

Diel timing of nest predation changes across breeding season in a subtropical shorebird

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Abstract

Predation is the most common cause of nest failure in birds. While nest predation is relatively well studied in general, our knowledge is unevenly distributed across the globe and taxa, with for example limited information on shorebirds breeding in sub-tropics. Importantly, we know fairly little about the timing of predation within a day and season. Here, we followed 444 nests of red-wattled lapwings (*Vanellus indicus*), a ground-nesting shorebird, for a sum of 7828 days to estimate a nest predation rate, and continuously monitored 230 of these nests for a sum of 2779 days to reveal how the timing of predation changes over the day and season in a subtropical desert. We found that 312 nests (70%) hatched, 76 nests (17%) were predated, 23 (5%) failed for other reasons and 33 (7%) had an unknown fate. Daily predation rate was 0.95% (95%CrI: 0.76% – 1.19%), which for a 30-day long incubation period translates into ~25% (20% – 30%) chance of nest being predated. Such a predation rate is low compared to most other avian species. Predation events (N = 25) were distributed evenly across day and night, with a tendency for increased predation around sunrise. Predation rate and events were distributed evenly also across the season, although night predation was more common later in the season, perhaps because predators reduce their activity during daylight to avoid extreme heat. Indeed, nests were never predated when mid-day ground temperatures exceeded 45°C. Whether the diel activity pattern of resident predators undeniably changes across the breeding season and whether the described predation patterns hold for other populations, species and geographical regions awaits future investigations.

KEYWORDS: continuous monitoring, diel pattern, diel timing, nest predation, predation rate, shorebirds, survival analyses, timing of predation, waders, red-wattled lapwing

INTRODUCTION

Predation affects the reproduction of wild populations (Ricklefs, 1969; Skutch, 1985; Caro, 2005). Indeed, predation is the most common cause of nest failure in birds (Ricklefs, 1969; Skutch, 1985). While nest predation is relatively well studied in general, our knowledge is biased toward the Northern hemisphere temperate and arctic regions (Vojtěch Kubelka *et al.*, 2018; Bulla *et al.*, 2019; Freeman *et al.*, 2020; Unzeta, Martin and Sol, 2020). Such bias then does not allow to generalize the conclusions from global comparative analyses. Moreover, regardless of the region, we know fairly little about when within a day nests are predated (Tulp *et al.*, 2001; hereafter “diel timing of predation”: Praus and Weidinger, 2010; Weidinger, 2010; DeGregorio *et al.*, 2015; Brynychová *et al.*, 2020; Laidlaw *et al.*, 2020), perhaps because it requires continuous nest monitoring (Weidinger, 2006; Pietz *et al.*, 2012).

Knowing when nests of a given species or population are predated may help in interpreting various behaviours of incubating parents, such as the timing of breeding season (Morton, 1971), pattern of nest attendance (Massaro *et al.*, 2008; Cervenci *et al.*, 2011; Skórka *et al.*, 2012; Kasun B Ekanayake *et al.*, 2015; Bakner *et al.*, 2019; Sládeček, Vozabulová, Brynychová, *et al.*, 2019), or daily rhythms of self-maintenance activities (Javůrková *et al.*, 2011; Brynychová *et al.*, 2020). Notably, given the lack of information on diel timing of predation, it is unclear whether there is a population- or species-specific, latitudinal or habitat dependent pattern in the timing of predation. For example, is there a day-night nest predation pattern around the equator and around the clock nest predation toward the poles, where it is light 24-hrs a day during the breeding season?

Diel timing of nest predation for a given avian species is likely to depend on its anti-predatory strategy (Eggers, Griesser and Ekman, 2008; Bulla *et al.*, 2016; Brynychová *et al.*, 2020), as well as on when their main predator species are active (DeGregorio *et al.*, 2015; Kämmerle, Rondeaux and Storch, 2020). For example, corvids (Corvidae) are active and search for their prey during daylight hours (Tahajjul Taufique, Jha and Kumar, 2016), but ground-nesting northern lapwings (*Vanellus vanellus*) actively protect their nests by chasing away corvids (and other day-light active avian predators). Thus, nests of northern lapwings are rarely predated during the day, and night predation prevails (Brynychová *et al.*, 2020). In contrast, temperate open-cup nesting and ground-nesting passerines do not actively defend their nests and consequently, both mammals and birds predate their nests, resulting in around the clock nest predation (Praus and Weidinger, 2010; Weidinger, 2010). In general, mammalian predators are nocturnal and predate nests and incubating parents at night, while avian nest predators are active during daylight and are the main daylight predators (Weidinger, 2010). In contrast, snakes, which are common predators of avian nests for example in the tropics (Robinson, Rompré and Robinson, 2005; Visco and Sherry, 2015) or North America (Weatherhead and Blouin-demers, 2004), predate nests around the clock (DeGregorio *et al.*, 2015). Importantly, the frequency of nest predation may also change over the breeding season. Such change may coincide with changes in vegetation density and nest concealment (Morton, 1971; Mezquida and Marone, 2001; Batáry, Winkler and Báldi, 2004; Sieving, 2019), and with changes in the presence of main predators, e.g. due to migration or due to dispersal of new generations (Patnode and White, 1992; Sloan, Holmes and Sherry, 1998; Sperry *et al.*, 2008).

Here, we estimated nest predation rate and investigated temporal dynamics of nest predation in the red-wattled lapwing (*Vanellus indicus*), in a population breeding in an arid and hot sub-tropical environment, south of Dubai, United Arab Emirates. Specifically, we followed 444 nests for a sum of 7828 days to estimate daily and total nest predation rate, as well as change in daily predation rate across the breeding season. We also continuously monitored 230 of these nests for a total of 2779 days to reveal the diel timing of predation and its changes over the breeding season.

We tested the following three predictions. First, because red-wattled lapwings actively defend their nests during the day (but not during the night) by alarm calling when a predator is at a great distance and by attacking a predator, often in cooperation with nearby breeding pairs (Narwade, Fartade and Fartade, 2010; Kaur and Khera, 2017), we expected day-time nest predation to be less common than night-time nest predation. Second, because

migrating avian predators pass through the study area early in the lapwing's breeding season (eBird, 2020) and because avian chicks – an alternative prey – are available later in the breeding season, we expected nest predation to decrease over the season. Third, because the presence of migrating avian predators – daylight predators of nests – declines over the breeding season (Table A0, eBird, 2020) and because ambient and ground temperatures increase dramatically over the breeding season (Figure 1) to the point where mid-day activity of most endotherm animals (Albright *et al.*, 2017; Streicher *et al.*, 2017; Abdu *et al.*, 2018) is close to impossible, we expected daylight nest predation (if any) to decline over the breeding season.

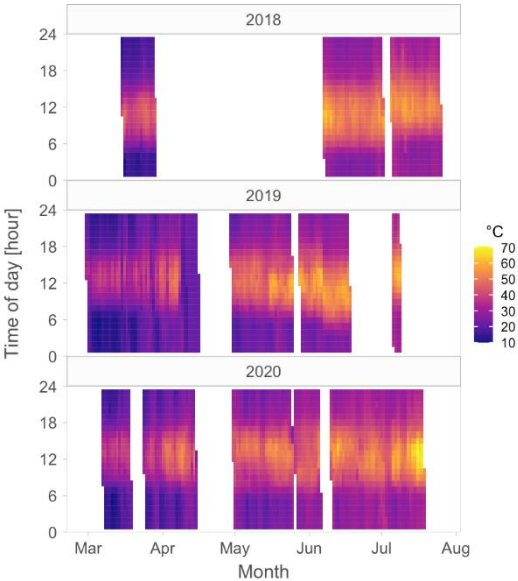


Figure 1 | Changes in hourly ground temperatures across day and season. Depicted are median hourly ground temperatures in the study area based on all recordings of sensors located next to the nests at a given hour (see Methods for details). White space indicates no temperature recordings.

