Original Research Article

How does human disturbance affect brood parasitism and nest predation in hosts inhabiting a highly fragmented landscape?

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ABSTRACT

Human disturbance represents a considerable challenge for the conservation of living organisms and has profound negative impacts globally. There is substantial variation in how species respond to human disturbance. The main aim of the present study is to examine how human activities influence the risk of brood parasitism and nest predation for three passerine species living in a highly fragmented landscape in Central Bangladesh. We use data collected from 518 nests over nine breeding seasons for three host species of the Asian koel (*Eudynamys scolopaceus*), a non-evicting brood parasite: i) long-tailed shrike (*Lanius schach*), ii) common myna (*Acridotheres tristis*) and iii) house crow (*Corvus splendens*). Two sources of disturbance were considered: i) houses and buildings inside the study area, the Jahangirnagar University campus and ii) the highly urbanized area outside the campus boundary. Additionally, we regarded iii) nest height, iv) number of days after egg laying until discovery (time unmonitored), v) distance to nearest fruit tree and vi) distance to nearest conspecific neighbor, as important habitat and nest characteristics. We found significantly lower predation risk with increasing time unmonitored in all three host species, thus more regular nest checks by fieldworkers lead to more predation. Moreover, we found that the distance to nearest fruit tree was the most important factor for the risk of parasitism. Although we could not find any significant impacts of distance to boundary or buildings on either predation or parasitism risk, we found a trend both in common myna and house crow that nesting success was higher closer to the boundary. Ultimately, increased monitoring time had the most consistent negative impact on nesting success among the host species. This study highlights the effect of disturbance caused by nest monitoring, exceeding the impact of permanent structures in an around the university campus i.e. boundary and buildings.

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1. Introduction

The continuously increasing human population reduces natural habitats and converts them to fragmented landscapes. Habitat fragmentation divides one continuous landscape into many small fragments, depending on the structure of the dominant landscape (Lienert, 2004; Saunders et al., 1991). Fragmentation is a distinctive feature of most human dominated habitats and it increases the amount of edge habitats (Cavitt and Martin, 2002; Stephens et al., 2003). Habitat edges change species richness, community structure as well as ecosystems (Laurance et al., 2007). Unlike other animals, birds usually face reduced reproductive success (high nest predation rates), lower species richness and emigration or immigration in edge habitats (Banks-Leite et al., 2010; Marini et al., 1995; Rolstad, 1991; Stephens et al., 2003; Watson et al., 2004). Such edge effects are particularly strong when fragments are small or unevenly shaped or when the transition between natural and changed habitats is sharp (Laurance and Yensen, 1991).

Human disturbance affects feeding areas (Sutherland and Crockford, 1993) and breeding success (Giese, 1996), and might pose serious negative impacts on avian conservation (Carney and Sydeman, 1999). Different species respond to human disturbance differently (Andrén, 1992; Kurki et al., 2000). Some studies have found that host species of the common cuckoo (*Cuculus canorus*) may avoid parasitism by breeding indoors and in close proximity to humans (Liang et al., 2013; Møller et al., 2016), while other studies have shown that the common cuckoo regularly parasitize host nests placed inside human houses, farm house etc. close to humans (Antonov et al., 2007b, 2007c, 2009; Mikulica et al., 2017).

A famous egg collector, Gerald Tomkinson, described in his notebooks (stored at the Natural History Museum, Tring, UK) that during the period of 1905−1945, the common cuckoo parasitized pied wagtail (*Motacilla alba yarrellii*) nests placed on his house in Worcestershire, UK. Parasitized nests were found over the dining room window, over the front door, in the ivy on a garden fountain, over the porch, on the balcony over the sitting room, at the top ledge of the house and on the wall of the vinery. Similarly, other brood parasites, such as the brown-headed cowbird (*Moluthrus ater*), seems to prefer inhabited areas. Cowbird parasitism is often more pronounced in areas with high human density due to abundance of foraging area and high host density (Airola, 1986; Burhans and Thompson, 2006; Chace et al., 2003; Goguen and Mathews, 2000; Robinson et al., 1995; Rodewald, 2009; Tewksbury et al., 1998, 2006). Thus, how human disturbance affect predation and parasitism risk seems to be highly condition dependent, probably related to complex interactions between habitat, parasites, predators and hosts. Studies assessing some or all of these interactions are currently few (see, Feng and Liang, 2020).

Another possible source of human disturbance towards avian breeding success is research activities or research disturbance (Hu et al., 2020; Border et al., 2018; Ibáñez-Álamo et al., 2012). Research work on birds includes several activities, like frequent nest visit (Ibáñez-Álamo and Soler, 2010) and handling the eggs and chicks (Orzechowski et al., 2019), often negatively influencing avian nesting success (Götmark, 1992). Research activities may damage nesting plants or leave human scent close to nesting areas (Götmark, 1992; Gutzwiller et al., 2002). Research disturbance may negatively influence the bird reproductive success directly through encouraging nest desertion (Piatt et al., 1990) and indirectly through increasing the risk of predation (Border et al., 2018). However, the effects of research activities on avian breeding success can vary widely among the species and even within the same habitat (Ibáñez-Álamo et al., 2012; Weidinger, 2008). Many studies have found that research activities can cause higher nest predation (Major, 1990; Zhao et al., 2020; Meixell and Flint, 2017) whereas, others found no significant effects on nest predation (Ibáñez-Álamo et al., 2012; Orzechowski et al., 2019; Ledwoń et al., 2016). Moreover, several studies have found positive effects of research activities on breeding success of some bird species, possibly due to human or their devices may deter some predators, especially mammalian (Ibáñez-Álamo and Soler, 2010; Richardson et al., 2009; MaCivor et al., 1990; Herranz et al., 2002).

