020), we identified potential predators of eggs and chicks in river lapwing. Line transect method was employed to assess abundance (number of individuals) of various predators in the study area (Burnham et al. 1980). 60 transects (500 m each) were selected covering an area of 30 km in length. The distance between the two transects was approximately 50 m in each study site. We estimated abundance (mean ± SE) of each predator encountered along the fixed line of the transect.

We recorded vigilance rate (scanning/minutes) in response to various sizes of flocks of river lapwing and distance from predators. In addition, the employment of camouflage as a defence against an approaching nest predator was examined in this study. We identified 15–20 pairs of river lapwings for detailed examination based on observability and accessibility. Sampling was shifted among these pairs with the intention that all were sampled approximately equally often at all times of the day. Focal sampling method was used to collect data on vigilance rate and anti-predator response (Altmann 1974). One or two pairs of lapwings were used as subjects in the samples. Samples collected in the study area were measured in 15-min observation sessions. Birds held territories long before and after breeding, so that responses of non-breeding territorial birds, as well as breeding birds, could be sampled.

During the entire field study, 2088 focal observations (18 focal observations/day, 72 focal observations/month) were taken into account. Data collection consisted of 116 days (4 days/month, 48 days/year). Mean frequencies of vigilance rate and anti-predator responses were recorded monthly, and subsequently all data were pooled together.

Focal samplings were conducted during peak activity period—early morning (6:00–9:00 AM) and late afternoon (3:00–6:00 PM). Foraging behaviour appears to be bimodal, with morning and evening types for both seasons and habitat types in river lapwings (Prateek et al. 2024a). These time windows were chosen as they correspond to increased feeding activity, with mornings offering optimal foraging conditions and evenings providing a final opportunity for lapwings to gather energy before nightfall. We observed the responses of the focal birds whenever a potential predator entered the study site. The vocabulary used by Gochfeld (1984) was utilised to categorise the observed reactions.

During the field investigation, two observers were involved to record the responses from two directions since this minimises the chances of missing the individuals being observed. However, if the individuals being observed were disturbed and flew away, or if the observer lost track of the target birds, we ended the observation process for those specific river lapwings. All the data collected from the two observers were pooled together for further analysis and interpretation. Binoculars (Olympus-10 × 50 DPS) were used to identify predators. Anti-predator reactions were captured using a Nikon Coolpix P900 digital camera with an 83 optical zoom lens and subsequently translated into field forms.

Statistical analysis

The Kolmogorov–Smirnov and Levene tests were used to assess the data's homogeneity and normality. When the data were found to be normally distributed, then the analysis of variance (one-way ANOVA) followed by Tukey's post hoc test was applied to examine the number of different predators encountered and the vigilance rate. ANOVA (Tukey's test) was used to determine the frequency of different anti-predator responses. Generalised linear mixed model (GLMM) was performed using the GLIMMIX macro of the SAS® (v. 8·2) statistical package (Littell et al. 1996), with Poisson distribution and logarithmic link function to examine variation in anti-predator response of river lapwing. GLMM was employed with both fixed and random effects, using Maximum Likelihood (ML) estimation. In this model, anti-predator response was considered as response variable which represents the duration during which any anti-predator behaviour was observed, hence taken as continuous variable. Reproductive stages, predator locations and predator types were fixed effects (predictors), while pair ID was a random effect. Significance testing of fixed effects was derived from Wald z, examining the *p* value associated with each term, when included in the null model containing only significant term. The significance of the random effect was determined based on its estimated variance. The statistical software SPSS (version 16.4) was used to complete statistical studies. Furthermore, the statistical analysis employed a significance level (α) of 0.05.

