




ORIGINAL RESEARCH

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 subtropics. Importantly, we know fairly little about the timing of predation within a day. Here, we followed 444 nests of the red-wattled lapwing (*Vanellus indicus*), a ground-nesting shorebird, for a sum of 7,828 days to estimate a nest predation rate, and continuously monitored 230 of these nests for a sum of 2,779 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 evenly distributed across day and night, with a tendency for increased predation around sunrise, and evenly distributed 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 midday 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 await future investigations.

KEYWORDS

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

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1 | INTRODUCTION

Predation affects the reproduction of wild populations (Caro, 2005; Ricklefs, 1969; Skutch, 1985). 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 (Bulla et al., 2019; Freeman et al., 2020; Kubelka, Šálek, et al., 2018; Unzeta et al., 2020), which hampers 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 nest predation”; Praus & Weidinger, 2010; Weidinger, 2010; DeGregorio et al., 2015; Brynychová et al., 2020; Laidlaw et al., 2020), perhaps because it requires continuous nest monitoring (Pietz et al., 2012; Weidinger, 2006).

Knowing when nests of a given species or population are predated may help in interpreting various behaviors of incubating parents, such as the timing of breeding season (Morton, 1971), pattern of nest attendance (Bakner et al., 2019; Cervencel et al., 2011; Kasun B Ekanayake et al., 2015; Massaro et al., 2008; Skórka et al., 2012; Sládeček et al., 2019), or daily rhythms of self-maintenance activities (Brynychová et al., 2020; Javůrková et al., 2011). Notably, given the lack of information on diel timing of nest 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 hr a day during the breeding season?

Diel timing of nest predation for a given avian species likely depends on its anti-predatory strategy (Brynychová et al., 2020; Bulla et al., 2016; Eggers et al., 2008), as well as on when its main predator species are active (DeGregorio et al., 2015; Kämmerle et al., 2020). For example, corvids (*Corvidae*) are active and search for their prey during daylight hours (Tahajjul Taufique et al., 2016), but ground-nesting northern lapwings (*Vanellus vanellus*) actively protect their nests by chasing away corvids (and other daylight 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 & 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 in the tropics (Robinson et al., 2005; Visco & Sherry, 2015) and parts of temperate North America (Weatherhead & 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 (Batáry et al., 2004; Mezquida & Marone, 2001; Morton, 1971; Sieving, 2019), and with changes in the presence of main predators,

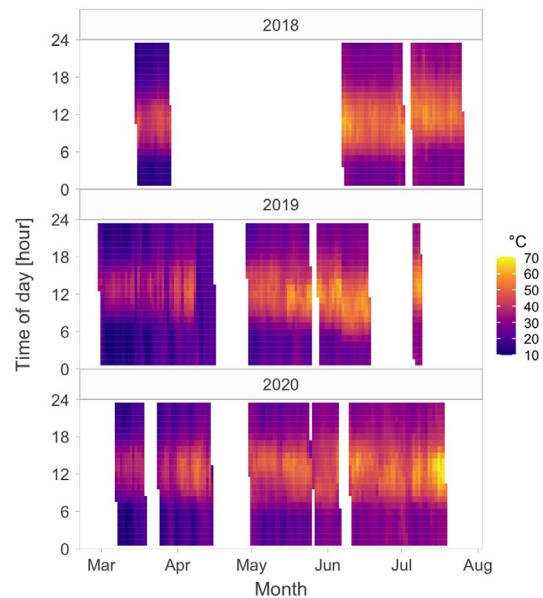


FIGURE 1 Changes in hourly ground temperatures across day and season. Depicted are median hourly ground temperatures in the study area based on all recordings of sensors located next to the nests at a given hour (see Methods for details). White space indicates no temperature recordings

for example, due to migration or due to dispersal of new generations (Patnode & White, 1992; Sloan et al., 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*), a shorebird breeding in an arid and hot subtropical environment. Specifically, we followed 444 nests south of Dubai, United Arab Emirates, for a sum of 7,828 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 2,779 days to reveal the diel timing of nest predation and its changes over the breeding season.

We tested the following three predictions. First, we expected daytime nest predation to be less common than night-time nest predation 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 (Kaur & Khera, 2017; Narwade et al., 2010). Second, we expected nest predation to decrease over the season because some overwintering avian predators migrate out and migrating avian predators pass through the study area early in the lapwing's breeding season (eBird, 2020) and because other avian chicks—an alternative prey to red-wattled lapwing nests—are available later in the breeding season (personal observation). Third, we expected daylight nest predation (if any) to decline over the breeding season, because the presence of migrating avian predators—daylight predators of nests—declines over the breeding season (Table A1 eBird, 2020) and because ambient and ground temperatures increase dramatically over the breeding season (Figure 1) to the point where midday activity of most endotherm animals is close to impossible (Abdu et al., 2018; Albright et al., 2017; Streicher et al., 2017).

2 | METHODS

2.1 | 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 (Figure 2).

The red-wattled lapwing is a poorly studied ground-nesting shorebird species that breeds mainly in human-altered habitats such as corn and grass fields, larger gardens, or waste, fallow and plowed 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 consists of approximately 80 breeding pairs. The breeding season lasts from early February to the beginning of August, and some individuals

have several (up to 5) breeding attempts (our unpublished data). The red-wattled lapwings nest on islands and within the tree plantations in the vicinity of lakes. They build their nests on the ground. Incubating parents are readily visible on the nest from afar (Figure 2). Both parents continuously attend the nest and nests are rarely left unattended. When eggs hatch, parents remove large eggshells 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.