Brood parasitism often leads to reproductive costs for the host, but nest predation is the key cause of nest failure in most bird species (Martin, 1993; Remeš et al., 2012; Thompson, 2007). Nest predation affects population density (George, 1987) as well as community structure (Martin, 1988; Söderström, 1999). Predator composition varies across habitats (Pietz and Granfors, 2000; Thompson et al., 1999), and often consists of a combination of reptilian, avian and mammalian species (Cavitt and Martin, 2002; Miller and Hobbs, 2000; Thompson et al., 1999). Human-influenced habitats may provide a good environment for predators (Soh et al., 2002), and many studies have found a positive relationship between nest predation and human habitation (Kluza et al., 2000; Liebezeit et al., 2009; Nilon et al., 1995; Smith and Wachob, 2006). Birds mainly face high egg loss and chick mortality in human disturbed areas (Madsen and Fox, 1995). Urban areas or human-disturbed habitats also provide good feeding grounds for raptors, which also act as nest predators (Cringan and Horak, 1989). In contrast, some studies have found negative effects of human activity on risk of predation (Leighton et al., 2010; Muhly et al., 2011; Seibold et al., 2013). For example, predation was lower for some species in urban areas than in natural habitats (Eden, 1985; Francis et al., 2009). The predator composition is sometimes lower in human-inhabited areas and only predators which coexist with disturbance can sustain (Tella et al., 1996). Animals can reduce their predation risk by living in urban areas, as predators avoid being in close proximity to humans (Møller, 2012). Sometimes, animals appear to trade-off food abundance to reduce levels of disturbance and avoid areas with high disturbance (Gill et al., 1996; Feng and Liang, 2020). The joint effect of human disturbance on predation and parasitism seems equivocal and require to be tested in areas with substantial human disturbance. Importantly, effects of predation and parasitism must be disentangled due to their potential opposing effects described above. Studies quantifying the relative effects of predation and parasitism in relation to gradients of human disturbance are

currently lacking, especially studies assessing sources of predation and parasitism in urban areas, and their impact on nesting success.

Habitat fragmentation negatively influence the avian reproductive success; however, the effects are more severe for hosts of brood parasites (Cavitt and Martin, 2002; Robinson et al., 1995; De Mársico and Reboreda, 2010). Hosts usually suffer higher reproductive loss due to nest predation and brood parasitism in fragmented areas (Donovan et al., 1995, 1997; Kosciuch and Sandercock, 2008). However, the fragmentation effects on nest predation and brood parasitism are often inconsistent across habitats and communities (Tewksbury et al., 1998, 2006). This inconsistency may arise because predators and brood parasites respond differently to habitat fragmentation (Sandercock et al., 2008; Tewksbury et al., 2006). Even though the effects of predation and brood parasitism often are independent, there has been shown that parasitism can lead to increased predation in some hosts species (Arcese et al., 1996; Burhans et al., 2010; Dearborn, 1999; Hannon et al., 2009; Heath et al., 2010). In fragmented habitats, host reproductive success depends in fact on the abundance and composition of predators and brood parasites (Tewksbury et al., 2006; Sandercock et al., 2008). Assessing the relative negative effects of predation and parasitism on reproductive success is thus key to understand how human disturbed areas may affect host species. Bangladesh, a small tropical country situated in south Asia, show high biodiversity, and hosts a total of 13 avian brood parasites (Khan, 2008). But this country also has a high human population of approximately 151.7 million people, resulting in one of the highest population densities in the world with 1063 people/km^2 (Bangladesh population census 2011, http://mof.gov.bd/en/budget/15_16/ber/en/06._Socio-Economic_Indicators.pdf). The proportion of forested area is continuously decreasing, and habitat fragmentation can potentially result in severe consequences for the indigenous wildlife. How human disturbance affects the costs of predation and parasitism for brood-parasite hosts in a densely populated region has thus far received little research attention. Here, we investigate whether distance to human habitation in a heavily fragmented landscape affects the probability of parasitism and predation for three host species parasitized by the Asian koel (*Eudynamys scolopaceus*), i) long-tailed shrike (*Lanius schach*), ii) common myna (*Acridotheres tristis*) and iii) house crow (*Corvus splendens*) in Bangladesh. If the Asian koel tends to avoid human habitation, we predict that distance to human buildings within our study area and distance to the abrupt boundary of human habitation outside our study area, which we considered as a source of disturbance, should be positively related to the risk of parasitism for the three host species. We furthermore compare the effect of human habitation on risk of parasitism and the risk of predation, also, assess the sensitivity of koels and predators on human disturbance. We also examine if research activities, another source of human disturbance, have any influence on nesting success of these hosts species. Finally, we examine the importance of human disturbance versus a set of other potentially important variables, and we test how these habitat and nest characteristics ultimately affected the probability of nesting success. pr p.

2. Materials and methods

2.1. Study area

The study was conducted in the campus area of Jahangirnagar University (23°52′ N and 90°16′ E). The study area is approximately 280 ha and located 32 km northwest of Dhaka, in Bangladesh (Fig. 1). The campus is a heterogeneous landscape and consists of wetlands, grasslands and cultivated lands, bushes, woodlands and human settlements, i.e. houses, academic and administrative buildings and shops which are made of tin, wood and bamboo at different sites of the campus. The study site is a highly fragmented area but supports large numbers of animals including 195 species of birds belonging to 43 families of which 74 species are recorded as breeding residents, 41 non-breeding residents and 65 migrants (Begum, 2016; Mohsanin and Khan, 2009).

2.2. Parasite and host community

2.2.1. Asian koel

Asian koel is the most common resident among the cuckoos in the study area, and it occurs throughout Bangladesh and Asia (Ali and Ripley, 1983; Begum et al., 2011a, 2011b; Payne, 2005). The Asian koel breeding season in the Indian subcontinent spans from December to October, but varies to some extent locally (Erritzøe et al., 2012; Payne, 2005). A total of 16 passerine species from different areas have been recorded as hosts of Asian koel (Mann, 2017). The Asian koel eggs are grey-bluish to greenish ground color and numerous brown or black spots (Fig. 2) (Erritzøe et al., 2012; Payne, 2005). Multiple Asian koel eggs can be found in a single host nest, generally 2–3, but up to 13 koel eggs have been recorded in one host nest (Erritzøe et al., 2012; Payne, 2005). The Asian koel eggs hatches after 13–14 days, and the fledgling leave the host nest after 19–27 days (Erritzøe et al., 2012; Payne, 2005).