Results

In this field study, snakes (Indian rock python, *Python molurus* and Indian rat snake, *Ptyas mucosa*), crows (House crow, *Corvus splendens splendens* and the Jungle crow, *Corvus macrorhynchos*), kites (Black kite, *Milvus migrans*), foxes (*Vulpes bengalensis)* and dogs (*Canis lupus familiaris*) were identified as potential predators to river lapwing. Crows (32.68 ± 5.69) and dogs (24.75 ± 3.72) were significantly ($F = 52.87$, df = 5, $p = 0.01$) highest, whereas kites (4.85 ± 1.98) and foxes (6.88 ± 2.38) were significantly lowest ($F = 43.58$, df = 5, $p = 0.05$) in number (Fig. 2). We estimated vigilance rate (scanning/minutes) with reference to flock size of river lapwing (Fig. 3). In this field investigation, vigilance rate was decreasing with the increasing flock size ($F = 48.26$, df = 3, $p = 0.02$). Similarly, it was significantly ($F = 29.57$, df = 5, $p = 0.04$) decreasing with the distance from predators increasing (Fig. 4).

We observed that river lapwing laid their eggs in a ground scrape nest. Eggs of river lapwings are olive in colour, brown with black specks or lines (Fig. 5a). This colour

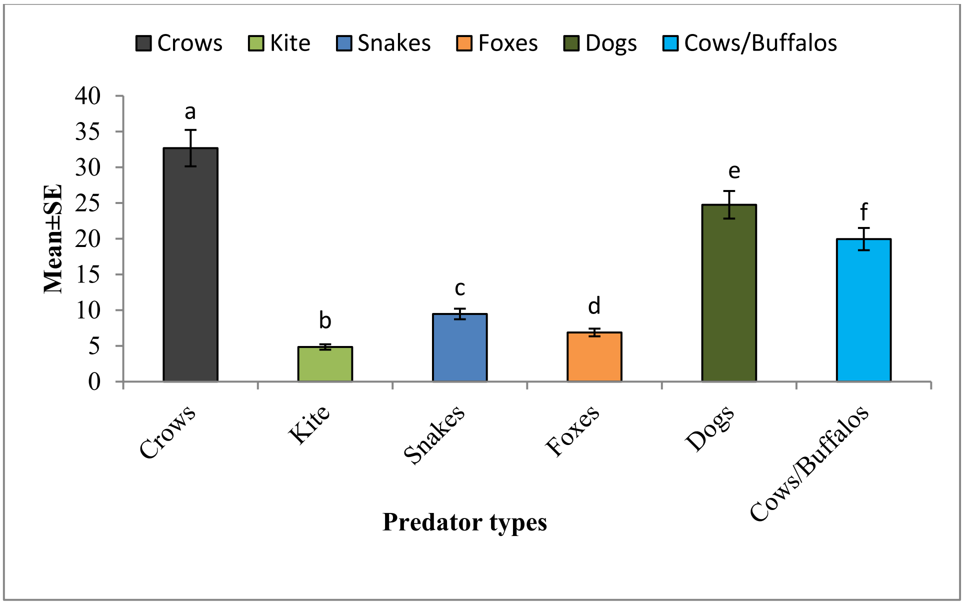

Fig. 2 Number of predators (mean ± SE) encountered during the field study. The locations marked with different small letters (**a**–**f**) are significantly different according to Tukey's test at $p < 0.05$ from each other