METHODS

Study site and species

The study was conducted in the central part of Al Marmoom Conservation Reserve, Dubai, United Arab Emirates (24.84°, 55.36°), during the 2018 - 2020 breeding seasons. The reserve hosts broad and rich array of animal communities, including nest predators (Table A1). The 6.6km² study area is in the heart of the reserve and consists of 26 artificial lakes, artificial plantations of desert shrubs and trees, and dunes (Picture 1).

The red-wattled lapwing is a poorly studied ground-nesting shorebird species that breeds mainly in man-made habitats such as corn and grass fields, larger gardens, or waste, fallow and ploughed land (Wiersma, 2020). Their global population is stable (not endangered, Wiersma, 2020) and growing on the Arabian Peninsula (Symes *et al.*, 2017). The local red-wattled lapwing population has approximately 80 breeding pairs. The breeding season lasts from early February to the beginning of August and some individuals have several (up to 4) breeding attempts (our unpublished data). The red-wattled lapwings nest on islands and plantations in the vicinity of lakes. They build their nests on the ground. Incubating parents are well visible on the nest from afar (Picture 1). Both parents continuously attend the nest and nests are rarely left unattended. Parents remove large eggshells from the nest upon hatching and take those far away from the nest. Precocial chicks leave the nest shortly after hatching (Wiersma, 2020, our observation). Families with chicks remain in the vicinity of the nest until fledging. We never observed chicks further than ~300 m from the nest and, with one exception, never on a different island than the one, on which they hatched.



Picture 1 | Study site and illustration of how readily visible are incubating Red-wattled lapwings. Note that the lapwings often breed close to irrigation pipes (right picture). Map base on ©OpenStreetMap contributors and our digitalization of the study site. Pictures: ©Miroslav E. Šálek.

Nest monitoring

We searched for nests by slowly driving a car through the study area, looking for incubating adults that are readily visible from a distance (Picture 1). We used the same method as a non-invasive way to check whether nests are being incubated. One observer (Esmat Elhassan) searched for nests and checked nests at least once (but usually 2-3 times) a week, across the whole breeding seasons. The rest of the research team searched for nests daily during two- to six-week-long expeditions (1-3 expeditions per year). Given the frequency of our visits and the visibility of incubating parents, we find nearly all nests within the study area and follow most of the parents that guide their chicks. Upon finding a nest we measured and floated the eggs to determine their age (and hence to estimate when a clutch was initiated and likely to hatch) based on the developmental stage of the oldest egg (van Paassen, Veldman and Beintema, 1984).

We trapped adults on nests using spring traps triggered from a distance by a fishing line and marked the adults with a unique combination of metal and 4 colour rings and a green flag embedded with a glass passive integrated transponder (Biomark: $\varnothing 2.1 \times 9.0$ mm, 0.087 g, ISO FDXB, <http://www.biomark.com/>, see Supplementary Picture S1 in (Bulla et al. 2013); or Smartrac 704487-09 Glass tag $\varnothing 2.12 \times 12$ mm, <https://rfid.averydennison.com>). We took a small (ca. 50 μ l) blood sample from a brachial vein for sexing. We left the nest undisturbed for at least one day between consecutive catching attempts. We then attempted to visit the nests at least once a week and around the estimated hatch date to monitor and determine their fate. Possible nest fates were hatched (at least

one egg hatched), predated (includes also partial predation events after which parents abandoned their nest), abandoned, or failed for other reasons (e.g. trampled or dead embryos due to overheating), and unknown.

We continuously followed (at least for some time) 230 nests with one incubation monitoring system or with a combination of incubation monitoring systems: 35 nests were monitored with a video recording system (Sládeček, Vozabulová, Šálek, *et al.*, 2019), 188 nests with dataloggers that recorded temperature and humidity inside and outside of the nest in 1-s intervals (DHT, <http://berg.fzp.czu.cz>) or recorded only temperature in 1-min intervals (Tinytag Talk 2, Bulla *et al.*, 2014), 144 nests were monitored with a radio frequency identification device (RFID) that detected a passive tag of an incubating parent in 5-s interval (Bulla *et al.*, 2014), 40 nests with multisensory datalogger that recorded temperature and humidity inside and outside of the nest and also detected passive transponders in 1-s intervals (ZAYDA 1.1, <http://berg.fzp.czu.cz>), and 15 nests with a dummy egg recording temperature and acceleration in 1-s to 30-s intervals (ANITRA, <https://anitracking.com>). The dummy eggs were placed into the nests with less than 4-eggs and were accompanied by a temperature logger (DHT) placed in the vicinity of the nest. The temperature-humidity dataloggers (DHT 2.1) and multisensory loggers (ZAYDA 1.1) were installed similarly to the other temperature loggers and RFIDs (Bulla *et al.*, 2014, Picture A1).

We then visualised and inspected all recordings to identify the data with device-caused errors and periods when a bird had removed a sensor from the nest, i.e. when a sensor had recorded outside, not inside nest parameters.

Clutch initiation and fate

We defined “clutch initiation” as the day when the first egg was laid, which also indicates the onset (day one) of the incubation period because red-wattled lapwings incubate their eggs and protect them against the extreme heat as soon as the first egg is laid (own observation). We assumed (based on our observations) that females lay eggs in 1.5-day intervals and hence that females finish laying a 4-egg clutch in 4.5 days. We further assumed a 30-day long incubation period from “clutch initiation” until the first egg hatches (mean = 30, median = 31, range: 25-34; N = 13 hatched nests found at laying). Thus, if a nest was found during egg-laying (N = 80) we estimated “clutch initiation” by subtracting the number of days it took to lay the clutch (e.g. for 3 eggs, 3 days; $1.5 \times (\text{found clutch size} - 1)$) from the date the nest was found. If a nest was found with a complete clutch, we estimated “clutch initiation” as the date when the oldest egg was laid based on the floating of the eggs (van Paassen, Veldman and Beintema, 1984). We calculated the “estimated hatch date” as “clutch initiation” plus 30 days.

We considered nests as hatched (N = 312), when at least one chick hatched, i.e. we found (i) a chick on or around the nest during the final nest-check (N = 197 nests), (ii) colour-marked parents guiding the chicks later than during the final nest-check (N = 36 nests) or (iii) small ($\leq 5\text{mm}$) eggshell pieces in the nest that result from a chick chipping its way out of its egg (N = 79) (Mabee, Wildman and Johnson, 2006; Brown *et al.*, 2014). This method is a standard to define successfully hatched nests in other shorebird species (Kentie *et al.*, 2015; Laidlaw *et al.*, 2020). Importantly, we ringed 233 chicks found off the nest and with an unknown nest identity. Most of these 233 chicks had to come from the 79 nests where we assumed hatching based on eggshell pieces, because (i) we follow nearly all nests within the study area, (ii) families with chicks stay within the study area as chicks would die in the surrounding desert, and (iii), with one exception, we have never observed chicks from a known nest on an island other than the one they hatched at. Convincingly, when we assume that the 233 chicks with an unknown nest identity come from the 79 nests where hatching was determined from eggshell pieces, the average number of chicks per nest is 2.95, which closely corresponds with an average of 2.75 chicks per nest in nests with known chick identity (641 chicks from 233 nests).