The Asian koel is a non-evicting brood parasite, feeding mostly on fruits and berries. Three passerine host species are parasitized by the Asian koel in our study area; the long-tailed shrike, the common myna and the house crow (Begum et al., 2011a, 2011b). Parasitized nests of long-tailed shrike, common myna and house crow with Asian koel egg is shown in Fig. 2.
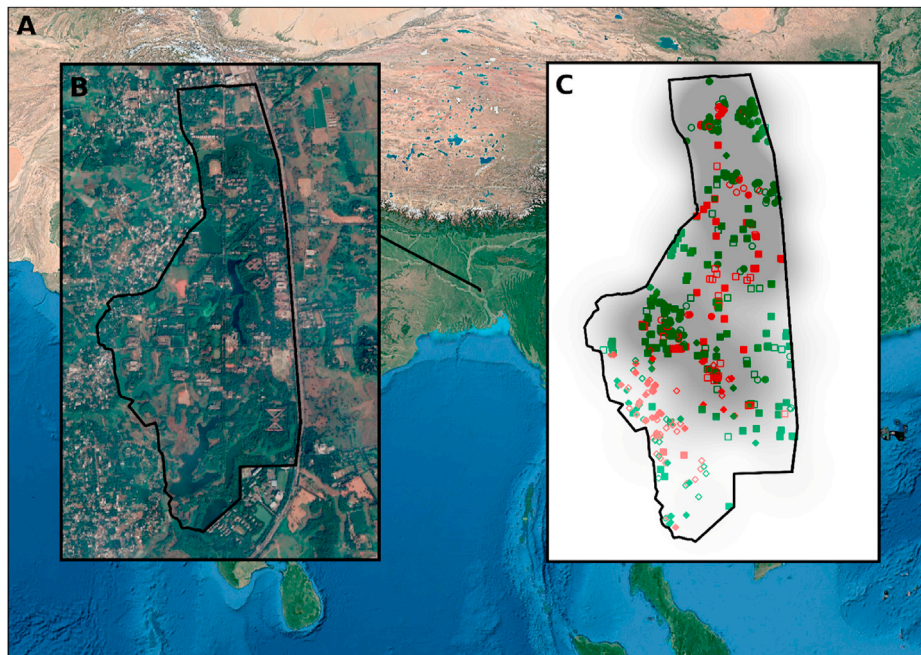
Fig. 1. Distribution of predation and parasitism across Jahangirnagar University campus. The main satellite image (A) shows the location of the campus in Bangladesh northwest of Dhaka. The campus area and the surroundings are shown in panel B, zoomed satellite image from Google Maps. Panel C shows location of all nests in relation to disturbed areas: buildings highlighted with shaded areas (heat map from QGIS) and boundary highlighted with black line. Closed symbols depict nesting success versus open unsuccessful breeding's. Green color indicates un-parasitized nests versus red parasitized nests. Symbol shape represents the different host species: common myna (circles), house crow (squares) and long-tailed shrike (diamonds). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Fig. 2. Illustrations of parasitized nests in three host species of the Asian koel. Note that multiple parasite eggs are common, and that these most likely stem from different females based on their differences in appearance. To the left a parasitized nest of long-tailed shrike, showing two shrike eggs (pale) and six Asian koel eggs (bluish with brown spots). In the middle a common myna nest with three common myna eggs (immaculate blue eggs) with two Asian koel eggs. To the right, a house crow nest with three house crow eggs (blue ground color with brown spots) together with two Asian koel eggs (darker, and somewhat smaller). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2.2. Long-tailed shrike

The long-tailed shrike is distributed throughout Asia, mainly south and southeast Asia (BirdLifeInternational, 2016; Yosef, 2019). It prefers open habitats for breeding and builds nests in trees and bushes (Begum et al., 2011a, 2011b; Whistler, 1949). The breeding season ranges from February to August and varies in different areas. The eggs have pinkish-cream ground color with greyish and reddish spots at the blunt end (Fig. 2), and the clutch size is 4–6 (Ali and Ripley, 1983; Begum et al., 2011b). The incubation period is 14 days and the fledgling period is 20 days (Baker, 1933).

2.2.3. Common myna

The common myna is a native bird of south and southeast Asia but introduced in middle east, Australia and some parts of Africa (BirdLifeInternational, 2017; Craig et al., 2019). As an opportunistic omnivore, the common myna builds nests in human habitats as well as natural areas. In Bangladesh, the breeding season is from March to August, however, it can breed throughout the year depending on area (Begum et al., 2011b). The common myna builds a variety of nest types, including nesting in tree holes, inside buildings or roofs, or in the small space between joining palm leaves of coconut (*Cocos nucifera*),

fishtail palm (*Caryota urens*) and fountain palm (*Livistona chinensis*) trees. Sometimes, common mynas use old pied myna (*Gracupica contra*) or house crow nests. Common myna eggs are immaculate blue (Fig. 2), and the clutch size is 4−5 (Begum et al., 2011b). The incubation period is 17 days whereas the chicks leave the nest after 20 days (Lamba, 1963; Ali and Ripley, 1983).

