



RESEARCH ARTICLE

Functions of extensive animal dung “pavements” around the nests of the Black Lark (*Melanocorypha yeltoniensis*)

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ABSTRACT

We used observational and experimental approaches to assess the possible functional significance of the often extensive “pavements” of livestock dung constructed by female Black Larks (*Melanocorypha yeltoniensis*) around their nests. These pavements are conspicuous to human observers, suggesting that they may also attract predators. The size of the pavement was correlated with, but not limited by, the density of dung in the vicinity of the nest. The relationship between pavement size and local dung density did not differ significantly between habitats or years, suggesting that females might scale their pavements according to the perceived trampling risk. Even in heavily grazed areas nest trampling was rare, and nest survival rates were similar to those in areas with few grazing animals, suggesting that pavements may reduce trampling risk without incurring an additional predation risk or, alternatively, that trampling is currently not an important threat to lark nests. An experimental manipulation of grazing animals around artificial nests yielded equivocal support for a trampling-deterrent effect of dung pavements. Dung pavements might also provide thermal benefits; experiments on artificial nests suggested that dung pavements buffer nests against extremes of heat and cold, and there was equivocal support for a positive effect of pavement size on chick tarsus growth rates. These pavements may therefore be multifunctional, but identifying the adaptive drivers of the behavior requires further research.

Keywords: nest construction, adaptive behavior, animal dung, thermoregulation, trampling risk, Alaudidae, Kazakhstan

Funciones de los amplios “pavimentos” de estiércol animal alrededor de los nidos de *Melanocorypha yeltoniensis*

RESUMEN

Usamos aproximaciones basadas en observaciones y experimentos para determinar el posible significado funcional de los amplios “pavimentos” de estiércol de ganado que construyen las hembras de *Melanocorypha yeltoniensis* alrededor de sus nidos. Estos pavimentos son conspicuos para los observadores humanos, lo que sugiere que también podrían atraer depredadores. El tamaño del pavimento se correlacionó con la densidad de estiércol en la vecindad del nido pero no estuvo limitada por ésta. La relación entre el tamaño del pavimento y la densidad local de estiércol no fue significativamente diferente entre hábitats y años, lo que sugiere que las hembras podrían cambiar el tamaño de sus pavimentos de acuerdo al riesgo percibido de pisoteo. El pisoteo fue raro aún en áreas de alto pastoreo y las tasas de supervivencia de los nidos fueron similares a las de áreas donde había pocos animales pastoreando. Esto sugiere que los pavimentos podrían reducir el riesgo de pisoteo sin incurrir en un riesgo adicional de depredación o, alternatively, que el pisoteo no es un riesgo importante para los nidos de *M. yeltoniensis*. Una manipulación experimental de animales que pastorean alrededor de nidos artificiales sustentó ambigüamente el efecto anti-pisoteo de los pavimentos de estiércol. Los pavimentos de estiércol también podrían proveer beneficios térmicos: experimentos en nidos artificiales sugirieron que los pavimentos de estiércol amortiguan los cambios extremos de temperatura en los nidos y encontramos sustento ambiguo de un efecto positivo del tamaño del pavimento en las tasas de crecimiento del tarso de los polluelos. Por lo tanto, los pavimentos podrían tener múltiples funciones, pero identificar las causas adaptativas del comportamiento requiere más investigación.

Palabras clave: Alaudidae, comportamiento adaptativo, construcción del nido, estiércol animal, Kazakhstan, termorregulación, riesgo de pisoteo.