2.2 | 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 (Figure 2). We used this same noninvasive method to monitor

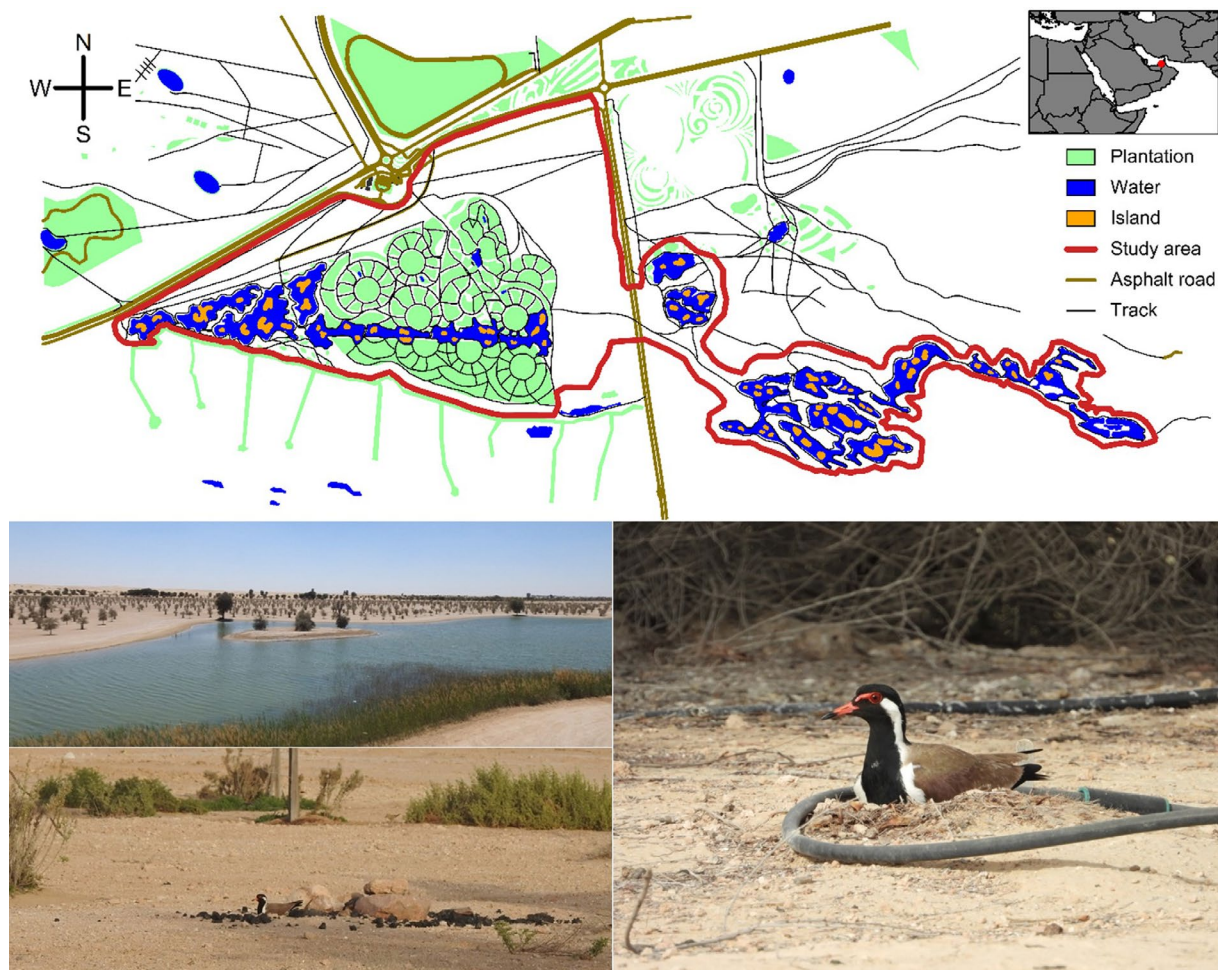


FIGURE 2 Study site and illustration of how readily visible are incubating red-wattled lapwings. Note that the lapwings often breed close to irrigation pipes (right picture). Map based on ©OpenStreetMap contributors and our digitalization of the study site. Pictures: ©Miroslav E. Šálek

nests during incubation. 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 likely found most lapwing nests within the study area and followed most of the parents that guided their chicks. Upon finding a nest, we measured and floated the eggs to estimate when a clutch was initiated and likely to hatch (see below).

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 color rings and a green flag embedded with a glass passive integrated transponder (Biomark: Ø 2.1 × 9.0 mm, 0.087 g, ISO FDXB, <http://www.biomark.com/>, see Appendix Picture A1 in (Bulla et al. 2013); or Smartrac 704487-09 Glass tag Ø 2.12 × 12 mm, <https://rfid.averydennison.com>). The transponder enabled us to determine the presence of the specific bird on the nest. We took a small (ca. 50 µl) blood sample from a brachial vein for sexing and 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 et al., 2019), 188 nests with data loggers 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 transponder of an incubating parent in 5-s interval (Bulla et al., 2014), 40 nests with multisensory data logger 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://anittracking.com>). The dummy eggs were placed into the nests with less than 4 eggs and were accompanied by a temperature logger (DHT 2.1) placed in the vicinity of the nest. The temperature-humidity data loggers (DHT 2.1) and multisensory loggers (ZAYDA 1.1) were installed similarly to the other temperature loggers and RFIDs (Picture A1 and Bulla et al., 2014).