2.2.4. House crow

The house crow has a very wide range of distribution throughout south and southeast Asia and has increased its geographic range to Africa, Middle east and some parts of Europe and North America (BirdLifeInternational, 2017; Madge, 2018). The house crow is a colonial breeder and builds nests close to human habitations where the food availability is high (Begum et al., 2011a). It can breed throughout the year (Akter et al., 1994; Lamba, 1963), but the breeding season is mainly from January to September and vary locally (Begum et al., 2011b; Grimmett et al., 1999). The house crow prefers large trees with big crowns and up to 9 nests can be found in a tree (Lamba, 1963, 1969). It builds open shallow-cup nests in trees and usually lays 3−6 eggs in a clutch. The eggs are bluish-green ground colored eggs with black or brown blotches (Fig. 2) (Begum et al., 2011b; Whistler, 1949). However, a recent study confirmed that house crow may lay immaculate blue eggs (Nahid et al., 2019). The incubation period is 16−17 days whereas the chicks leave the nest after 30 days (Ali and Ripley, 1987; Ali et al., 2007).

2.3. Predators

The study area holds a range of reptilian, avian and mammalian predators which are distributed throughout the study area. Common potential predator species in the area are large-billed crows (*Corvus macrorhynchos*), house crows, rufous treepies (*Dendrocitta vagabunda*), Bengal monitor lizards (*Varanus vengalensis*), Irrawaddy squirrels (*Callosciurus pygerythrus*), small Indian mongooses (*Herpestes auropunctatus*) and different species of snakes (pers. observation). Domestic cats (*Felis catus*) and dogs (*Canis lupus*) and jungle cats (*Felis chaus*) are also very common in the study area. All these animals can predate nests in trees except mongooses and dogs. For cases of nest predation, the present study did not identify the various predator species.

2.4. General methodology

The study was carried out over nine successive breeding seasons from 2008 to 2013 and 2015 to 2017. All data were collected during the breeding period of the three hosts and the Asian koel (i.e. January−August). Asian koel regularly parasitized the three host species in the study area (Fig. 1). Multiple parasitism was very common (mean ± SD number of koel eggs in long-tailed shrike nests: 2.05 ± 1.00, n = 66, common myna nests: 2.55 ± 1.60, n = 89 and house crow nests: 1.33 ± 0.48, n = 27, unpublished results). Different sizes and ground color of Asian koel eggs are often found in the same nest and therefore it was likely that more than one parasitic female laid eggs in a single host nest at our study site. A handheld global positioning system (GPS) device (Garmin eTrex 20) was used to plot each nest position. Each nest was checked regularly (almost daily during the egg laying and nestling period) after the first observation in order to record breeding variables including progress in building, egg laying, number of host and parasite eggs, number of host and cuckoo eggs hatched, number of host and cuckoo chicks fledged and final fate of the nest, which was either successful (at least one young fledged) or un-successful (no young fledged). Buildings inside the campus and the area outside the boundary were considered as human disturbance. Distance from the nest to the nearest building in the campus area and distance from the nest to the nearest boundary of the campus area were measured using the distance tool in Google Earth. The buildings in the study area consist of academic administrative offices or dormitories for students, residences that are densely occupied by daily activities of humans. Outside the campus boundary, there is also a high density of permanent human settlements. We ensured that the distance from building was not related to the distance from boundary (correlation = −0.17) i.e. that buildings are evenly distributed across the campus area, in order to include both variables in the same models (see, Fig. 1).

Besides human disturbance, we have considered four other variables in the statistical analyses: i) nest height, ii) number of days with eggs and nestlings present before discovery (time unmonitored), iii) distance to fruit trees and iv) distance to nearest active neighboring nests of the same host species. Previous studies have found that these factors influence risk of parasitism in our study area (Begum et al., 2011a). Risk of parasitism increased in host nests closer to fruit trees, however, long-tailed shrike suffered higher parasitism when nests were located in lower height and risk of parasitism increased with distance to conspecific neighbors in house crows and long-tailed shrikes (Begum et al., 2011a).

2.5. Statistical analyses

We examined the effects of nest height, time unmonitored, distance to nearest building, boundary, fruit tree, and nearest conspecific neighbor, respectively on the probability of parasitism, and predation, in binomial mixed-effects models using the R-package '*glmmTMB*' (Brooks et al., 2017). We added random intercepts for year. To model the effect of parasitism on predation we ran an additional model including parasitism as a fixed effect. In that way we could also examine the effect of habitat and nest characteristics on predation that was not caused by parasitism. To study the host population consequences of parasitism and predation related to habitat and nest characteristics, we examined their effect on an important fitness

component for annual reproductive success i.e. probability of nesting success. We analyzed nesting success as a binomial response in a mixed-effects model, including the same fixed-effects as mentioned above. Random intercepts were added for year. All statistical analyses were performed in the statistical software R (R Core Team, 2018). Due to the behavioral differences, e.g. nest site choice, nest structure and nest position, for these host species, we analyzed the data separately for each host. In order to ensure that fixed-effects were not correlated, we used the '*check_collinearity*' function from the '*performance*' package (James et al., 2013).

3. Results

A total of 518 nests of three host species (122 long-tailed shrike, 231 common myna, 165 house crow) were monitored within the study period. The parasitism rate of each host species was 54.1% in long-tailed shrike, 32% in common myna and 16.4% in house crow respectively. The predation rates were 50.8% in long-tailed shrike, 27.7% in common myna and 38.2% in house crow. A large proportion of nests were located within 50 m distance of buildings for common myna and house crow, while for the long-tailed shrike, the highest proportion of nests were located within 200 m (Fig. 3). However, there was no such clear pattern on nest distribution regarding the distance to campus boundaries. The number of nests was less dependent on the distance to campus boundaries, but decreased most in long-tailed shrike, thereafter house crow and the least in common myna (Fig. 3). In long-tailed shrike, the distance from nest to nearest boundary varied from 18 m to 623 m, whereas the ranges were 9 m–622 m and 4 m–606 m in common myna and house crow respectively (Fig. 3).

3.1. Parasitism effect on predation

The effects of nest parasitism on the probability of nest predation differed among the three hosts (Table 1). Parasitized long-tailed shrike nests had the same predation rate as non-parasitized nests, whereas in common myna, parasitized nests were significantly more predated. Also, in house crow there was a tendency for increased predation in parasitized nests.