We estimated the hatch date in the following way and order. First, if we knew when the chicks left the nest (i) based on the visualised continuously recorded data (N = 91) or (ii) freshly hatched chicks found around the nest (N = 24), we assumed that the nest hatched 1 day ago. Second, if during the nest visit both eggs and chicks were found in the nest (i.e. eggs were in the process of hatching), we assumed that the nest hatched 12 hours ago (N

= 50). Third, if a nest was found empty but with the signs of hatching (N = 57), older chicks were found around the nest during the final nest visit (N = 73) or parents were found later with chicks (N = 14), we assumed that nest hatched on the estimated hatch date (N = 144), unless the estimated hatch date was earlier than the last visit when the nest was seen active (without signs of hatching), in which case we assumed that chicks hatched one day after such visit (N = 3). Finally, 18 nests were found during or shortly after hatching (chicks in the nest cup). These 18 nests were not used in the analyses.

We considered nests as predated (N = 76) when nests were found (i) empty without signs of hatching, i.e. without tiny egg-shell pieces that indicate hatching, and if parents were ringed, they were seen without chicks and were not alarming (N = 69; for 25 of these nests predation was also confirmed by the continuous recording, which indicated the abrupt end of incubation - as described below and visible in Figure A1), when nests were found (ii) with remains of predated eggs (N = 5) or (iii) with some eggs missing and some eggs abandoned (no parents around) before expected hatching, i.e. partially predated (N = 2). Note, red-wattled lapwings continuously incubate or shade the nest to prevent overheating of the embryos; hence, abandoned (unattended) nest are obvious. Moreover, incubating parents arrange the pyriform eggs with sharp ends to the middle of the nest (Picture A1b). Thus, whenever we were suspicious of nest abandonment, we turned the eggs with the sharp ends out. If during the next visit the eggs remained the way we have left them, the nest was surely abandoned.

For the nests that were not continuously monitored, we estimated the date of predation as a midpoint between the last time when the nest was seen alive and the last nest visit, i.e. visit when the nest fate was determined, unless the expected hatch date was earlier, in which case the date of predation corresponds to the expected hatch date (N = 43). If the last time when the nest was seen alive was after the expected date of hatching, we assumed that the nest was predated one day after such visit (N = 8).

For the continuously monitored predated nests (N = 25, none of which was detected by video camera) we estimated the date and time of predation as the time when incubation temperature and humidity abruptly changed and reached the temperature and humidity values recorded outside of nests or as the time when incubating parent was last recorded with the RFID (Figure A1a). We considered this as the time of predation even if one of the parents visited the nest shortly after the predation event (Figure A1a). The nest fate estimated from temperature loggers matches well with the nest fate recorded by cameras (Weidinger, 2006). In addition, although the RFID method is less precise when only a single parent is tagged with a passive transponder and the nest temperature is not recorded (N = 3 nests), the parents exchange frequently on the nest (~hourly; Figure A1), so the bias in the time of predation should be minimal.

We define an observation period as a number of days for which a nest was followed and survived. Thus, the observation period starts when we found the nest and ends with the estimated date of hatching or predation. For nests that failed for other reason than predation (e.g. with infertile eggs or trampled; N=23) or nests with unknown fate (e.g. covered by sand after a windy day; N = 33), the end of the observation period indicates the last time when a nest was seen alive (based on visits or logger data). Such estimation results in a zero-observation period for additional 39 nests (15 failed for other reason and 24 with unknown fate), thus these 39 nests were not used in the analyses.

Ground temperatures

To investigate the relationship between the timing of predation and ambient temperature, the temperature loggers used for continuous nest monitoring recorded also ground temperatures next to the nest. We used these data to compute hourly median, mean, min and max temperature for each hour and each day of the year, for which we had the data (Figure 1). For the 25 predated nests we then assigned a median ground temperature during the hour when the nest was predated, as well as a median mid-day ground temperature of the day when the nest was predated.

Data analysis

General procedures

All statistical analyses and visualizations were performed in R 4.0.2 (R-Core-Team, 2019). The figures were created with the “ggplot” function from the “ggplot2” R-package (Wickham, 2016). Whenever we fitted linear and generalized models, we used the “sim” function from the “arm” R package and non-informative prior distribution (Gelman and Hill, 2007; Gelman *et al.*, 2016) to create a sample of 5000 simulated values for each model parameter (posterior distribution). We then reported the effect sizes and model predictions by the medians and the uncertainty of the estimates and predictions by Bayesian 95% credible intervals represented by 2.5 and 97.5 percentiles (95%CrI) of the posterior distribution of the 5000 simulated or predicted values.

Daily predation rate

We estimated the daily nest predation rate according to Mayfield (1961) using “logistic regression” with a number of days in which a nest was predated (0 or 1) and a number of days in which a nest survived as a binomial denominator (Aebischer, 1999). We then calculated a total nest predation rate (a chance of a nest being predated over the whole incubation period) as $1 - (1 - \text{daily predation rate})^{\text{30 days-long incubation period}}$ (Mayfield, 1961). We further tested whether the daily predation rate changed over the breeding season (“day of the year”). “Day of the year” reflects the midpoint of the period for which each nest was observed. We have then compared the fit of the two models by Akaike’s Information Criterion corrected for sample size (Anderson, 2008) generated by the “AICc” function from the “MuMIn” R package (Bartoń, 2019).

Of the 192 banded individuals, some were recorded at multiple nests (34% at two nests, 14% at three nests, 5% at four nests and 8% at > 4 nests). In an attempt to control for this non-independence of data points, we have refitted the models and included female, male and pair identities as random intercepts, while treating birds at nests with unringed parents as unique identities. Such models did not converge or provided nonsensical estimates. The same was the case for models with only pair identity, only male identity or only female identity. Our simulations reveal that this is due to the low number of nests associated with a particular pair or bird (i.e. low number of multiple observations per random factor level). Consequently, we use models without random intercepts and acknowledge that some nests may not be independent of each other - an issue common to most studies of daily nest predation (Weiser *et al.*, 2016, 2018; McGuire *et al.*, 2020; Meyer *et al.*, 2020).

Diel timing of predation

For the predation events with known timing (N = 25 cases), we visualized their distribution across the day, season and temperature. We then used a generalized linear model with a Poisson error distribution to test whether the number of predation events (count per hour) changed over the day. To account for circular properties of time, time (in hours) was transformed to radians ($2 \times \text{time} \times \pi/2$) and fitted as sine and cosine of radians (Bulla *et al.*, 2016). Since the hourly distribution of predation centred around sunrise (Figure 2), we also tested whether the probability of predation increased around sunrise by specifying time relative to sunrise (absolute hours) as a continuous predictor.

To further investigate whether the distribution of night and day predation changed over the season, we classified a predation event as “night” when the sun was at least 6° below the horizon (which demarcates the end of the “civil twilight” in the evening and its start in the morning), else we classified the predation event as “day”. The start and the end of each night were estimated for the latitude and longitude of the study site with the “crepuscule” function from the “maptools” R-package (Bivand and Lewin-Koh, 2020). We then fitted a binomial generalized linear model to test how the probability of night predation – a binary response with 1 (night) and 0 (day) – changed over the “breeding season” – day of the year when predation occurred.

The temperatures at the study site increase dramatically over the breeding season (Figure 1). We thus also investigated whether the probability of night predation changed with increasing mid-day temperatures. We then explored the relative importance of breeding season (day of the year) and mid-day temperatures by specifying

three additional models. First, despite the breeding season and mid-day temperatures being strongly correlated ($r_{\text{Pearson}} = 0.87$), we fitted both as predictors within the same model. Second, we have specified a model with breeding season and residual mid-day temperature as predictors. The residual mid-day temperature represents residuals of a model with the mid-day temperature as a response and the breeding season as a predictor. Third, we specified a complementary model with the mid-day temperature and the residual breeding season as predictors. The residual breeding season represents residuals from a model with the breeding season as a response and the mid-day temperature as a predictor. Apart from comparing the change in the effect sizes, we have also compared the model fits by Akaike's Information Criterion corrected for sample size (Anderson, 2008).