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

2.3 | 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 et al., 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, based on observations of (i) at least one chick on or around the nest during the final nest-check ($N = 197$ nests), (ii) color-marked parents guiding chicks after the final nest visit ($N = 36$ nests), or (iii) small (≤ 5 mm) eggshell pieces in the nest that result from a chick chipping its way out of its egg ($N = 79$; Brown et al., 2014; Mabee et al., 2006). The use of eggshell pieces has been used to define successfully hatched nests in other shorebird species (Kentie et al., 2015; Laidlaw et al., 2020). Importantly, we ringed 233 chicks whose identity was unknown as they were found away from nests. Most of these 233 chicks likely came from the 79 nests where we assumed hatching based on eggshell pieces, because (a) we follow nearly all nests within the study area, (b) families with chicks stay within the study area as chicks would die in the surrounding desert, and (c), 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 came 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). Moreover, these 79 nests where we identified hatching based on tiny eggshell pieces have little influence on our estimation of predation rate; treating these nests as unknown (i.e., observation period ending at the last visit when the nest was still active) generates similar predation rate as when we treat these nests as hatched.

We estimated the hatch date in the following way and order. First, we assumed that the nest hatched 1 day ago if we knew when the chicks left the nest (a) based on the visualized continuously recorded data ($N = 91$) or (b) freshly hatched chicks found around the nest ($N = 24$). Second, we assumed that the nest hatched 12 hr earlier than our nest visit if during the nest visit both eggs and chicks were found in the nest (i.e., eggs were in the process of hatching; $N = 50$). Third, if a nest was found empty but with 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 discovered 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 (a) empty without signs of hatching, that is, without tiny egg-shell pieces that indicate hatching, and if parents were ringed, they were never seen with chicks and did not alarm call ($N = 69$; 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 (b) with remains of predated eggs ($N = 5$) or (c) with some eggs missing and some eggs abandoned (no parents around) before expected hatching (i.e., partially predated $N = 2$). Note that 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, that is, 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 the 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 estimated 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). This approach resulted in 39 additional nests with no observation period (15 failed for other reason and 24 with unknown fate); these 39 nests were not used in the analyses.

2.4 | 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 midday ground temperature of the day when the nest was predated.

2.5 | Data analysis

2.5.1 | 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 noninformative prior distribution (Gelman & Hill, 2007; Gelman et al., 2016) to create a sample of 5,000 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 (95%CrI) represented by 2.5 and 97.5 percentiles of the posterior distribution of the 5,000 simulated or predicted values.

2.5.2 | Daily nest 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 $1 - (1 - \text{daily predation rate})^{\text{days-long incubation period}}$ (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 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: 35% (67 adults) at two nests, 14% (27 adults) at three nests, 5% (11 adults) at four nests, and 8% (16 adults) at >4 nests. In an attempt to control for this nonindependence of data points, we 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 non-sensical estimates. The same was the case for models with only pair identity, only male identity, or only female identity. Our simulations revealed that this was 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 used 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 (McGuire et al., 2020; Meyer et al., 2020; Weiser et al., 2016, 2018). Importantly, this issue seems negligible because when we removed the known re-nesting events within each year (i.e., used only the first nesting attempts, where known), the estimate and uncertainty in daily and total predation rate were similar to those from our original model (see Results).

2.5.3 | 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 events was centered around sunrise (Figure 3), 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 “mapprootools” R package (Bivand & 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; midday temperatures strongly positively correlated with the breeding season: $r_{\text{Pearson}} = 0.87$). To investigate whether the probability of night predation changed with increasing midday temperatures, we explored the relative importance of breeding season and midday temperatures by specifying and comparing

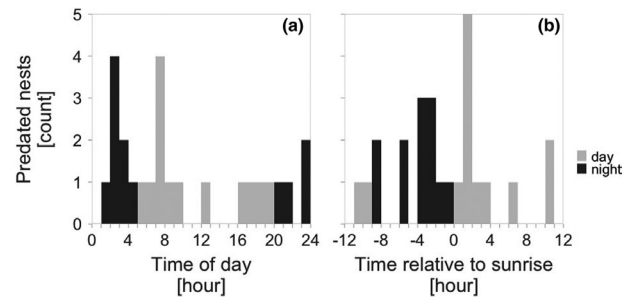


FIGURE 3 Diel timing of nest predation on red-wattled lapwing nests. Distribution of nest predation events across the day (a) and in relation to sunrise (b) with night predation (sun $>6^\circ$ below the horizon) in black, daylight predation in gray. Each bar represents a single hour

three alternative models. First, within the same model we fitted breeding season and midday temperature as predictors. Second, to evaluate whether the effect of breeding season (based on the first model) is confounded by midday temperature, we specified a model with breeding season and residual midday temperature as predictors. The residual midday temperature represents residuals of a model with the midday temperature as a response and the breeding season as a predictor. Third, to evaluate whether the effect of midday temperature (based on the first model) is confounded by breeding season, we specified a complementary model with the midday 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 midday 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 & Forstmeier, 2018; Schielzeth et al., 2020), we 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 generalized linear models (Table A3, A4).

3 | 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 7,828 days (median = 17.4, mean = 17.6, range: 0.3–67.8 days per nest). Note that some parents truly incubated (likely infertile eggs) for excessively long periods. The daily nest 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 nest predation rate was insensitive to the exceptionally long observation periods, nests with unknown fate, or multiple nesting attempts. In other words, when 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%), and when we used only the first nesting attempts, where known, predation rate was 0.93% (0.74%–1.17%, $N = 456$ nests). 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, that is, the simple model fitted the data better (Table A2).

We continuously monitored 230 nests (52% of nests) for an average of 10.3 days (median = 7.7, range: 1.2h – 44 days). During the 2,779 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 3a). Also, 64% of nests (16 out of 25) were predated during the first part of the day (between midnight and midday; Figure 3a, Table A3a), and nests tended to be predated around sunrise (Figure 3b, Table A3b). Early in the season, nests were predated mainly during the day, while later in the season mainly during the night (Figure 4, Table A4a). Nests were never predated when the ground temperatures exceeded 45°C (Figure 4b). Accordingly, the probability of night predation increased with increasing midday temperatures (Figure 5, Table A4b). We were unable to statistically distinguish the effect of season and temperature (Table A4c, d), although the model containing only the breeding season seemed 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 were nearly identical.