3.2. Nest height

The height above the ground where a nest was located had significant impact on the parasitism risk in long-tailed shrike, where nests located lower in the trees were more significantly parasitized (Table 1). Consequently, we found a trend for increased nesting success for nests located higher in the trees. However, nest height had no influence on predation risk in long-tailed shrike. In common myna and house crow nest height was not related to either predation or parasitism risk, and thus had no influence on the nesting success.
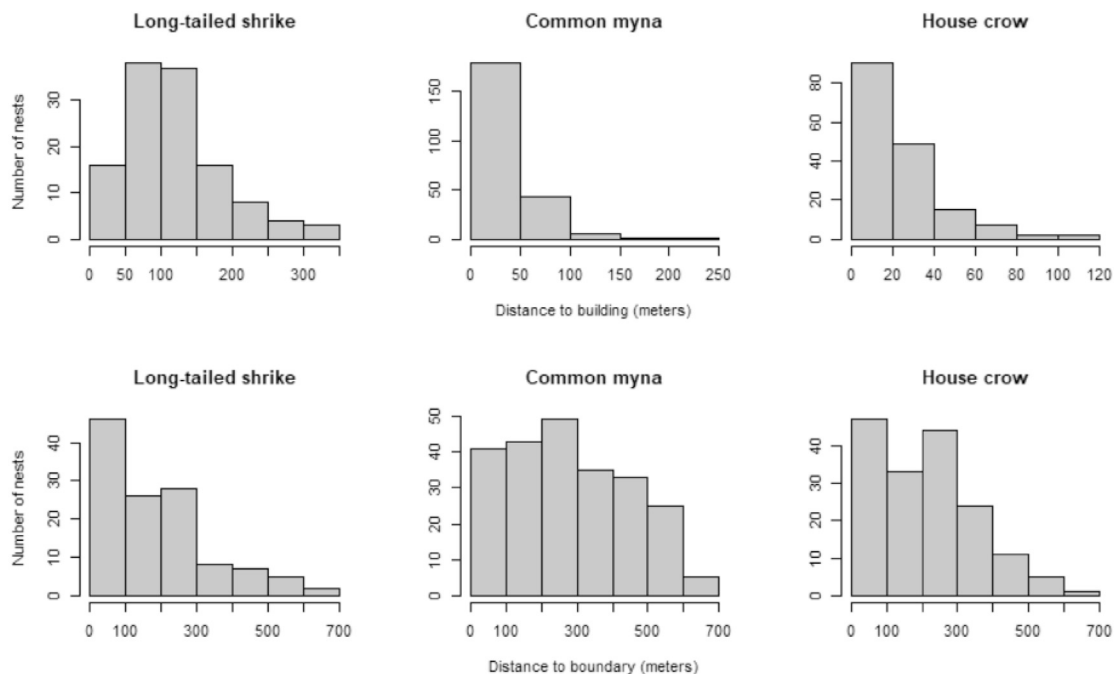

Fig. 3. The distribution of nests in relation to distance to nearest building (upper panel) and nearest boundary (lower panel) for the three host species parasitized by the Asian koel.

Table 1

Generalized linear mixed-effects models on probability of predation (* separating effects of parasitism), parasitism and nesting success, with year as random intercept. a) long-tailed shrike (n = 113), b) common myna (n = 221) and c) house crow (n = 157). Significant effects depicted in bold font. § high collinearity, ¥ moderate collinearity.