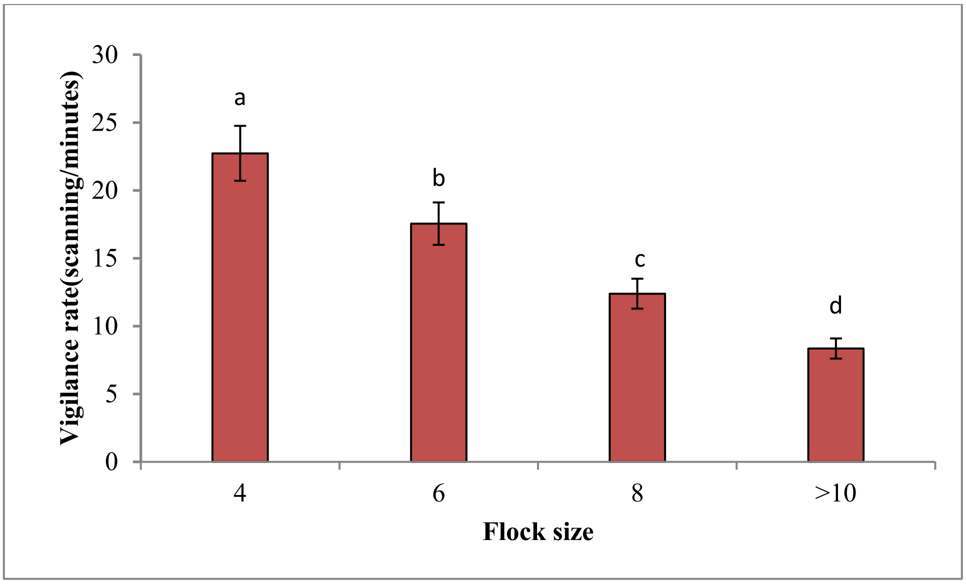

Fig. 3 Relationship between vigilance rate (scanning/minutes) in response to various sizes of flocks of river lapwing. The locations marked with different small letters (**a**–**d**) are significantly different according to Tukey's test at $p < 0.05$ from each other

pattern provided efficient masking pattern towards the predators. We further documented that the colour pattern of chicks appeared to be analogous with the nearby vegetation cover and sand as well (Fig. 5b). In a nutshell, we identified three distinct anti-predator responses, mainly alarm call, distraction display and aggression. Furthermore, these anti-predator responses were classified into eight distinct categories (Table 1). Representative images of anti-predator responses were enshrined (Fig. 6). All the anti-predator responses were estimated in three dimensions (reproductive stages, predator locations and predator types) simultaneously (Table 1). In this field investigation, results of ANOVA followed by Tukey's post hoc test exhibited that alarm calls, mobbing, crouch run and swooping attack were significantly predominant ($F = 42.85$, df = 8, $p = 0.01$) anti-predator responses (Table 1). Pecking attack and ungulate display were significantly lowest ($F = 11.53$, df = 8, $p = 0.05$) anti-predator responses (Table 1). Pecking attack and ungulate display were only recorded when river lapwing encountered reptilian (snakes) and mammalian (cows/buffaloes) predators, respectively (Table 1).

Results of GLMM analysis manifested that reproductive stage significantly affects the anti-predator response. Incubation showed increased ($p < 0.01$) anti-predation response, while tending young revealed somewhat reduced response (Table 2). Predator location and type both strongly influenced the anti-predation response, with ground predators ($p < 0.01$) and certain predator types such

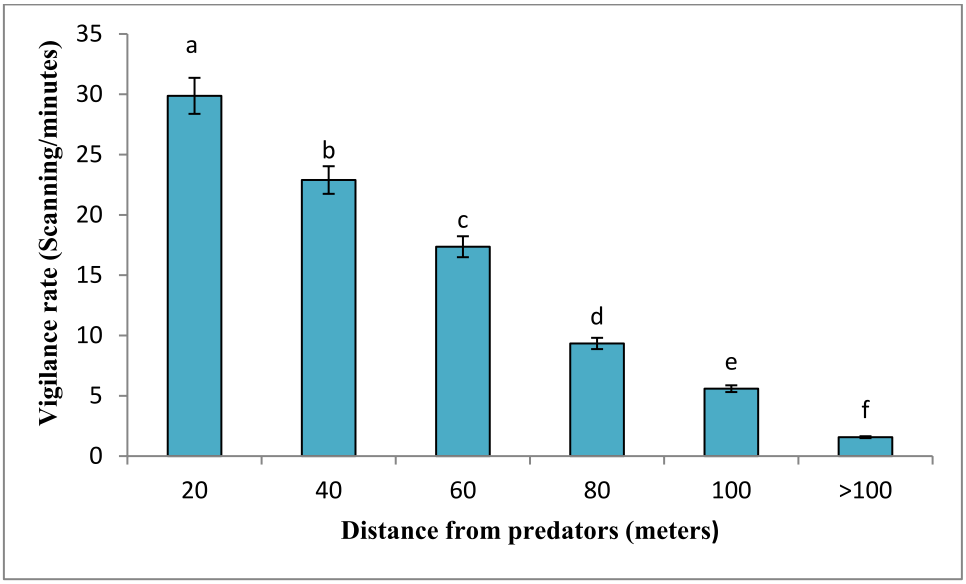

Fig. 4 Vigilance rate (scanning/minutes) in response to distance from predators. The locations marked with different small letters (**a**–**f**) are significantly different according to Tukey's test at $p < 0.05$ from each other