4 | DISCUSSION

Our results indicate that the red-wattled lapwings, breeding in the subtropical, 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 midday temperatures are high.

4.1 | Daily nest predation rate

The relatively low nest predation rate (~25%) in our red-wattled lapwing population 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), suburban and agricultural population of masked lapwings (*Vanellus miles*) from Australia (0% and 5%, Cardilini et al., 2013), and the population of spur-winged lapwings (*Vanellus spinosus*) nesting in agricultural landscape and rooftops in Israel (14%, Yogev et al., 1996; 31%, Yogev & Yom-tov, 1997). Note that most of these predation estimates represent apparent predation rate (not controlled for observation period) and are based

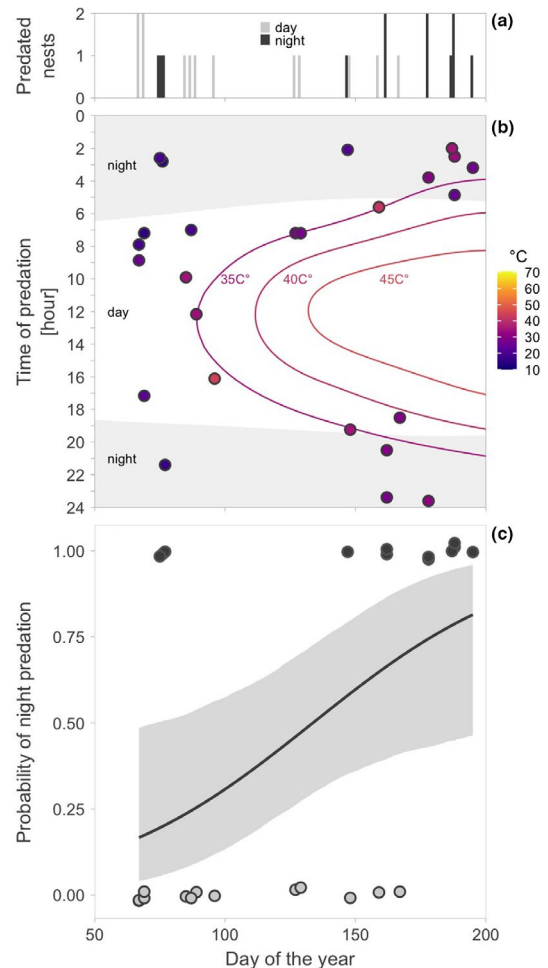


FIGURE 4 Change in diel timing of predation on red-wattled lapwing nests across the breeding season. Distribution of nest predation events across the breeding season (day of the year), gray color indicating the day and black color the night predation events (a), and in relation to the time of the day (b). b. Each dot represents a single predation event, dot color 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 color scale represents the recorded range of hourly median ground temperatures in the study area, and the gray polygons indicate night (sun $>6^\circ$ below the horizon). Note that no nests were predated when ground temperatures $>45^\circ\text{C}$. c. Increase in probability of night predation across the breeding season. 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 A4a). The dots represent single cases of the day (gray) and night (black) predation

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 human-altered habitats. Such adaptations may include colonization of safe sites (such as islands) with generally low density of predators (Sethi et al., 2011; Yogev & Yom-tov, 1997) and/or an active nest defense (Królikowska et al., 2016; Larsen, 1991).

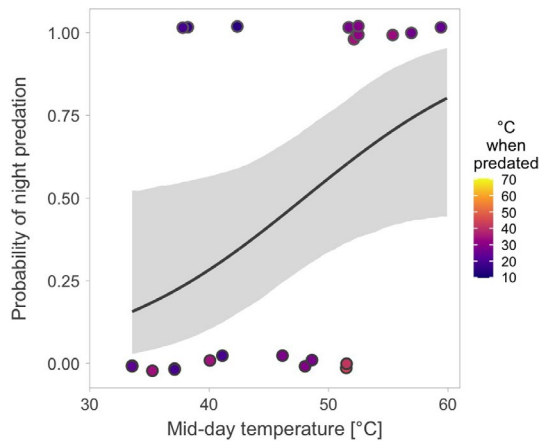


FIGURE 5 Change in diel timing of predation on red-wattled lapwing nests in relation to midday temperatures. Each dot represents a single predation event. Top dots represent night predation (sun $>6^\circ$ below the horizon), and bottom dots represent daylight predation. Dot color indicates median hourly temperature (on the ground, next to the nest) at the time of predation, and the color scale represents the range of hourly median ground temperatures recorded 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 (Figures 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)

In contrast, the relatively low nest predation rate in our red-wattled lapwing population (~25%) 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 subtropical plover species (35%–75%; Makrigianni et al., 2008; Lomas et al., 2014; AlRashidi, 2016; Mishra et al., 2020). The low predation rate also contrasts with nest predation rate of most other plovers and shorebirds (Šálek & Šmilauer, 2002; Watson et al., 2006; Cepáková et al., 2007; Macdonald & 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 nonarid environments (Freeman et al., 2020; Mezquida & Marone, 2001; Shkedy & Safriel, 1992; Weidinger, 2002).

Given that our red-wattled lapwing population breeds in human-altered 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; Kubelka, Zámečník, et al., 2018) breed in or depend on human-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 (Cardilini et al., 2013; Narwade et al., 2010; Yogev & Yom-tov, 1997).