	Predation				Predation*				Parasitism				Nesting success			
	Est	±SE	Z	P	Est	±SE	Z	P	Est	±SE	Z	P	Est	±SE	Z	P
a) Long-tailed shrike																
Intercept	4.804	1.525	3.151	0.002	4.601	2.236	2.057	0.040	167.853	77.169	2.175	0.030	−6.510	1.566	−4.157	<0.001
Parasitism	NA	NA	NA	NA	0.140	1.139	0.123	0.902	NA	NA	NA	NA	NA	NA	NA	NA
Nest height	−0.185	0.163	−1.136	0.256	−0.179	0.171	−1.042	0.297	**−8.235**	**3.584**	**−2.298**	**0.022**§	0.280	0.148	1.896	0.058
Time unmonitored	**−0.326**	**0.077**	**−4.261**	**<0.001**	**−0.328**	**0.078**	**−4.220**	**<0.001**	**1.356**	**0.689**	**1.969**	**0.049**	**0.099**	**0.035**	**2.837**	**0.005**
Distance to boundary	−0.003	0.002	−1.482	0.138	−0.003	0.002	−1.475	0.140	0.061	0.042	1.433	0.152¥	0.003	0.002	1.275	0.202
Distance to building	−0.001	0.004	−0.244	0.808	−0.001	0.004	−0.241	0.810	−0.184	0.099	−1.860	0.063§	−0.004	0.005	−0.802	0.423
Distance to fruit tree	−0.177	0.105	−1.683	0.092	−0.161	0.165	−0.977	0.329	**−18.039**	**8.914**	**−2.024**	**0.043**¥	**0.357**	**0.108**	**3.313**	**0.001**
Distance to neighbor	0.002	0.001	1.362	0.173	0.002	0.001	1.359	0.174	0.038	0.028	1.359	0.174	0.000	0.001	0.019	0.985
b) Common myna																
Intercept	0.997	0.815	1.223	0.221	0.500	0.847	0.590	0.555	3.169	1.250	2.535	0.011	−1.457	0.747	−1.950	0.051
Parasitism	NA	NA	NA	NA	**1.194**	**0.552**	**2.163**	**0.031**	NA	NA	NA	NA	NA	NA	NA	NA
Nest height	0.015	0.074	0.205	0.838	0.018	0.075	0.241	0.810	−0.026	0.092	−0.286	0.775	−0.027	0.054	−0.503	0.615
Time unmonitored	**−0.258**	**0.039**	**−6.583**	**<0.001**	**−0.265**	**0.041**	**−6.488**	**<0.001**	−0.014	0.025	−0.552	0.581	**0.102**	**0.020**	**5.063**	**<0.001**
Distance to boundary	0.002	0.001	1.257	0.209	0.001	0.001	0.440	0.660	**0.003**	**0.001**	**2.536**	**0.011**	−0.002	0.001	−1.744	0.081
Distance to building	−0.009	0.007	−1.355	0.175	−0.012	0.007	−1.694	0.090	**0.018**	**0.008**	**2.306**	**0.021**	0.001	0.005	0.280	0.780
Distance to fruit tree	**−0.116**	**0.053**	**−2.192**	**0.028**	−0.040	0.062	−0.652	0.514	**−1.068**	**0.175**	**−6.086**	**<0.001**	**0.192**	**0.049**	**3.910**	**<0.001**
Distance to neighbor	**0.005**	**0.001**	**3.575**	**<0.001**	0.005	0.001	3.184	0.001	**0.004**	**0.002**	**2.174**	**0.030**	−0.001	0.001	−0.824	0.401
c) House crow																
Intercept	−0.587	1.247	−0.470	0.638	−1.545	1.349	−1.145	0.252	7.561	3.837	1.971	0.049	−0.145	1.039	−0.140	0.889
Parasitism	NA	NA	NA	NA	1.272	0.671	1.896	0.058	NA	NA	NA	NA	NA	NA	NA	NA
Nest height	0.043	0.076	0.563	0.574	0.049	0.075	0.645	0.519	0.115	0.218	0.528	0.597	−0.075	0.067	−1.116	0.264
Time unmonitored	**−0.180**	**0.042**	**−4.258**	**<0.001**	**−0.189**	**0.044**	**−4.269**	**<0.001**	−0.037	0.046	−0.805	0.421	**0.082**	**0.023**	**3.602**	**<0.001**
Distance to boundary	0.003	0.002	1.539	0.124	0.003	0.002	1.565	0.118	0.005	0.006	0.759	0.448	−0.002	0.001	−1.773	0.076
Distance to building	−0.015	0.010	−1.441	0.150	−0.016	0.010	−1.521	0.128	−0.023	0.048	−0.467	0.641	0.005	0.009	0.531	0.595
Distance to fruit tree	0.054	0.069	0.791	0.429	0.143	0.085	1.683	0.092	**−1.764**	**0.442**	**−3.994**	**<0.001**	0.073	0.063	1.165	0.244
Distance to neighbor	0.002	0.002	1.226	0.220	0.002	0.002	0.833	0.405	**0.012**	**0.005**	**2.586**	**0.010**	−0.001	0.002	−0.642	0.521

3.3. Time unmonitored

Nests were found from 12 January to 26 July, where 159 were found during building, 218 during egg laying or incubation and 148 nests during chick rearing. The longer time a nest was present without being discovered (time unmonitored), the nest experienced lower probability of predation in the remaining nest period in three host species (Table 1). In contrast, time unmonitored did not affect the probability of being parasitized (Table 1). Consequently, monitoring time significantly influenced nesting success negatively in all host species (Fig. 4), suggesting substantial impact from the nest visits from researchers (Table 1).

3.4. Human disturbance

There was no consistent effect of distance to boundary or distance to buildings on predation or parasitism risk. Only in common myna we found some evidence that parasitism risk increased farther away from boundary and buildings. However, we found a trend for increased nesting success closer to the boundary in common myna and house crow (Table 1; Fig. 5b and c).
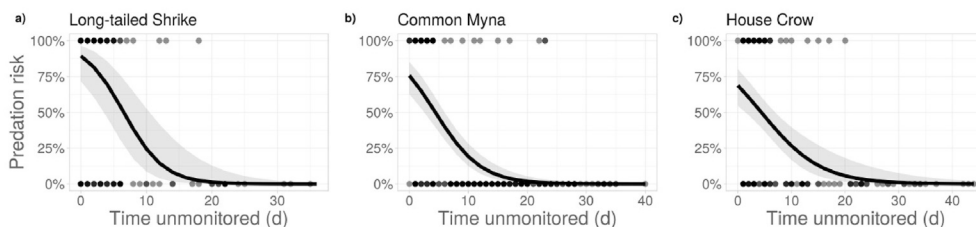

Fig. 4. The effect of time unmonitored on predation risk, highlighting the negative impact of human presence and nest checks on the probability of being predated. Darker dots indicate multiple data points on top of each other.
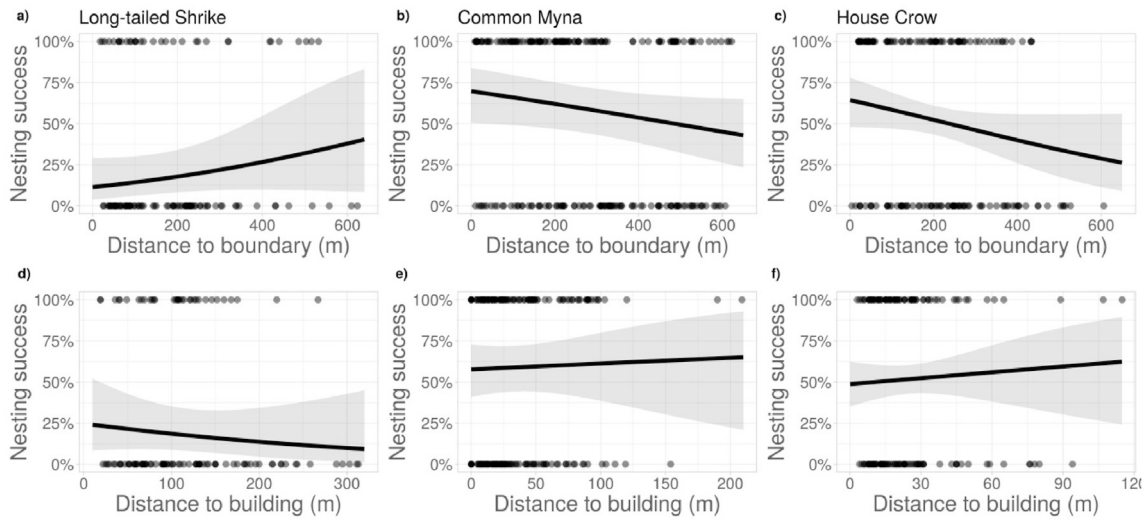
Fig. 5. The effect of distance to boundary and distance to building on nesting success. Darker dots indicate multiple data points on top of each other.