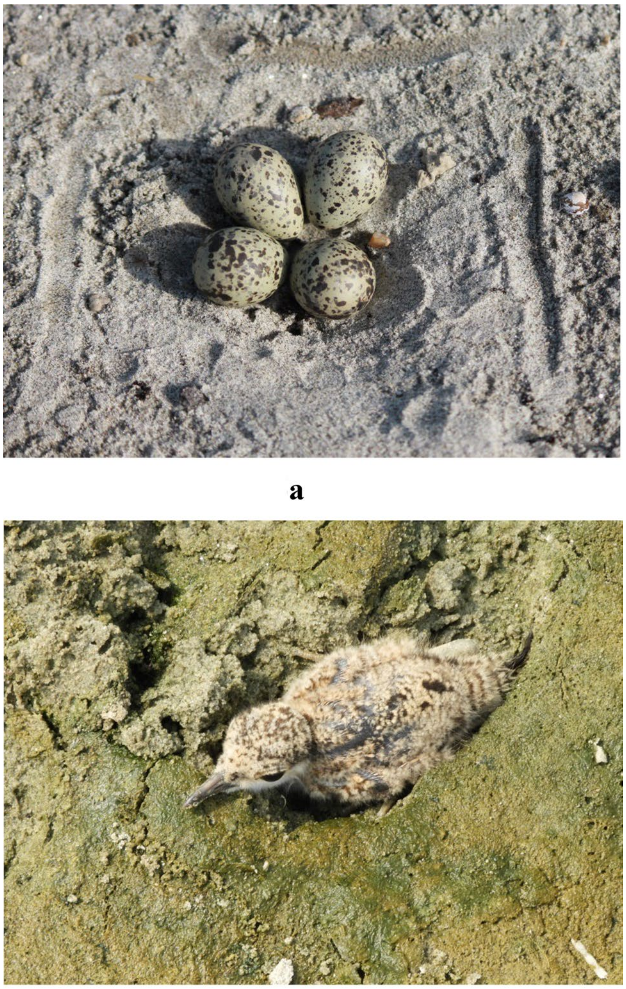

Fig. 5 **a**, **b** Photographic record of eggs and chicks of river lapwing showing camouflage as a defence against an approaching predator

as crows ($p < 0.01$), dogs ($p = 0.02$) and cows/buffaloes ($p = 0.03$) eliciting strong positive responses (Table 2). The model estimated a variance of 4.56 (SD = 2.14) for pair ID, indicating considerable individual-level variability in anti-predator responses (Table 2).

Discussion

We encountered crows and dogs as most potential and abundant predators in both the reproductive stages (incubation and tending small young). The similar pattern of nest predation was documented in previous studies (Claassen 2004; Sethi et al. 2011; Mishra and Kumar 2022; Elas and Witkowska 2024; Prateek and Kumar 2025).Crows and dogs usually predate eggs by consuming it or accidental crushing (Mishra et al. 2020). Furthermore, vultures, snakes, cows/buffaloes and foxes appeared as other plentiful predators at the nests of river lapwing. Comparable outcomes have been documented for the two lapwing species, *Vanellus indicus* and *Vanellus vanellus* (Seymour et al. 2003; Mishra and Kumar 2022). Nonetheless, herbivore predators (buffalo and cows) were more common, which could crush eggs or small young (Walters 1990).

Predator avoidance is a crucial habit in most animals, with clear repercussions for their fitness (Bar-Ziv et al. 2023). Beyond the consumptive (direct predation) effect, remaining alert to threats and the potential need to escape takes time and energy away from other activities (Krebs et al. 1983), highlighting the trade-offs that animals must make when selecting a predator avoidance strategy (Wirsing et al. 2021). Our results indicated that vigilance rate was decreasing with the flock size increasing. A similar study was done in southern lapwing, *Vanellus chilensis* (Maruyama et al.