Second, even seemingly pristine study sites are often located in accessible regions, close to roads and cities (Bulla et al., 2014; Liebezeit et al., 2009; Liebezeit & Zack, 2009) that attract mammalian and avian predators. In other words, human-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. If our nest predation rates are comparable with those from other studies, the low predation rate in our subtropical population deviates from 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 & Morton, 2013). However, whether our finding holds for other subtropical species, especially those with less active nest-defense strategies, or is just an exception to the rule requires further investigations. Furthermore, it might be worth investigating whether predation rates follow gradients of human-altered landscapes and whether predation rates differ between landscapes designated to support wildlife and those altered or built by humans for other purposes (e.g., agriculture, recreation).

4.2 | Diel timing of nest predation

The predation events were distributed evenly across day and night, with a tendency for higher predation around sunrise (Figure 3; 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 daylight predators, often in groups of up to seven individuals (Kaur & Khera, 2017; Narwade et al., 2010, own observations). Second, the closely related northern lapwings—breeding in the temperate region and having a two to three times higher nest predation rate (Macdonald & Bolton, 2008; Šálek & Šmilauer, 2002)—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 A1, versus 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 did not record a single predation event. Knowing who predated the red-wattled lapwing nests is essential for clarifying why (despite active nest defense) 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 subarctic and arctic regions (Laidlaw et al., 2020; Tulp & Schekkerman, 2001), and anecdotal evidence suggests that the lack of diel pattern in nest predation may be found also in species from regions with a similar composition of predator community (Kosztolanyi et al., 2009; Shkedy & Safriel, 1992). Moreover, around the clock predation is common in ground-nesting passerines (Pietz et al., 2012; Praus & Weidinger, 2010; Weidinger, 2010), as well as in small shorebirds, that do not actively deter predators (Ekanayake, Weston, et al., 2015; Macdonald & Bolton, 2008).

Despite the overall even distribution of predation events across day and night (i.e., despite fairly constant diel predation pattern; Figure 3), and although daily predation rate changed little over the breeding season (Table A2), the diel timing of predation changed over the breeding season (Figure 4, Table A4 and A5). Specifically, daylight predation nearly disappeared, and the probability of night predation increased, as the season progressed. We offer two (mutually nonexclusive) explanations of this pattern.

First, some birds of prey (daytime predators, such as harriers, kites, and eagles; Table A1, 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).

Second, the ambient and surface temperatures dramatically increase over the breeding season (Figure 1) to the point where midday activity of endotherms is close to impossible (Abdu et al., 2018; Albright et al., 2017; Streicher et al., 2017). During such high temperatures, lapwing parents incubate (often rather shade) their eggs continuously to avoid lethal overheating of the embryos (Brown & Downs, 2003; Grant, 1982). Such continuous presence of parents on the nest may protect the nest from smaller avian predators that do not depart the study area—such as common maynas (*Acridotheres tristis*), southern gray shrikes (*Lanius meridionalis*), or Indian rollers (*Coracias benghalensis*)—that can predate eggs, but not the incubating adults (Feare et al., 2015; Verboven et al., 2001). Perhaps more importantly, to minimize energy expenditure and other costs, most animals are inactive during the hottest part of the day (Alagaili et al., 2020; Brown & Downs, 2003; Streicher et al., 2017). Indeed, we found that all predation events with a known time of predation occurred when temperatures were lower than 45°C (Figure 4b). In other words, when midday temperatures were high, predation was more likely to occur at cooler parts of the day, usually at night (Figures 4, 5; Table A4).

We speculate that the departure of 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 would decrease daily nest predation across the breeding season (Shkedy & Safriel, 1992), which was not the case (Figure 4a, Table A2). However, the potential 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 avian predators (Table A1)—such as egrets and herons (*Ardea* spp.), brown-necked ravens (*Corvus ruficollis*), common maynas, gray 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 & White, 1992; Sloan et al., 1998). Second, common nonmigratory predators (that hunt by day) live within the study area (Table A1), which lends support to the idea that temperature extremes are driving the seasonal increase of night nest predation. Third, most migratory avian predators start leaving the study area

in March and are gone 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 4b). In contrast, ground temperatures gradually increase over the whole breeding season until the end of July (Figure 1). Importantly, nest predation events start occurring during the colder parts of the day as midday temperatures increase and well before the migratory predators leave the study site (Figure 4b). Thus, midday temperature is likely a stronger driver for the diel change in nest predation than the absence of migratory predators. Nevertheless, whether such change in the timing of predation—linked to midday temperatures—is present in other locally breeding species or avian and nonavian 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 behavior of incubating red-wattled lapwing parents and parents of any other biparentally incubating species experiencing a similar diel pattern of nest 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, we expect parents to reduce their activity around the nest at night (i.e., increase constancy of incubation, decrease number of nest reliefs), as the season progresses because (i) active nest-defense during the night is unlikely (e.g., because a parent sees an approaching predator only at a short distance) and (ii) activity at the nest increases nest predation (Martin et al., 2000; Smith et al., 2012). Second, as the season progresses and temperatures increase, we expect the parents to reduce their alertness during the day, spending more time preening and sleeping on the nest, 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.

5 | CONCLUSION

We found nest predation to be relatively low in a subtropical population of the poorly studied red-wattled lapwing, breeding in an arid, artificial habitat. Such low predation rate contrasts with higher predation rates found in many related and unrelated species breeding both in the desert and other habitats (Mezquida & Marone, 2001; Mayfield based predation rates in Bulla et al., 2019; Freeman et al., 2020; Kubelka, Zámečník, et al., 2018). Although we found little variation in daily nest predation rate across the breeding season, the probability of night predation increased over the season, likely due to the extreme heat during the midday. These results help us understand the evolution of different defense behaviors and 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

We have no competing interests.