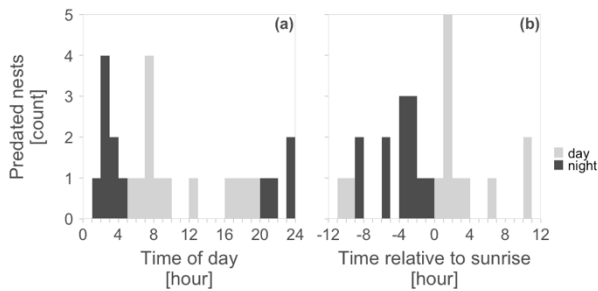
As Gaussian models are robust against the violation of model assumptions and perform well on data with the binomial and Poisson distributions (Knief and Forstmeier, 2018; Schielzeth *et al.*, 2020), we have also refitted the models on the diel pattern of predation (Table A3) and models on the probability of night predation (Table A4) with Gaussian error distribution. Such models generated similar results to the initial generalised linear models (Table A3, A4).

RESULTS

During 2018-2020, we followed 444 nests, of which 76 nests (17%) were predated, 312 (70%) hatched, 23 (5%) failed for other reason and 33 (7%) had an unknown fate. We followed the 444 nests in total for 7828 days (median 17.4, mean 17.6, range 0.3 – 67.8 days). Note that some parents truly incubated (likely infertile eggs) for excessively long periods. The daily predation rate was 0.95% (95%CrI: 0.76% – 1.19%, Table A2), which for a 30-day long incubation period translates into ~25% (20% – 30%) chance of nest being predated. The estimation of daily predation rate was insensitive to the exceptionally long observation periods or nests with unknown fate. In other words, if we limited the long observation periods (in 45 nests) to 30 days, predation rate was 0.99% (0.78% - 1.24%), when we removed the 33 nests with unknown fate, predation rate was 1.02% (0.81% – 1.29). The probability of nest predation did not change over the breeding season, and the model with breeding season was three times less likely than the simple model without breeding season, i.e. the simple model fitted the data better (Table A2).

We have continuously monitored 230 nests (52% of nests), on average for 10.3 days (median = 7.7 days, range: 1.2h – 44 days). During the 2779 continuously monitored nest-days 25 nests were predated. Of the 25 predation events recorded via the continuous monitoring, 12 nests (48%) were predated during the night (the sun was more than 6° below the horizon; Figure 2a), 16 nests (64%) were predated during the first part of the day (between midnight and midday; Figure 2a, Table A3a), and nests tended to be predated around sunrise (Figure 2b, Table A3b). Early in the season, nests were predated mainly during the day, while later in the season mainly during the night (Figure 3, Table A4a). Nests were never predated when the ground temperatures exceeded 45°C (Figure 3b). Accordingly, the probability of night predation increased with increasing mid-day temperatures (Figure 4, Table A4b). We were unable to distinguish the effect of season and temperature (Table A4c, d). Although the model containing only the breeding season seems the one most supported by the data and twice as likely as the second-best model with midday temperature (Table A5), the AICc difference between these two models was only 1.48, suggesting that the models are nearly identical.

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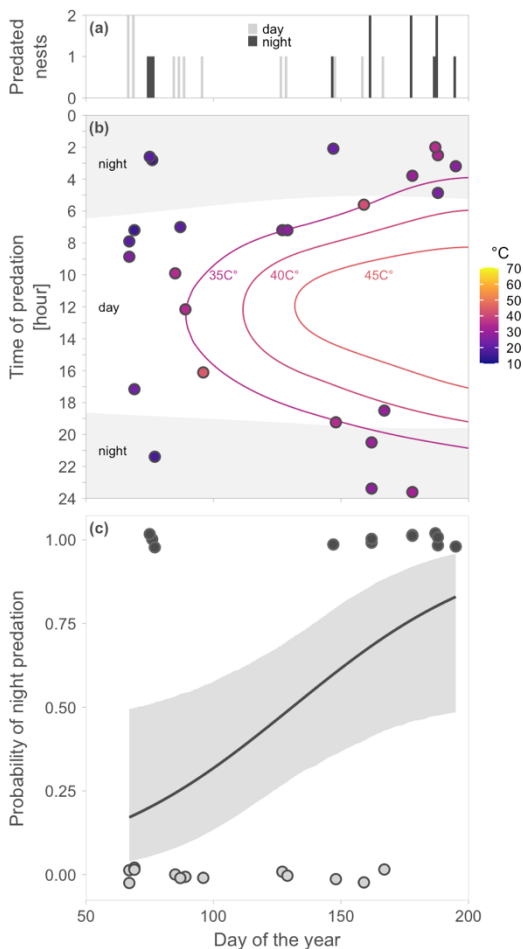
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Figure 2 | Diel timing of nest predation on red-wattled lapwing nests. Distribution of nest predation across the day (a) and in relation to sunrise (b) with night predation (sun >6° below the horizon) in black, daylight predation in grey. Each bar represents a single hour.



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Figure 3 | Change in diel timing of predation on red-wattled lapwing nests across the breeding season. Distribution of nest predation events across the breeding season (day of the year) indicating the day (grey) and night (black) predation events (a,c) and the time of the day (b). b, each dot represents a single predation event, dot colour indicates hourly-median temperature (on the ground, next to the nest) at the time of predation. Lines represent predicted isotherms (based on ground temperatures recorded next to nests). The colour scale represents the range of hourly-median ground temperatures in the study area and the grey polygons indicate night (sun >6° below the horizon). Note that no nests were predicated when ground temperatures > 45°C. c, Increase in probability of night predation across the breeding season. The line with shaded area represents the predicted relationship with 95% CIs based on the joint posterior distribution of 5,000 simulated values generated by the "sim" function in R (Gelman et al., 2016) from the output of the binomial model (Table A4a). The dots represent single cases of the day (grey) and night (black) predation.

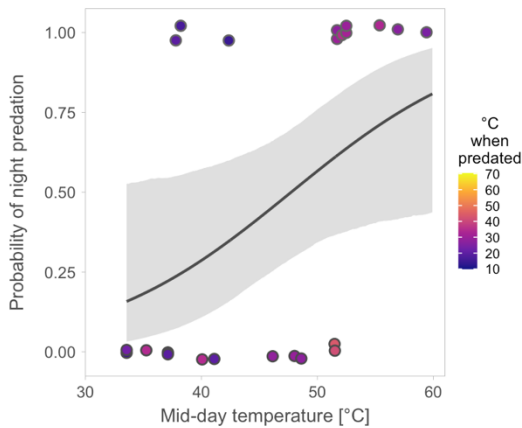


Figure 4 | Change in diel timing of predation on red-wattled lapwing nests in relation to mid-day temperatures. Each dot represents a single predation event. Top dots represent night predation (sun $>6^\circ$ below the horizon), bottom dots daylight predation. Dot colour indicates median hourly temperature (on the ground, next to the nest) at the time of predation and the colour scale represents the range of hourly-median ground temperatures within the study area. Note that ground temperatures at the time of predation never exceed 45°C , despite higher ground temperatures during daylight hours being common later in the breeding season (Figure 1 and 3b). The line with shaded area represents the predicted relationship with 95%CrIs based on the joint posterior distribution of 5,000 simulated values generated by the "sim" function in R (Gelman *et al.*, 2016) from the output of the binomial model (Table A4b).