Table 1 Anti-predator response (mean ± SE) of river lapwing to different potential predators

Stage of reproductive cycle	Predator location	Predator type	Frequency of response								
			No response	Alarm call	Mobbing	Crouch run	Pecking attack	Swooping attack	Ungulate display	False brooding	Injury feigning
Incubation	Flying high	Crows	0	4.23 ± 1.98	1.21 ± 0.36	0	0	0	0	0	0
		Vultures	2.08 ± 0.12	3.64 ± 1.37	0.73 ± 0.19	0	0	0	0	0	0
	Flying low	Crows	3.13 ± 1.15	8.16 ± 3.05	3.84 ± 1.23	9.28 ± 2.47	0	9.39 ± 3.36	0	9.79 ± 3.58	7.69 ± 3.08
		Kites	1.12 ± 0.06	5.92 ± 2.34	2.11 ± 1.82	3.77 ± 2.14	0	5.12 ± 2.69	0	5.97 ± 2.12	6.11 ± 2.87
	Ground, perched	Crows	0	27.21 ± 5.88	23.93 ± 4.81	28.46 ± 8.79	0	15.59 ± 4.95	0	17.42 ± 5.96	12.38 ± 4.28
		Kites	0	20.97 ± 4.21	18.85 ± 6.21	13.88 ± 4.12	0	12.32 ± 3.94	0	11.85 ± 3.51	5.92 ± 2.15
		Snakes	1.05 ± 0.63	9.15 ± 2.89	9.68 ± 2.47	7.06 ± 2.03	31.73 ± 3.51	9.05 ± 4.11	0	0	0
		Foxes	4.96 ± 1.85	7.06 ± 1.92	5.33 ± 1.93	9.33 ± 2.37	0	8.13 ± 3.93	0	3.12 ± 1.16	6.29 ± 2.94
		Dogs	2.28 ± 0.16	21.91 ± 4.77	21.75 ± 3.45	23.16 ± 7.26	0	13.96 ± 5.07	0	14.69 ± 4.77	10.84 ± 3.91
		Cows/buffalos	1.72 ± 1.12	15.16 ± 3.75	19.89 ± 4.19	15.92 ± 5.34	0	12.95 ± 3.84	39.94 ± 4.51	1.96 ± 0.95	2.37 ± 1.36
Tending small young	Flying high	Crows	0	3.08 ± 1.17	1.15 ± 0.35	0	0	0	0	0	0
		Kites	0	2.13 ± 1.13	1.04 ± 0.11	0	0	0	0	0	0
	Flying low	Crows	4.29 ± 2.05	7.32 ± 2.03	8.96 ± 1.78	5.56 ± 2.12	0	16.09 ± 4.41	0	1.16 ± 0.18	2.43 ± 1.05
		Kite	1.11 ± 0.09	4.16 ± 2.01	5.14 ± 1.15	2.29 ± 1.95	0	9.36 ± 3.01	0	1.82 ± 1.03	1.21 ± 0.62
	Ground, perched	Crows	1.84 ± 1.11	14.55 ± 4.96	34.47 ± 4.27	18.15 ± 3.35	0	25.27 ± 6.11	0	11.36 ± 4.75	3.91 ± 1.83
		Kites	2.03 ± 0.98	12.32 ± 5.11	27.25 ± 4.38	10.84 ± 3.95	0	17.55 ± 5.17	0	5.73 ± 2.17	1.12 ± 0.07
		Snakes	3.45 ± 1.01	5.11 ± 2.25	19.96 ± 2.15	5.93 ± 2.08	14.19 ± 26	17.85 ± 5.51	0	0	0
		Foxes	3.06 ± 1.17	4.08 ± 2.11	10.43 ± 3.95	7.77 ± 3.32	0	18.26 ± 4.04	0	1.15 ± 0.64	1.78 ± 0.53
		Dogs	0	17.26 ± 6.87	39.72 ± 8.26	19.34 ± 12.27	0	29.04 ± 11.47	0	6.47 ± 2.88	4.18 ± 1.97
		Cows/buffalos	0	11.95 ±	27.19 ±	20.17 ±	0	20.68 ± 37	17.38 ± 2.96	0.37 ± 0.12	1.25 ± 0.53