AUTHOR CONTRIBUTIONS

Martin Sládeček: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (equal); Resources (equal); Software (lead); Validation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Kateřina Brynychová:** Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Writing-original draft (supporting). **Esmat Elhassan:** Conceptualization (supporting); Funding acquisition (lead); Investigation (lead); Project administration (equal); Resources (equal); Writing-original draft (supporting). **Miroslav E Salek:** Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Project administration (lead); Resources (lead); Supervision (lead); Writing-original draft (equal); Writing-review & editing (equal). **Veronika Janatová:** Data curation (supporting); Investigation (equal); Project administration (equal); Writing-original draft (supporting). **Eva Vozabulová:** Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Writing-original draft (supporting). **Petr Chajma:** Data curation (supporting); Investigation (equal); Project administration (supporting); Writing-original draft (supporting). **Veronika Firlová:** Data curation (supporting); Investigation (equal); Project administration (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Lucie Peřková:** Investigation (equal); Project administration (equal); Writing-original draft (supporting). **Aisha Almuheri:** Resources (equal); Writing-review & editing (equal). **Martin Bulla:** Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (equal); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead).

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This article has been awarded Open Materials, Open Data Badges. All materials and data are publicly accessible via the Open Science Framework at <https://doi.org/10.17605/OSF.IO/BQ4DR> (Sládeček & Bulla, 2021).

DATA AVAILABILITY STATEMENT

All data and computer code to replicate our analyses, as well as plots of model assumptions, are freely available from OSF: <https://doi.org/10.17605/OSF.IO/BQ4DR> (Sládeček & Bulla, 2021).

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APPENDIX

TABLE A1 Potential predators of red-wattled lapwing eggs in the study site at Al Marmoom Conservation Reserve, Dubai, UAE

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

Note: 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 in bold. Note that none of the migratory predators forages at night.

TABLE A2 Daily predation rate on red-wattled lapwing nests

Model	Effect	Logit scale			AICc	Δ AICc ^a	w_i ^b	ER ^c
		Estimate	95% CrI					
(a)	(Intercept)	-4.65	-4.89	-4.42	615.86	0	0.7	1
(b)	(Intercept)	-4.44	-5.19	-3.67	617.54	1.68	0.3	2.33
	Season	0	-0.01	0				

Note: Shown are the posterior estimates (medians) of the effect sizes with the 95% credible intervals (CrI) from a posterior distribution of 5000 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. The intercept in (a) represent daily predation rate. The AICc comparison was performed with the "AICc" function from the "MuMIn" R-package (Kamil Bartoň 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	0.356
			sin(time)	0.533	-0.035	1.124
			cos(time)	0.481	-0.11	1.072
(a) Time of day	Predation per hour	Gaussian	(Intercept)	1.039	0.469	1.63
			sin(time)	0.535	-0.283	1.335
			cos(time)	0.471	-0.335	1.292
(b) Time relative to sunrise	Predation per hour	Poisson	(Intercept)	0.709	0.043	1.368
			Absolute time from sunrise	-0.121	-0.246	0
(b) Time relative to sunrise	Predation per hour	Gaussian	(Intercept)	1.84	0.848	2.798
			Absolute time from sunrise	-0.13	-0.278	0.014

Shown are the posterior estimates (medians) of the effect sizes with the 95% credible intervals (CrI) from a posterior distribution of 5000 simulated values generated by the "sim" function in R. Response is specified as a number of predation events per hour of the day (a; $N = 24$ h) and per each hour, centered around sunrise (b; $N = 23$ h).

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

Note: Shown are the posterior estimates (medians) of the effect sizes with the 95% credible intervals (CrI) from a posterior distribution of 5000 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).

TABLE A5 Probability of night predation on red-wattled lapwing nests—AICc model comparison

Model	Predictors	AICc	$\Delta AICc^a$	w_i^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

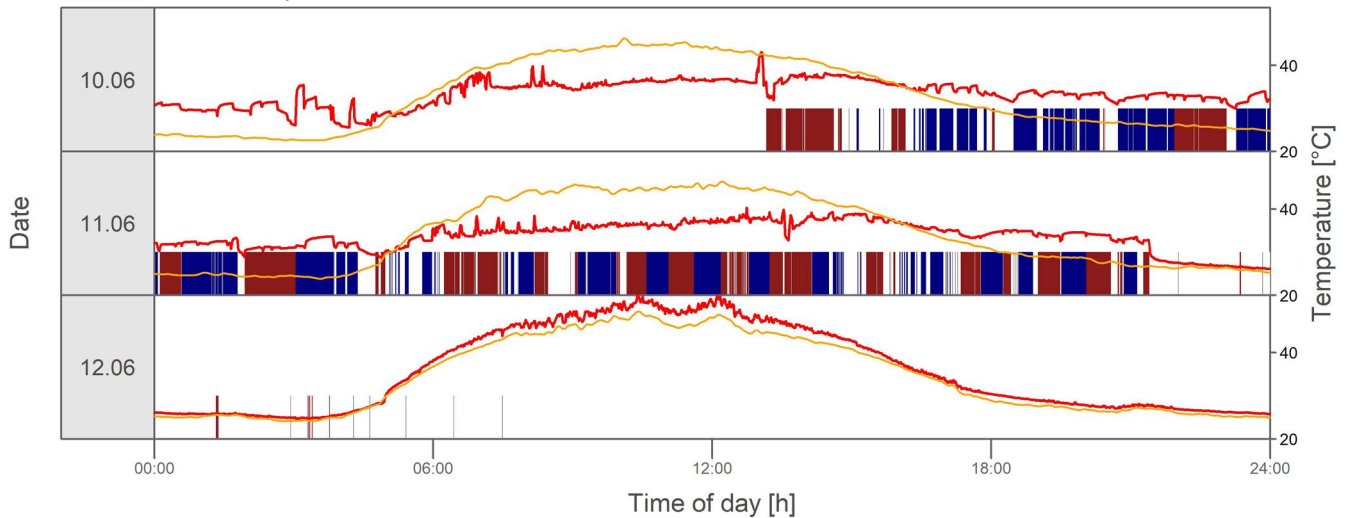
Note: Model names correspond to the model names in Table A4. The AICc comparison was performed with the AICc function from the MuIn R-package (Kamil Bartoń 2020) and separately for binomial and Gaussian models, which generated identical results.