DISCUSSION

Our results indicate that the red-wattled lapwings, breeding in the sub-tropical, arid, artificial habitat, had a low nest predation rate that was constant over the breeding season. Our data further revealed that the predation events tended to concentrate around sunrise, and night predation was more common later in the season when mid-day temperatures are high.

Daily predation rate

The relatively low nest predation rate ($\sim 25\%$) in our red-wattled lapwing population dramatically contrasts with the 60% nest predation rate of red-wattled lapwings breeding in rural India (Sethi *et al.*, 2011), as well as with the nest predation rate of other related sub-tropical plover species (35-75%; Makrigianni *et al.*, 2008; Lomas *et al.*, 2014; AlRashidi, 2016; Mishra, Kumar and Kumar, 2020). The low predation rate also contrasts with nest predation rate of most other plovers and shorebirds (Šálek and Šmilauer, 2002; Watson *et al.*, 2006; Cepáková *et al.*, 2007; Macdonald and Bolton, 2008; Sheldon *et al.*, 2013; Mayfield based predation rates in Vojtěch Kubelka *et al.*, 2018; and Bulla *et al.*, 2019), as well as with nest predation rate of many other birds breeding in arid and also non-arid environments (Shkedy and Safriel, 1992; Mezquida and Marone, 2001; Weidinger, 2002; Freeman *et al.*, 2020).

In contrast, the relatively low nest predation rate in our red-wattled lapwing population ($\sim 25\%$) is reminiscent of low predation rates found in the suburban population of red-wattled lapwings breeding on rooftops in India (15% Sethi *et al.*, 2011), (ii) suburban and agricultural population of masked lapwings (*Vanellus miles*) from Australia (0% and 5% Cardilini *et al.*, 2013), or population of spur-winged lapwings (*Vanellus spinosus*) nesting in agricultural landscape and rooftops in Israel (14% Yogeve, Ar and Yom-tov, 1996; 31% Yogeve and Yom-tov, 1997). Note that most of these predation estimates represent apparent predation rate (not controlled for observation period) and are based on limited sample sizes. Nonetheless, if the reported findings are close to reality, lapwings of genus *Vanellus* may be flexible and well adapted for the suburban and man-altered habitats. Such adaptations may include colonisation of safe sites (such as islands) with generally low density of predators (Yogeve and Yom-tov, 1997; Sethi *et al.*, 2011), and/or an active nest defence (Larsen, 1991; Królikowska, Szymkowiak and Laidlaw, 2016).

Given that our red-wattled lapwing population breeds in man-altered breeding habitat, it may be debated whether the reported nest predation rate is comparable with the nest predation rate from other populations, species or geographical regions. There are two reasons why we believe that our results are comparable. First, pristine habitats are becoming increasingly scarce and many shorebird species (e.g. European population of northern lapwings or black-tailed godwits; Beintema, 1986; Vojtěch Kubelka *et al.*, 2018) breed in or depend on man-altered habitats (e.g. arable fields, fishponds, or intensively managed meadows). Red-wattled lapwings breeding on Arabian Peninsula and other plover species are not an exception (Yogev and Yom-tov, 1997; Narwade, Fartade and Fartade, 2010; Cardilini *et al.*, 2013). Second, even seemingly pristine study sites are often located in accessible regions, close to roads and cities (Liebezeit and Zack, 2009; Liebezeit *et al.*, 2009; Bulla *et al.*, 2014) that attract mammalian and avian predators. In other words, man-altered habitats are currently “natural” breeding habitats for red-wattled lapwings and for many avian species and hence we consider our results representative of the red-wattled lapwing population and comparable with other nest predation data. As such, the low predation rate in our sub-tropical population undermines the general assumption about latitudinal gradient in predation rates that expects the increase in nest predation rates from the north to the south (Ricklefs, 1969; Stutchbury and Morton, 2013). However, whether our finding holds for other sub-tropical species, especially those with less active nest-defence strategies, or is just an exception to the rule requires further investigations.

Diel timing of nest predation

The predation events were distributed evenly across day and night, with a tendency for higher predation around sunrise (Figure 2, Table A3). The lack of distinct day-night difference is surprising and goes against our initial prediction. First, red-wattled lapwings actively protect their nests against day-light predators, often in groups of up to seven individuals (Narwade, Fartade and Fartade, 2010; Kaur and Khera, 2017, own observations). Second, the closely related northern lapwings - breeding in the temperate region and having a two to three-times higher nest predation rate (Šálek and Šmilauer, 2002; Macdonald and Bolton, 2008) - also drive away approaching predators during daylight, but ~82% of nest predation events occur at night (Brynychová *et al.*, 2020). It is unclear whether such difference arises because red-wattled lapwings face a different community of predators (Table A0, vs. predators in: Brynychová *et al.*, 2020) and/or might be less effective in driving away some predators than northern lapwings. To identify nest predators, we continuously video-recorded ~116 days of incubation, but (given the low predation rate in our population) have not recorded a single predation event. Knowing who predated the red-wattled lapwing nests is essential for clarifying why (despite active nest defence) their nests are predated around the clock.

The lack of overall differences between day and night predation are described, but not formally tested, from the sub-arctic and arctic regions (Tulp *et al.*, 2001; Laidlaw *et al.*, 2020), and anecdotal evidence suggests that it may be found also in species from regions with a probably similar composition of predator community (Shkedy and Safriel, 1992; Kosztolanyi *et al.*, 2009). Moreover, around the clock predation is common in ground-nesting passerines (Praus and Weidinger, 2010; Weidinger, 2010; Pietz *et al.*, 2012), as well as in small shorebirds, that do not actively deter predators (Macdonald and Bolton, 2008; Kasun B. Ekanayake *et al.*, 2015).

Despite the overall even distribution of predation events across day and night (i.e. despite fairly constant diel predation pattern; Figure 2), and although daily predation rate changed little over the breeding season (Table A2), the diel timing of predation changed over the breeding season (Figure 3, Table A4 and A5). Specifically, daylight predation nearly disappeared, and the probability of night predation increased, as the season progressed. We offer two (mutually non-exclusive) explanations of this pattern.

First, birds of prey (daytime predators, such as harriers, kites and eagles; Table A0, eBird, 2020) migrate from and through the study area early in the breeding season while mammalian predators (mostly nocturnal predators) stay year-round (Table A1). The lack of migratory birds of prey later in the breeding season certainly reduces predation pressure during the day (Figure A2).

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Second, the ambient and surface temperatures dramatically increase over the breeding season (Figure 1) to the point where mid-day activity of endotherms is close to impossible (Albright *et al.*, 2017; Streicher *et al.*, 2017; Abdu *et al.*, 2018). During such high temperatures, lapwing parents incubate (often rather shade) their eggs continuously to avoid lethal overheating of the embryos (Grant, 1982; Brown and Downs, 2003). Such continuous presence of parents on the nest may protect the nest from smaller predators - such as common maynas (*Acridotheres tristis*), southern grey shrikes (*Lanius meridionalis*), or Indian rollers (*Coracias benghalensis*) - that can predate upon eggs, but not upon incubating adults (Verboven, Ens and Dechesne, 2001; Feare *et al.*, 2015). Perhaps more importantly, to minimize energy expenditure and other costs, most animals are inactive during the hottest part of the day (Brown and Downs, 2003; Streicher *et al.*, 2017; Alagaili *et al.*, 2020). Indeed, we found that all predation events with a known time of predation occurred when temperatures were lower than 45°C (Figure 3b). In other words, when mid-day temperatures were high, predation was more likely to occur at cooler parts of the day, usually at night (Figure 3, 4, Table A4).