INTRODUCTION

The use of objects such as feathers, flowers, stones, and pieces of plastic in birds' nests has been documented for many species and serves various purposes, such as in bowerbirds (Borgia et al. 1987) and Rock Sparrows (*Petronia petronia*; García-Navas et al. 2015). A number of bird species collect and add mammal dung to their nests, but the adaptive reasons for this behavior are poorly understood (Smith and Conway 2011). A number of nonmutually exclusive hypotheses have been investigated; dung in the nests of White Storks (*Ciconia ciconia*) may act as insulation for the chicks during periods of inclement weather (Tortosa and Villafuerte 1999), and Common Waxbills (*Estrilda astrild*) may collect predator dung to deter predators from the nest (Schuetz 2005). Levey et al. (2004) suggested that Burrowing Owls (*Athene cunicularia*) line their burrows with dung as bait for dung beetles (Scarabaeoidea) to increase food availability near the nest, although these results could not be replicated in a second study (Smith and Conway 2011).

The Black Lark (*Melanocorypha yeltoniensis*) is a medium-sized songbird endemic to the Eurasian steppes, with 95% of the population confined to Kazakhstan. Within this region, it is one of the largest ground-nesting passerines. The species breeds in open steppe grassland with a structure shaped historically by wild, largely nomadic ungulates but is today largely determined by the grazing of domestic livestock (Kamp et al. 2011). Prior to egg-laying, female Black Larks often collect horse or cattle dung from the surrounding steppe grassland and use this to construct dung "pavements" around the nest cups (Figure 1, Appendix Figure 5). This behavior was first described by Moiseev (1980), who found that 73% of all nests ($n = 48$) had dung arranged around them.

Ramparts of stone pebbles or pieces of dried earth have been observed around the nests of other lark species, such as the Horned Lark (*Eremophila alpestris*) and Eurasian Skylark (*Alauda arvensis*; Cannings and Threlfall 1981, Beason 1995, Donald 2004); however, the use of animal dung and the large size of the resulting pavements in relation to the nest seem to be unique to Black Larks.

Some females place their clutches in or near existing dung piles, but in our study population the majority of nest pavements appear to be constructed from individually collected dung pieces (Figure 1). The construction of large dung pavements requires a considerable investment of time (Moiseev 1980), and probably also energy, and might thus be costly from an evolutionary perspective. The construction process might also increase exposure to predators because vigilance might be lowered during the collection of dung. After construction is complete, the pavements themselves are conspicuous to trained human observers. For nest predators, the pavements could conceal



FIGURE 1. Black Lark nest with a large assembled dung pavement. The arrows mark the nest entrance (nest predated). Korgalzhyn, Kazakhstan, May 2011.

the nest or might, just as for human observers, act as cues. For the pavement-construction behavior to be adaptive, the costs would have to outweigh the benefits, so the pavements would have one or several adaptive functions. We used observational and experimental approaches to shed light on potential functions of the dung pavements.

First, we assessed whether the pavements reduce the risk of nest predation. Predation of the nests of ground-breeding birds in our study area has been attributed mainly to mammalian predators. A study using nest cameras identified red fox (*Vulpes vulpes*), long-eared hedgehog (*Hemiechinus auritus*), and steppe polecat (*Mustela erminei*) as the main predators of ground-breeding wader nests in the same study area (Sheldon et al. 2013). Birds have recently been shown to be able to deliberately camouflage their nests (Bailey et al. 2014). A camouflaging effect of the dung (e.g., by "dissolving" the breeding female or the conspicuous eggs in the open nest cup) could help to hide nests from visually searching mammalian and avian predators during the day. Female plumage coloration in Black Larks is similar to that of the dry dung used for pavements (Appendix Figure 5). Additionally, the smell of the dung could act as an olfactory deterrent to predators searching for nests during the night, as has been suggested for Common Waxbills (Schuetz 2005). Experienced nest predators might, however, just as our trained observers, recognize the arranged pavements as a potential nest site that could attract predators. Either way, we expected that nest predation rates were not independent of pavement size.