Crouch run **False brooding**

Injury feigning **Ungulate display**

Swooping attack

Fig. 6 Representative images of different anti-predator responses in river lapwing identified during field study

2010; Prateek et al. 2024a, 2024b). The size of flock and its relation to vigilance behaviour is well documented in birds (Lima 1995; Roberts 1996). There are two theories that have been put out to explain this inverse relationship: as a group grows, more eyes are looking for predators, according to the "many eyes hypothesis" (Lima 1995). As a result, an individual can spend less time scanning without lowering the group's overall vigilance. According to Roberts (Roberts 1996) "predation risk hypothesis," when a group grows in size, the individual danger of predation decreases,

Table 2 Generalised linear mixed model (GLMM) explaining various factors affecting anti-predator responses in river lapwing

Predictor	Level	Estimate	SE	Wald z	*p* value
Fixed effects					
Intercept		1.254	0.342	3.67	< 0.01
Reproductive stages	Incubation	0.823	± 0.131	6.28	< 0.01
	Tending small young	− 0.427	± 0.124	− 3.44	0.03
Predator locations	Flying high	− 0.053	± 0.031	− 1.71	0.07
	Flying low	0.187	± 0.059	3.16	0.02
	Ground, perched	0.753	± 0.121	6.22	< 0.01
Predator types	Crows	0.912	± 0.092	9.91	< 0.01
	Kites	− 0.396	± 0.211	− 1.87	0.08
	Snakes	0.417	± 0.149	2.79	0.04
	Foxes	− 0.238	± 0.076	− 3.13	0.03
	Dogs	0.768	± 0.086	8.93	0.02
	Cows/buffalos	0.506	± 0.068	7.44	0.03
Random effects					
Grouping factor		Variance	SD		
Pair ID		4.56	2.14		

The model included fixed effects such as reproductive stage, predator location and predator type and random effects for pair ID to account for individual variation

so vigilance should decrease as well. Similarly, vigilance rate was also decreasing as the distance from the predators increasing. In this investigation, river lapwings appear to be extremely alert birds. When the stimulus animal was well over a hundred metres away from the river lapwings, responses to those potential predators that elicited responses usually started. This field study is consistent with the previous investigation on three species of lapwings (Walters 1990).

Evidence suggested that offspring producing ability and guarding those until independence are critical aspects that usually determine how successful their reproductive attempts are (Larsen et al. 1996). As a result, river lapwings must respond accurately to predators that pose a threat to themselves, their offspring, or both. The right course of action relies on the kind of predator and the circumstances surrounding the prey–predator encounter (Walters 1990). Many encounters began with cautious posturing and calling in response to a potential predator, but many evolved into more dramatic behaviours.

River lapwing displayed camouflage response to avoid nest predators. This study is consistent with previous studies in northern lapwing and the little ringed plover (Salek and Cepakova 2006). To blend in with their surroundings and remain undiscovered, camouflage frequently entails matching the visual appearance of the background (Jagati et al. 2023). Egg crypsis is a common response of open-nesting waders to an approaching visually orientated nest predator (Salek and Cepakova 2006). According to Skrade and Dinsmore (2013), the less the contrast between egg colour and nest environment, the higher the camouflage and consequently egg survival chances are. In addition, the colour pattern of river lapwing chicks frequently blends with sand and plants. Many ground-nesting birds display plumage, colours and markings to mix with their surroundings (Gupta et al. 2002).

Furthermore, while their partners guarding the nests are ready to attack any intruders, lapwings can incubate more closely (Sasvari and Hegyi 2000). The parent may reveal the clutch to the predator by pointing out its location while it is still at the nest (Cresswell 1997; Roper and Goldstein 1997; Muchai and du Plessis 2005). However, when the birds return to the nest, it becomes evident how crucial it is for the lapwing parents to disguise the location of the nest. They generally land a few tens of metres away from the nest. They either head straight for the nest or circle it as soon as they land (Cramp 1990).