We speculate that leaving of the migratory avian predators might be less important in driving the temporal trend in diel timing of predation than the increase in temperatures. First, if migratory birds of prey were the key nest predators, their departure from the study site for northerly breeding grounds would decrease daily nest predation across the breeding season (Shkedy and Safriel, 1992), which was not the case (Figure 2a, Table A2). However, the decrease of seasonal change in daily nest predation rate might be masked by increase in predation pressure from other predator communities. For example, later in the season when days get extremely hot, resident predators (Table A1) - such as egrets and herons (*Ardea* spp.), brown-necked ravens (*Corvus ruficollis*), common maynas, grey shrikes, or Indian rollers - concentrate around the artificial water bodies and hence in the vicinity of lapwing nests (personal observation). Also, the offspring of these predators disperse (Patnode and White, 1992; Sloan, Holmes and Sherry, 1998). Consequently, both, the concentration of predators around water bodies and dispersing offspring of predator species, may increase the daylight nest predation pressure, and hence offset the decrease in day-light predation pressure from migratory birds. Second, most migratory avian predators start leaving the study area in March and most disappear from the study area by the end of April (Figure A2, Table A1, eBird, 2020). However, despite the absence of migratory predators, we recorded cases of daylight predation in May, and daylight predation disappeared only from June onwards (Figure 3b). In contrast, ground temperatures gradually increase over the whole breeding season (Figure 1) and such increase continues until the end of July. Importantly, the nest predation cases follow such increase in mid-day temperatures by moving into the colder parts of the day well before the migratory predators leave the study site, i.e. despite the presence of migratory predators (Figure 3b). Thus, mid-day temperature is likely a stronger driver for the diel change in nest predation than the absence of migratory predators. Nevertheless, the current information on the precise timing of predation is limited. Thus, whether such change in the timing of predation – linked to mid-day temperatures – is present in other locally breeding species or avian and non-avian species from other hot environments awaits further investigations.

Regardless of the likely drivers of the changes in the diel pattern of nest predation, the finding generates three predictions (worth future investigations) about the behaviour of incubating red-wattled lapwing parents and parents of any other biparentally incubating species experiencing a similar diel pattern of predation. First, given the seasonal changes in the diel pattern of nest predation, we expect seasonal changes in the diel pattern of nest attendance. Specifically, as active nest-protection during the night is unlikely (e.g. because a parent sees an approaching predator only at a short distance) we expect increasing constancy of incubation (decreasing movement on the nest and decreasing number of parental exchanges on the nest) as the season progresses and night predation becomes more likely. Second, as the season progresses, the parents may afford to reduce their alertness in the hottest part of the day. Specifically, they are expected to preen and sleep on the nest during the day, similarly to the northern lapwings (Brynychová *et al.*, 2020). Also, an off-nest parent on the watch for predators may not be necessary. The off-nest parent may thus forage, preen or sleep instead.

Conclusions

We found a relatively low predation rate in the sub-tropical population of poorly studied red-wattled lapwings, breeding in arid, artificial habitat. Such low predation rate contrast with higher predation rates found in related and unrelated species breeding both in the desert and other habitats (Mezquida and Marone, 2001; Mayfield based predation rates in Vojtěch Kubelka *et al.*, 2018; and Bulla *et al.*, 2019; Freeman *et al.*, 2020). These results suggest that man-made sites are suitable breeding habitats in deserts, where natural water sources are scarce. In addition, the low nest predation rate in our population may be a general phenomenon driving the recent increase of red-wattled lapwings on the Arabian Peninsula. The predation in our population tended to concentrate around sunrise. Whereas we found little variation in daily predation rate across the breeding season, the probability of night predation increased over the season, likely due to the extreme heat during the mid-day. These results highlight the need for continuous monitoring to reveal the temporal pattern of predation on multiple time scales, as well as the need for further studies on the timing of predation to evaluate whether the seasonal pattern in temperature-driven predation is a general rule or an exception to the rule.

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Conflict of interest

None

Author contributions (<https://casrai.org/credit/>):

Conceived and supervised the long-term study: MŠ
Conceptualized the long-term study: MŠ, MS, MB
Administered the long-term study: MŠ
Funding acquisition: MŠ, MS, EV, EE
Data collection / Investigation: MŠ, MS, EE, KB, VJ, EV, PC, VF, LP
Data curation / management: MS, KB, MB
Conceptualized the manuscript: MB and MS
Formal analyses: MS and MB
Visualization: MB and MS
Repository: MB and MS
Writing – original draft: MB and MS
Writing – review & editing: all authors
Writing – revising and finalizing: MB and MS

Data and computer coded availability statement

All data and computer code to replicate our analyses, as well as plots of model assumptions, are freely available from GitHub: https://github.com/MartinBulla/RWLE_predation_timing.

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Appendix

Table A1 | Potential predators of red-wattled lapwing eggs in the study site at Al Marmoom Conservation Reserve

Common name	Scientific name	Abundance	Activity	Present
Montagu's harrier	<i>Circus pygargus</i>	Regular, but not abundant	day	October - March
Pallid harrier	<i>Circus macrourus</i>	Regular, but not abundant	day	October - March
Black-eared kite	<i>Milvus lineatus</i>	Rare	day	October - March
Western marsh harrier	<i>Circus aeruginosus</i>	Common and abundant	day	September - April
Common mayna	<i>Acridotheres tristis</i>	Common and abundant	day	year-round
Common moorhen	<i>Gallinula chloropus</i>	Common and abundant	day	year-round
Brown-necked raven	<i>Corvus ruficollis</i>	Common and abundant	day	year-round
Herons/Egrets	<i>Ardea spp.</i>	Common and abundant	day	year-round
Indian roller	<i>Coracias benghalensis</i>	Regular, but not abundant	day	year-round
Common kestrel	<i>Falco tinnunculus</i>	Regular, but not abundant	day	year-round
Southern grey shrike	<i>Lanius meridionalis</i>	Regular, but not abundant	day	year-round
Feral cats	<i>Felis catus</i>	Common and abundant	day/night	year-round
Black rat	<i>Rattus rattus</i>	Common and abundant	night	year-round
Arabian red fox	<i>Vulpes v. arabica</i>	Regular, but not abundant	night	year-round
Desert monitor	<i>Varanus griseus</i>	Regular, but not abundant	day	year-round

Avian predators are at the top, other predators at the bottom. The species are ordered according to their presence in the study area and from most to least abundant (based on Dubai municipality internal reports and our haphazard observations). Migratory predators are highlighted in grey. Note that none of the migratory predators forages at night.

Table A2 | Daily predation rate on red-wattled lapwing nests

Model	Effect	Original scale			Binomial scale			AICc	$\Delta AICc^a$	w_i^b	ER ^c
		Estimate	95%CrI		Estimate	95%CrI					
(a)	(Intercept)	0.95%	0.76%	1.18%	-4.65	-4.89	-4.42	615.86	0	0.7	1
(b)	(Intercept)	1.18%	0.55%	2.47%	-4.44	-5.19	-3.67	617.54	1.68	0.3	2.33
	Season	49.95%	49.80%	50.11%	0	-0.01	0				

Shown are the posterior estimates (medians) of the effect sizes with the 95% credible intervals (CrI) from a posterior distribution of 5,000 simulated values generated by the "sim" function in R. Response variable indicates whether a nest was predated (0 or 1) and the number of days in which a nest survived as a binomial denominator. We present both, back-transformed estimates representing daily predation rate in percentages and estimates on the binomial scale. The AICc comparison was performed with the "AICc" function from the "MuMIn" R-package (Kamil Bartoń 2020). N = 444 nests of red-wattled lapwings from a population near Dubai.