^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).

(a) Illustration of predation



(b) Illustration of hatching

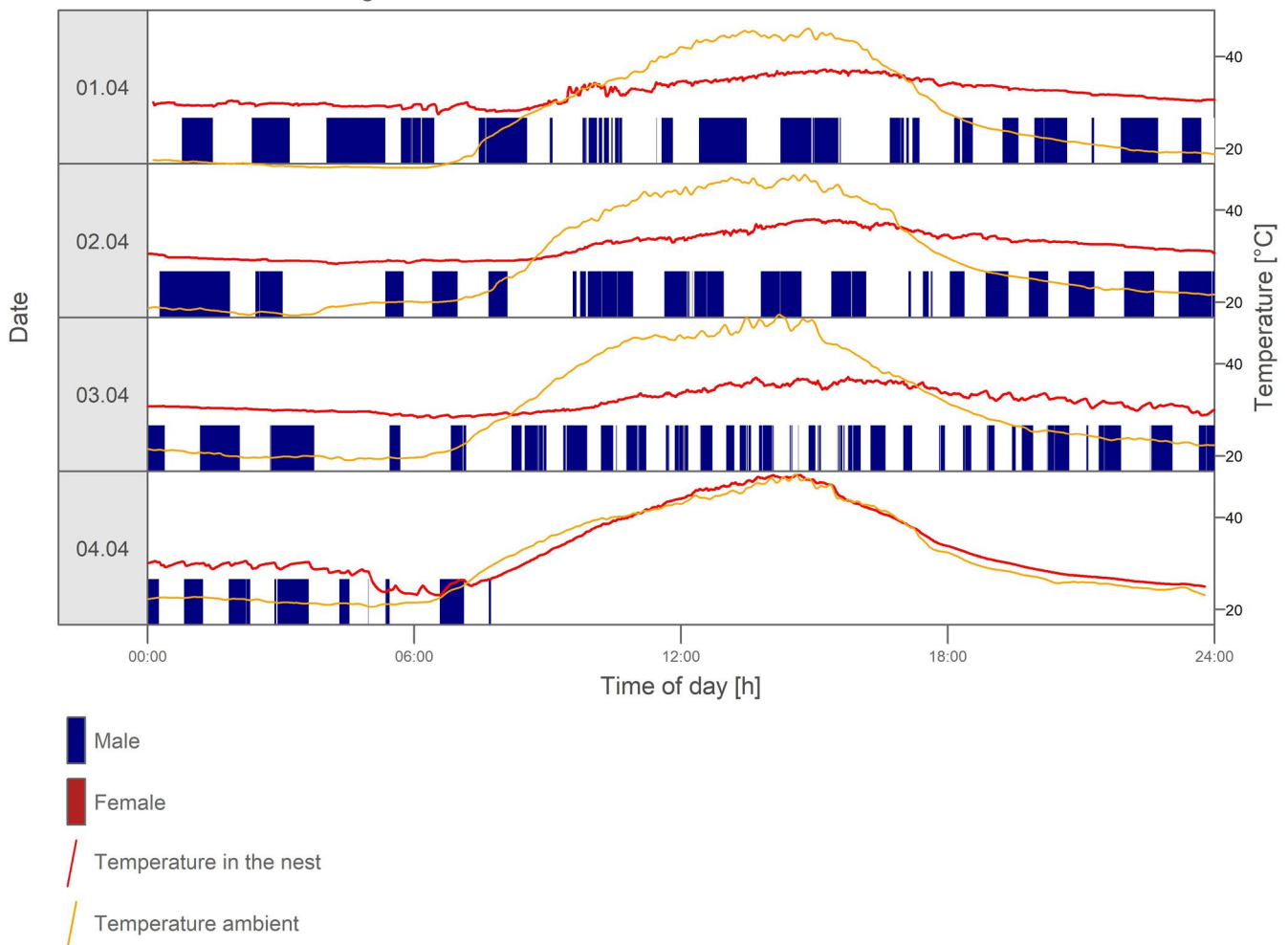


FIGURE A1 Illustration of predation and hatching on continuous recordings from red-wattled lapwing nests. (a, b) Red line indicates nest temperatures, orange line ground temperatures next to the nest. Bars indicate RFID recording of female (dark red) and male (blue) on the nest. (a) Nest was predated 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