3.5. Distance to fruit trees

We found consistent effects of increased parasitism risk closer to fruit trees (Table 1; Fig. 6). In common myna, predation also increased closer to fruit trees, however, in long-tailed shrike and house crow, predation risk was not related to distance to fruit trees. Consequently, this resulted in a lower nesting success closer to fruit trees in long-tailed shrike and common myna, but not in house crow.

3.6. Distance to conspecific neighbor

We found no consistent effects of distance to nearest conspecific neighbor (Table 1). In common myna, both predation and parasitism risk increased when breeding farther away from conspecifics; however, distance to conspecific neighbor had no effect on nesting success. Moreover, house crow also experienced higher parasitism risk when breeding farther from nearest conspecific (Table 1).

4. Discussion

We found large impacts of human disturbance on nesting success in all hosts, however, not from the sources of disturbance we set out to test. Instead we found large negative effects from nest monitoring on nesting success in all host species, mainly through increased predation risk. Additionally, we found increased parasitism risk closer to fruit trees, affecting nesting success of long-tailed shrike and common myna. However, there was only a tendency for support to our hypothesis in common myna and house crow, which experienced somewhat higher nesting success closer to campus boundary. Moreover, we found a tendency for a positive relationship between nesting success and nest height in long-tailed shrike, likely caused by the significant lower parasitism risk in nests located higher in the vegetation.

4.1. Nest height

In the long-tailed shrike, nests placed higher from the ground experienced significantly lower parasitism risk than nests placed closer to the ground. A previous study confirm that risk of parasitism increased in long-tailed shrike when nests placed
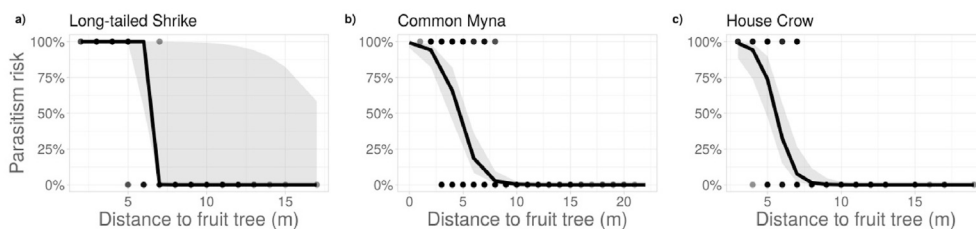

Fig. 6. The effect of distance to nearest fruit tree on parasitism risk. Darker dots indicate multiple data points on top of each other.

at lower height (Begum et al., 2011a). Host nests in lower height of the trees where foliage and branches are sparse may be easier to detect by brood parasites (Øien et al., 1996; Moskát and Honza, 2000; Clarke et al., 2001). However, predation was not influenced by nest height in long-tailed shrike indicating that the trend for lower nesting success lower in trees was mostly due to increased parasitism risk (Table 1). The influence on parasitism and not predation may also suggest that parasites and predators differ in how they search for host nests. Moreover, no significant influence of nest height were found on risk of predation and parasitism as well as nesting success in common myna and house crow. Common myna builds a variety of nest types in trees, electric poles, building roofs, ventilators. Similarly, house crow builds nests in colonies in trees and poles. Both common myna and house crow nests are large and easy to detect even in dense foliage. Thus, nests placed higher or lower in trees did not provide an advantage of avoiding risk of predation and parasitism in common myna and house crow. A previous study also found that nest height did not have a significant influence on risk of parasitism in common myna and house crow (Begum et al., 2011a).

4.2. Time unmonitored

There was no relationship between the time a nest was left unmonitored (i.e. during breeding when a nest was discovered), and parasitism risk. These results indicate that probably Asian koel do not follow human activities or the damage of the habitat causes by human activities to select the nest for parasitized. Instead, Asian koel seems to use fruit trees to search for nests, and may not rely on human cues to find nests. In contrast, there was a consistent negative relationship between the duration of monitoring and the probability of being predated in all three hosts (Table 1). Although a more complete monitoring of a nest revealed more predation could indicate that some nests were predated before discovery, these findings may also suggest substantial impacts of nest visits by researchers. Similar negative impacts of nest visits have been reported from long-term studies in common eiders (*Somateria mollissima*) (Stien and Ims, 2016), White-fronted Chats (*Ephthianura albifrons*) (Major, 1990), Chinese grouse (*Tetrastes sewerzowi*) (Zhao et al., 2020) and European nightjar (*Caprimulgus europaeus*) (Lowe et al., 2014). Despite an experimental test among passerines failed to find support for this effect, regular visited nests experienced somewhat more predation and revealed large variation among passerine species (Mayer-Gross et al., 1997). Another experimental test in Eurasian oystercatcher (*Haematopus ostralegus*) revealed a positive relationship between the level of disturbance and the rate of egg predation (Verboven et al., 2001). In this study human disturbance related to regular nest checks resulted in significant lower nesting success in all hosts. As our study area is a fragmented habitat which consists of many potential predators as well as human, predators might rely on human trails or their activities to find nests. Advantages of relying on human cues may even lead to such predators being more common in human disturbed habitats. These effects highlights the importance of including the effect of researchers in studies involving nest monitoring.