We identified three distinct anti-predator responses: primarily alarm call, distraction display and aggression, and these anti-predator responses were classified into nine distinct categories. During the investigation, we also observed that river lapwing elicited a non-aggressive response. The parent may either skulk away from the nest or take flight and fly away from it as part of this non-aggressive reaction. In a nutshell, alarm calls, mobbing, crouch run and swooping attack were the predominant anti-predator responses, while pecking attack and ungulate display were the least recorded anti-predator responses.

In this study, river lapwing elicited alarm calls of various grades to eliminate predators from the breeding grounds. This study is coincident with previous investigations (Elliot 1985; Mishra et al. 2020; James et al. 2023). Among the most investigated anti-predator adaptations are alarm calls or vocalisations (Hollen and Radford 2009; Garcia and Favaro 2017). To alert others to the presence of a predator, lapwing species use alarm calls (Magrath et al. 2015). In addition, individuals can respond by increasing alertness (Griesser 2008), leaving the area (Forsman and Monkkonen 2001), or actively engaging the predator (Krams and Krama 2002). In addition, this alarm call escalated into one that drew specific attention and sparked a mobbing reaction. It attracted both territorial and non-territorial vagrants. It was also suggested that once the threats had disappeared, the residents abruptly impelled the attracted birds out of their area (Walters 1990).

River lapwing displayed mobbing response against predators. This study coincided with preceding research in red-wattled lapwing and northern lapwing (Elliot 1985; Mishra et al. 2020). It has been proposed that lapwings employed group mobbing to reduce nest predators like crows (Elliot 1985). One of the aggressive anti-predatory responses is mobbing in which members of prey species aggregate around a predator and collectively attack it to protect their progeny (Pawlak et al. 2019). Generally, mobbing is used by birds to recruit particular mates for the attack (Kalb and Randler 2019). The mobbing response, in which birds attack predators directly, was assumed to be a costly behaviour in terms of time and energy expenditure (Caro 2005). It may efficiently thwart predators from entering the nesting regions, ensuring increased offspring survival (Kontiainen et al. 2009).

In this field investigation, river lapwing displayed injury feigning as a sort of displacement response to avoid predators in the nesting area. The similar results were registered in previous studies (Walters 1990; Ristau 2013). Lapwings exhibit distraction activities including injury feigning, crouch run and false brooding (Gupta et al. 2002). River lapwings frequently displayed early, stealthy departure by quietly running from the nest in a crouched position. Both the wings are spread out and the head is down, while crouch run is performed to eliminate potential predators from the nesting ground. This investigation is coincided with previous studies (Brown 1962; Elliot 1985; Takahashi and Ohkawara 2007).

We registered mainly two kinds of attack (swooping and pecking attack) in river lapwing. Swooping attacks are employed to deter avian predators. They swoop quickly close to the predator, astonishing it and sometimes even hitting it (Buitron 1983). During nest or chick defence, swooping attacks on predators have also been reported in lapwing (Brown 1962) and banded plover (Smith 1966). In this study, another type of attack was reported as pecking attack, which was restricted to interactions with reptiles. It was the least estimated anti-predator response in river lapwings. Occasionally, a reptile alarm call would be heard, followed by a pecking attack. The noise caused the chicks to quickly relocate away from the source and stay upright and vigilant (Walters 1990).

Ungulate display was recorded when river lapwings appeared to eliminate herbivore predators (cows/buffaloes) from the active nests. In this process, the bird raises its wings up over its back, showing the brightly coloured underwings, while standing in an almost squat stance with its head kept low (Gupta et al. 2002). Furthermore, injury feigning (broken wing display), a kind of distraction display, was documented to disguise different predators of eggs and chicks of river lapwing. Distraction displays are fairly prevalent in birds, in which they try to draw the attention of predators by performing embellished activities such as standing stationary, hampered combat, and injury feigning to shield their nests, eggs, or young ones (Humphreys and Ruxton 2020).

False brooding is recorded as a kind of displacement type anti-predator response in river lapwing to deceive the predators. It has also been described as a nest defence tactic for double-banded plover (Bomford 1986) and red-capped plover (Davis and Recher 2000). False brooding is a method in which a bird perches far away from its nest and imitates incubation. In addition, they move away from the claimed nest site and bow down to appear as though they are sitting at a fake nest, which encourages the predator to follow it closely before running away (Gupta et al. 2002).