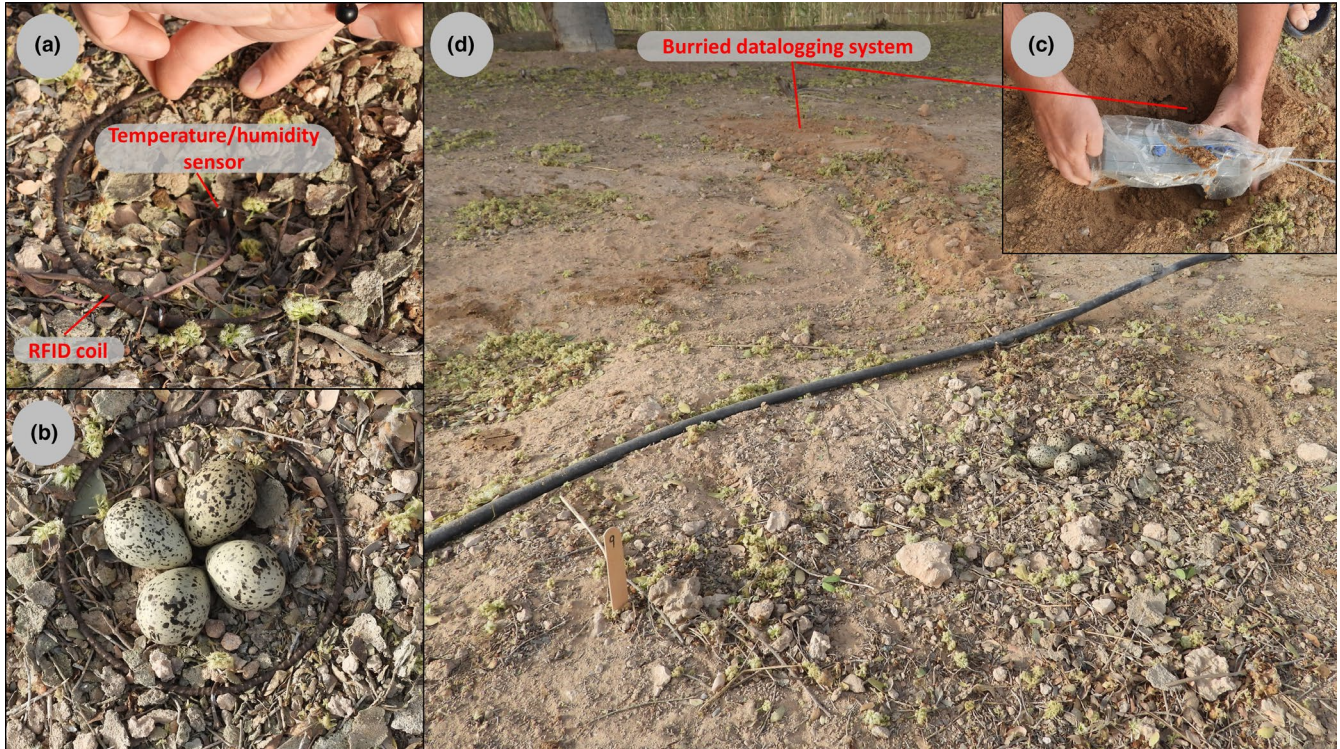


FIGURE A1 Installation of the ZAYDA incubation monitoring system on a red-wattled lapwing nest. Minute temperature/humidity probe is placed between the eggs (a), RFID coil around the eggs (a, b), the system, including the cables, is hidden under the ground (c, d)

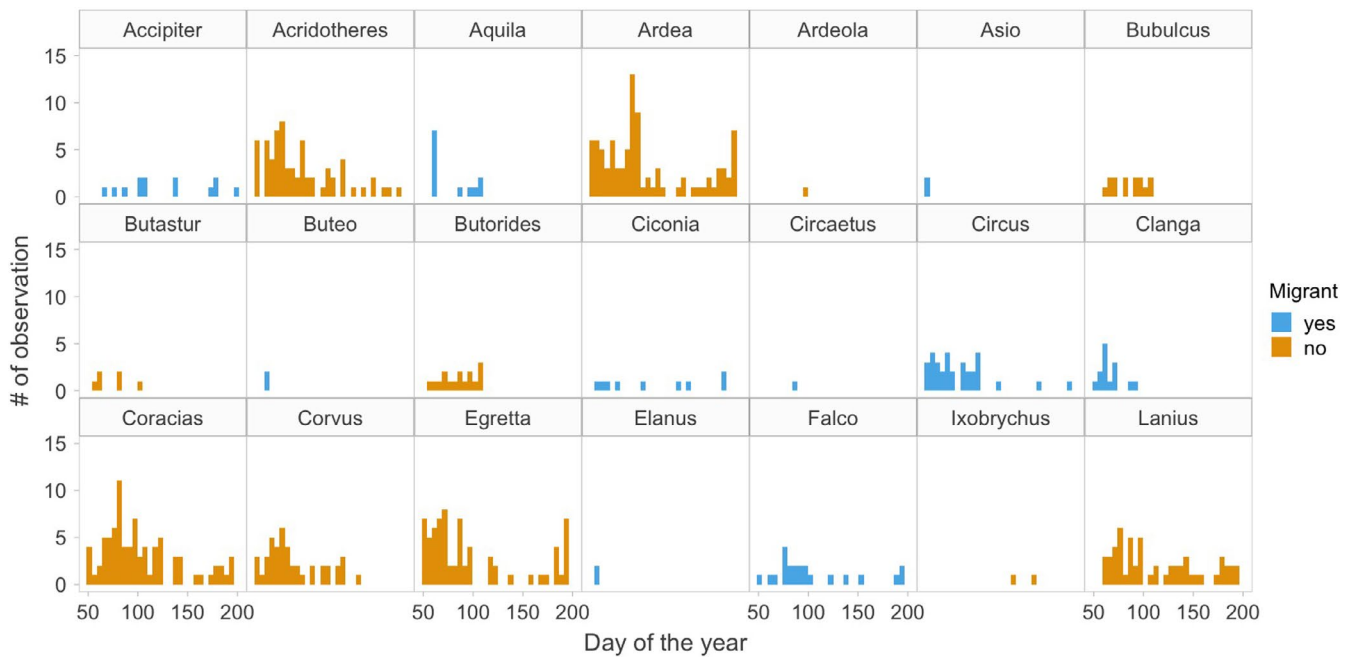


FIGURE A2 Changes in observations of potential avian predators of red-wattled lapwing nests over the breeding season. Bars represent a number of observations of a given genus during each day of the breeding season based on all eBird data ($N = 557$ observations) available for Dubai until 1. March 2021, color indicates whether the observed species migrate through or out of the study area during breeding season (blue) or not (orange) (eBird, 2020). Note that despite local (non-migrating) populations, individuals of the given genus may migrate through the study area. Number of observations are used, instead of the number of seen individuals, because the latter varies between observations and in 74% of observations only 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