^aThe difference in AICc between the first-ranked model and the given model.

^bAkaike weight – the weight of evidence that a given model is the best approximating model (i.e. probability of the model).

^cEvidence ratio – the model weight of the first-ranked model relative to that of the given model (i.e. how many times is the first-ranked model more likely than the given model).

Table A3 | Diel pattern of predation on red-wattled lapwing nests

Model	Response	Error structure	Effect	Estimate	95%CrI
(a) Time of day	Predation per hour	Poisson	(Intercept)	-0.087	-0.532
			sin(time)	0.533	-0.035
			cos(time)	0.481	-0.11
(a) Time of day	Predation per hour	Gaussian	(Intercept)	1.039	0.469
			sin(time)	0.535	-0.283
			cos(time)	0.471	-0.335
(b) Time relative to sunrise	Predation per hour	Poisson	(Intercept)	0.709	0.043
			Absolute time from sunrise	-0.121	-0.246
(b) Time relative to sunrise	Predation per hour	Gaussian	(Intercept)	1.84	0.848
			Absolute time from sunrise	-0.13	-0.278

Shown are the posterior estimates (medians) of the effect sizes with the 95% credible intervals (CrI) from a posterior distribution of 5,000 simulated values generated by the "sim" function in R. Response is specified as a number of predation events per hour of the day (a; N = 24 hours) and per each hour, centred around sunrise (b; N = 23 hours).

Table A4 | Probability of night predation on red-wattled lapwing nests

Model	Response	Error structure	Effect	Estimate	95%CrI	
(a) Season	Night predation (0,1)	binomial	(Intercept)	-3.195	-6.058	-0.419
			Season	0.024	0.004	0.045
(b) Midday Temperature	Night predation (0,1)	Gaussian	(Intercept)	-0.202	-0.746	0.333
			Season	0.005	0.001	0.009
	Night predation (0,1)	binomial	(Intercept)	-5.629	-11.149	-0.331
			Midday temperature	0.117	0.008	0.23
(c) Midday Temperature & season	Night predation (0,1)	Gaussian	(Intercept)	-0.717	-1.823	0.395
			Midday temperature	0.026	0.002	0.049
			Season	-3.461	-9.5	2.657
	Night predation (0,1)	binomial	(Intercept)	0.01	-0.19	0.21
			Midday temperature	0.023	-0.015	0.06
			Season	-0.276	-1.597	1.056
(d) Residual midday temperature & season	Night predation (0,1)	Gaussian	(Intercept)	0.002	-0.042	0.048
			Midday temperature	0.005	-0.003	0.013
			Season	-3.229	-5.966	-0.489
	Night predation (0,1)	binomial	(Intercept)	0.01	-0.19	0.208
			Residual temperature	0.025	0.004	0.044
			Season	-0.199	-0.743	0.344
(e) Residual season & midday temperature	Night predation (0,1)	Gaussian	(Intercept)	0.002	-0.042	0.047
			Residual temperature	0.005	0.001	0.009
			Season	-5.678	-10.952	-0.431
	Night predation (0,1)	binomial	(Intercept)	0.023	-0.015	0.06
			Residual season	0.118	0.011	0.227
			Midday temperature	-0.733	-1.766	0.281
(f) Residual temperature	Midday temperature	Gaussian	(Intercept)	0.005	-0.002	0.013
			Midday temperature	0.026	0.005	0.047
			Season	26.9	21.61	32.14
(g) Residual season	Season	Gaussian	(Intercept)	0.16	0.12	0.2
			Midday temperature	-94.24	-152.61	-38.65
				4.7	3.53	5.9

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Shown are the posterior estimates (medians) of the effect sizes with the 95% credible intervals (CrI) from a posterior distribution of 5,000 simulated values generated by the "sim" function in R. N = 25 nests. Note that residuals from (f) were used in (d) and residual from (g) in (e).

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Table A5 | Probability of night predation on red-wattled lapwing nests – AICc model comparison

Model	Predictors	AICc	$\Delta AICc^a$	w^b	ER ^c
(a) Season	Season	32.53	0	0.43	1
(b) Midday Temperature	Midday temperature	34.01	1.48	0.21	2.05
(c) Midday T & season	Season & Midday temperature	35.12	2.59	0.12	3.58
(d) Residual T & season	Season & Residual midday temperature	35.12	2.59	0.12	3.58
(e) Residual season & T	Midday temperature & Residual season	35.12	2.59	0.12	3.58

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Model names correspond to the model names in Table A4. The AICc comparison was performed with the AICc function from the MuMIn R-package (Kamil Bartoń 2020) and separately for binomial and Gaussian models, which generated identical results.

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^aThe difference in AICc between the first-ranked model and the given model.

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^bAkaike weight – the weight of evidence that a given model is the best approximating model (i.e. probability of the model).

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^cEvidence ratio – the model weight of the first-ranked model relative to that of the given model (i.e. how many times is the first-ranked model more likely than the given model).

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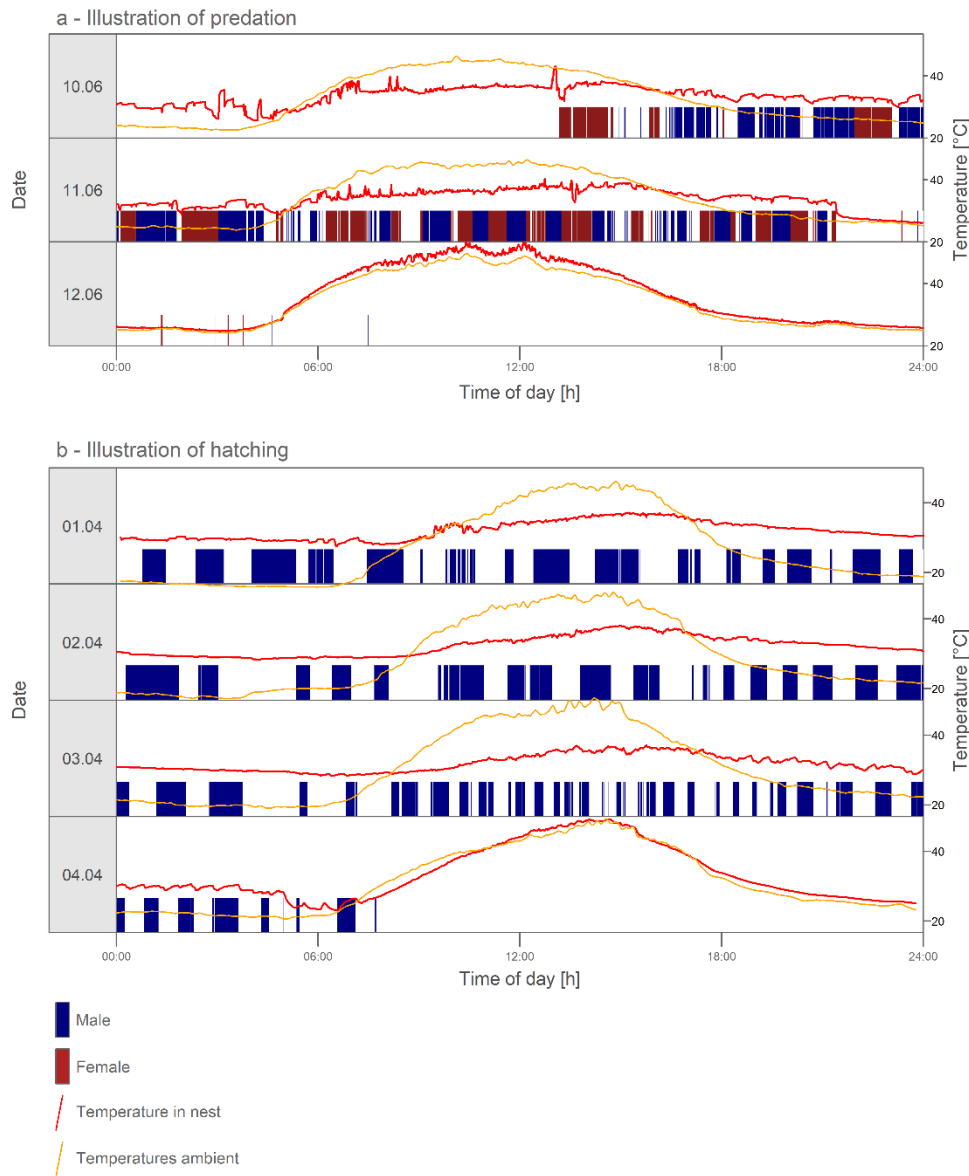