In this study, river lapwing elicited more significant anti-predator responses at incubation period as compared to tending small young (chick) since lapwings exhibited more investments in defending large-egg nests or clutches nearing hatch (Andersson et al. 1980; Montgomerie and Weatherhead 1988) and the survival scenario of lapwing chicks reduces over the breeding season (Galbraith 1988; Thompson et al. 1994). Furthermore, ground and perched predators were more responsive to predators. This observation coincides with previous study (Walters 1990). Distance to vantage point and habitat edge may be predicted to correspond to daily predation rate, as predators take advantage of these factors (Sheldon et al. 2007; MacDonald and Bolton 2008). It was anticipated that predators were more inclined to forage around the borders of fields or other linear features of habitats (Seymour et al. 2003). Since ground and perched predators were frequently sighted in close proximity to nests and might easily gain access to incubating nests as well as chicks of river lapwings, they had to respond very quickly to these predators.

Our results exhibited significant individual-level variation in anti-predator responses, as indicated by the random effect of pair ID. This recommended that individual differences account for a meaningful portion of the variability in the observed behaviour, beyond what is explained by the fixed effects. These findings indicated that certain individuals consistently exhibited stronger or weaker anti-predator responses, regardless of reproductive stage, predator location and predator type. Such consistent behavioural differences among individuals are evocative of animal personality traits or behavioural syndromes, which are increasingly accredited as ecologically and evolutionarily important (Sih et al. 2004; Reale et al. 2007).

These patterns may arise from differences in age, sex, prior experience with predators, physiological condition, or inherent boldness (Magnhagen and Borcherding 2008). Essentially, this variation can persuade fitness outcomes, especially in high-risk environments, and may shape how populations adapt to changing predator regimes (Khater et al. 2016). A more sophisticated knowledge of how animals balance risk and reproductive trade-offs in intricate ecological environments is made possible by incorporating individual variation into behavioural research (Dall et al. 2004; Wolf et al. 2007).

Furthermore, crows, dogs and cows/buffaloes elicited maximum anti-predator responses since they appeared as the most prominent predators of river lapwings. The similar pattern was documented in few species of waders (Walters 1990; Mishra and Kumar 2022). Crows and dogs responded to predators primarily by alarm calls, mobbing, crouch run and swooping attack. False brooding and injury feigning were relatively less frequently elicited anti-predator responses. Cows/buffalo predominantly responded to predators by ungulate display. Other anti-predator responses (alarm call, mobbing, crouch run, swooping attack, false brooding and injury feigning) were also elicited to eliminate herbivore predators from the active nests of river lapwing. In addition, river lapwings responded to snakes only by pecking attack.

Conclusions

Predation is the leading cause of reproductive failure in the majority of bird species; hence, they engage in various forms of anti-predator behaviour to improve the chance of successful breeding. In this study, snakes, crows, kites, foxes and dogs were identified as predators to river lapwing. However, crows and dogs were registered as the most potential and abundant predators in both the reproductive stages (incubation and tending small young). We conclude that vigilance and camouflage response were the first line of defence to avoid nest predators in river lapwing. Furthermore, we observed three distinct anti-predator responses including alarm call, distraction display and aggression which were further classified into nine distinct categories. In a nutshell, the most common anti-predator responses were alarm calls, mobbing, crouch run and swooping attack, with pecking attack and ungulate display being the least common.

This study highlights that River lapwings reconcile their anti-predator behaviour based on reproductive stages, predator locations and types. Stronger responses during incubation suggest higher parental investment when the risk to eggs is greatest. Ground and perched predators elicited the strongest responses likely due to their close proximity to nests and ease of accessing both eggs and chicks. The anti-predator response of lapwings is not uniform but varies significantly across individuals due to a combination of internal (e.g. age and boldness) and external factors (e.g. predator type and nest visibility). Understanding this variation is essential for accurate behavioural ecological interpretations and for conservation strategies, especially in human-altered landscapes where predation pressures can change rapidly.

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Declarations

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