4.3. Human disturbance

Our results revealed only a trend that common myna and house crow nests closer to the nearest boundary to the campus have higher probability of nesting success. In terms of predation and parasitism risk, distance to nearest boundary and nearest building inside the campus affected only the parasitism risk in common myna, experiencing more parasitism further away from both sources of disturbance. In our study area, most of the long-tailed shrike nests were found in an area close to the boundary, and the parasitism rate in this host was higher than in both house crow and common myna. Hence, the Asian koel seem to parasitize long-tailed shrike nests close to the boundary area even though levels of human disturbance are high. We assumed that if Asian koels tend to avoid human disturbance areas, the risk of parasitism would be lower in nests close to disturbance areas for all host species, which was not the case. The house crow built nests in colonies and all colonies were found close to building areas where food availability was high. As with shrikes, it seems that koels parasitizing house crow nests are not particularly affected by human disturbance. This study did not find any significant effects of distance to building on risk of predation for any host species. The study area has different habitat types including human habitation, wetland, grassland, agricultural land, natural and monotypic plantation. Predation pressure is common in all habitats, but different habitats could differ in predator species composition. Since the three host species in general are distributed in different parts of the campus area with differing habitats, they are also likely to face different predators. Predator composition may be higher inside the study area than close to human disturbed boundaries which may be the main cause of the tendency for lower nesting success for common myna and house crow in the core area of the study site. Due to the habitat characteristics, the campus area can be considered as an edge habitat. However, the dense permanent human settlements with very poor vegetation or natural habitats outside the campus boundary made the campus area a wildlife refuge where animals are sustained for food and breeding habitats and can act as "ecological lungs" surrounded by a densely populated human settlements. The diverse ecological habitat of the campus including human habitation, roads, water body, grassland, natural or monotypic plantation contributes to the campus functioning like an urban park, where animals including predators can coexist with humans. However, the campus area may as well act as an ecological trap for these host species with high probability of predation and risk of parasitism (Yang et al., 2014).

4.4. Distance to fruit tree

The risk of parasitism increased with shorter distance to fruit trees consistently for all hosts (Table 1). These results support the Begum et al. (2011a) hypothesis, which states that Asian koel feeds on fruits and spend more times in fruit trees and therefore also use these fruit trees as a vantage points to monitor and time its egg laying (Perch proximity hypothesis: Anderson and Storer, 1976; Øien et al., 1996; Røskaft et al., 2002). Similar dependence of vantage points was found in studies of the common cuckoo (Antonov et al., 2006, Antonov et al., 2007; Moskát and Honza, 2000; Øien et al., 1996; Røskaft et al., 2006) as well as cowbirds (Clotfelter, 1998; Freeman et al., 1990; Hauber and Russo, 2000). In contrast to the large effect of fruit trees on parasitism, distance to fruit trees had significant influence only on nest predation in common myna but not in long-tailed shrike and house crow. Probably, Asian koel parasitism increased the predation risk in common myna nests close to fruit trees. In the present study, the predation in common myna nests were significantly determined by whether the nests were parasitized or not. Predators generally do not use fruit trees as vantage points to select the nests for predation. This might also suggest that sometimes koels themselves might act as important nest predators. Nesting success in long-tailed shrike and common myna increased with nests farther away from fruit trees. This relationship was mainly explained by the risk of parasitism decreasing for nests further away from the fruit trees, resulting in hosts may experience higher nesting success by building nests away from the fruit trees. Additionally, parasitized nests of common myna closer to fruit trees were more predated, and long-tailed shrike nests closer to fruit trees also tended to be more predated (Table 1).

4.5. Distance to nearest conspecific neighbor

The present study revealed large heterogeneity in the effect of distance to conspecifics. Common myna experienced generally more predation and parasitism when breeding farther away from conspecifics, while in house crow only the risk of parasitism was positively associated to the distance from conspecific. In a previous study, the house crow and long-tailed shrike nests farther away from the nearest conspecific nest had significantly higher risk of parasitism but this was not found in common mynas (Begum et al., 2011a). In contrast, long-tailed shrike was equally predated and parasitized independent of distance to conspecifics. Importantly, our results showed that distance to conspecific neighbor had no significant effects on nesting success in either of the host species studied. House crows in the study area may breed solitary occasionally, but usually in colonies of variable sizes, whereas, common myna breed both in close proximity as well as solitary. In general crows suffered relatively low levels of parasitism relative to the solitary breeding mynas and shrikes. Birds breeding in colonies or close proximity to neighbors may experience lower risk of parasitism and predation as colonial or cooperative breeding increases nest vigilance or defense (Canestrari et al., 2009; Martinez et al., 1996; Götmark and Andersson, 1984). Red bishops (*Euplectes orix*) in larger breeding colonies experienced lower parasitism by Diederik cuckoo (*Chrysococcyx caprius*) than hosts breeding in smaller colonies (Brown and Lawes, 2007; Ferguson, 1994; Lawes and Kirkman, 1996). However, some birds experienced higher predation in colonies if the potential predators were conspecific (Davis and Dunn, 1976).

5. Conclusion

In conclusion, we found a large negative impact on nesting success resulting from increased predation caused by human disturbance related to nest visits. However, we found little support for our hypotheses of disturbance from the vicinity (boundary) and buildings inside the campus area, maybe due to the large negative effects related to nest visits. We found only a trend for increased nesting success closer to the boundary in common myna and house crow. Additionally, we found a consistent increase in parasitism risk closer to fruit tree, negatively impacting nesting success in long-tailed shrike and common myna. Our results highlight the negative impact of nest monitoring as a source of human disturbance significantly affecting nesting success of all three host species.

Author's contributions

MIN, FF, BGS, SB, ER and PSR conceived the study and wrote the manuscript. MIN and SB collected the data. PSR, MIN, FF, BGS and ER analyzed the data. All authors read and approved the final manuscript.

Ethical standards

All research and data collection followed the ethical laws of Bangladesh and there was no harm made to any bird in this study.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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