Figure A1 | Illustration of predation and hatching on continuous recordings from red-wattled lapwing nests. a, b, Red line indicates nest temperatures, orange line ground temperatures next to the nest. Bars indicate RFID recording of female (dark red) and male (blue) on the nest. **a,** Nest was predated in the evening of June 11 when nest temperatures quickly drop and reach ground temperatures. Despite the nest predation, parents still occasionally passed over the nest until the morning of June 12. **b,** Nest hatched in the morning on April 4. Note the difference between the changing nest temperatures in the morning on April 4 (indicating chick presence on the nest) and smooth nest temperatures in the morning on April 3. The change in temperature and RFID pattern is visible even if only a single parent (here male) is tagged.

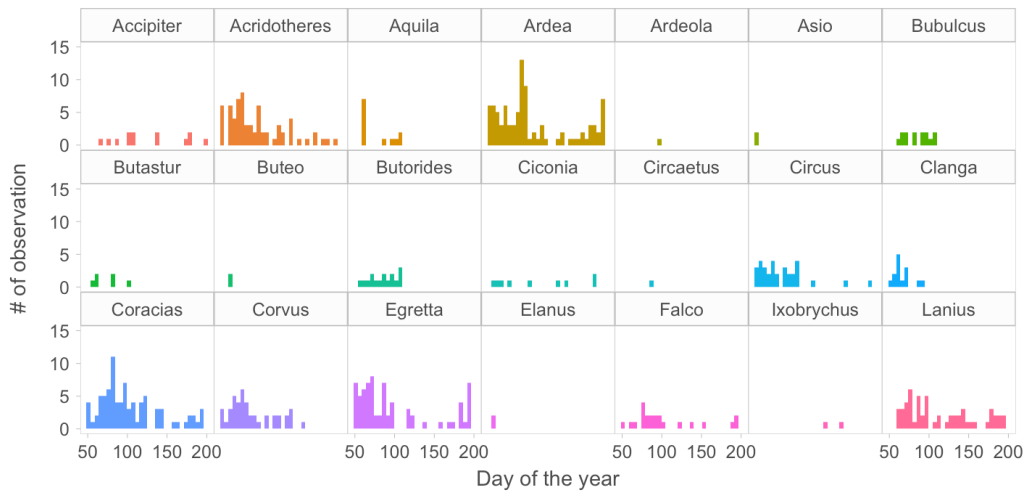
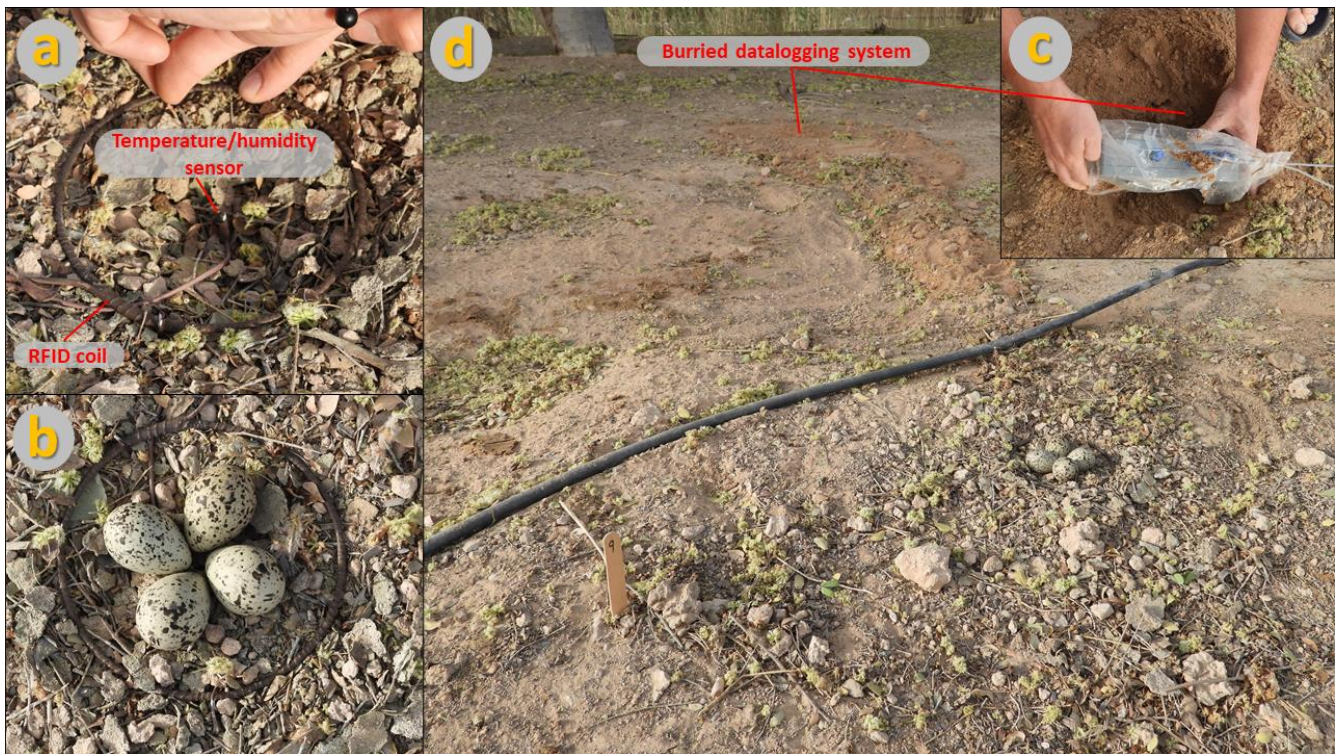


Figure A2 | Changes in numbers of potential avian predators of red-wattled lapwing nests over the breeding season. Bars represent a number of observations of a given genus during each day of the breeding season based on all eBird data (N = 557 observations) available for Dubai until 1. March 2021 (eBird, 2020). The number of seen individuals varies between observations, but in 74% of observations one or two individuals were observed or the number of individuals was unreported. In 5% of observation >10 individuals were observed. Although these data confirm the suspected pattern with migrating species disappearing over the breeding season, the pattern can also reflect increasing mid-day temperatures accompanied by a decrease in bird watching activities of local inhabitants.



Picture A1 | Installation of the ZAYDA incubation monitoring system on a red-wattled lapwing nest. Minute temperature/humidity probe is placed between the eggs (a), RFID coil around the eggs (a, b), the system, including the cables, is hidden under the ground (c, d).