Second, we assessed whether dung pavements might reduce the risk of a nest being trampled by domestic livestock. Livestock trampling can significantly reduce nest success in ground breeding passerines (Donald et al. 2002, Fondell and Ball 2004, Beja et al. 2014). In our study area, high livestock trampling rates have been observed in

ground-breeding waders (Watson et al. 2006, Sheldon et al. 2013). For Black Larks, Moiseev (1980) found that more than 60% of the failed nests had been trampled, although that study was conducted in a period of much higher livestock densities than those recorded during our study. Cattle, sheep, and horses avoid grazing near patches of their own dung (Marten and Donker 1964, Lütge et al. 1995, Bosker et al. 2002). Nests surrounded by dung might thus be less prone to trampling by domestic livestock. Livestock are also known to occasionally eat chicks and eggs of ground-nesting songbirds (Nack and Ribic 2005), so dung pavements might additionally reduce the risk of disturbance and predation by livestock.

Third, we assessed whether the pavements create any thermal benefits by buffering changes of the temperature of the soil surrounding the nest, and therefore the nest cup itself. Decaying horse dung is known to have a “self-heating” capacity (exploited, for example, in gardeners’ “hot-beds”), resulting from its insulation capacity and heat release due to microbial activity during the decay process (Gerretsen et al. 1949). We predicted that if nest cup temperature was positively influenced by the dung pavement, less time was needed for incubating eggs and brooding chicks (brooding is common in the first 5 days of chick development). Females might therefore spend more time foraging or collecting food for the chicks, thereby potentially increasing their own fitness or that of the offspring. To address these 3 hypotheses, we used a combination of nest monitoring, a trampling experiment with livestock, and an experiment on the thermal properties of dung pavements.

METHODS

Study Area

In 2011 and 2013, we monitored nests and conducted field experiments in a study area in the Tengiz–Korgalzhyn depression ~120 km southwest of Kazakhstan’s capital, Astana, near the village of Korgalzhyn (N50°34′59.00″, E70°00′01.14″). The area comprises ~14,000 ha of steppe grassland and agricultural habitats and is situated close to the geographical center of the Black Lark’s breeding range. The northern part of the study area is dominated by arable fields and hay meadows used for wheat cultivation in Soviet times, but this became unprofitable after the breakup of the Soviet Union in 1991 (Kamp et al. 2011). Currently, the northern area is grazed by a flock of ~1,000 horses and several hundred sheep and cattle, which are kept for meat and dairy production. This area holds high densities of Black Larks (on average 0.65 males ha⁻¹; Kamp et al. 2011). The southern part of the study area comprises mainly pristine steppe grassland that was never plowed and always used for low-density grazing. During our study,

it supported ~300 horses, 100 cattle, and 100 sheep. Here, densities of Black Lark are much lower (on average 0.2 males ha⁻¹; Kamp et al. 2011).

Nest Monitoring

We searched for Black Lark nests from April 28 until the end of June in both years, 2011 and 2013. Nests were found by driving and walking transects in suitable habitat, thereby flushing incubating females (82% of all found nests), or by following birds carrying nesting material, dung, or food for chicks to nests (18%).

We stored nest locations in a GPS unit. We measured the length and width of all eggs found during the incubation stage with calipers to the nearest 0.1 mm and weighed them with a portable scale to the nearest 0.1 g.

Every third day, we revisited the nests to record nest contents and status. We assumed no effect of visits on nest survival (Ibáñez-Álamo et al. 2012), although precautions were taken to avoid attracting predators to the nest (short visits, one visitor, no insect repellent worn). Lark chicks usually leave the nest well before their wing feathers are fully grown and before they can feed independently. Fledging was defined as the point when chicks left the nest. We recorded nests as successful if at least one chick fledged, indicated by a flattened nest margin and scattered chick droppings around the nest around the expected fledging date (Donald et al. 2002).

Nests were classified as depredated when found empty before the observed or predicted hatching date (prediction method discussed later), or when the lining was removed and egg shell fragments were found. Predation of chicks was assumed and the nest recorded as unsuccessful when chicks disappeared from the nest before an age of 10 days (the observed minimum age of leaving the nest in our study), when no chick droppings were found around the nest, and the nest margin was not flattened. Trampling by livestock was assumed to have happened where crushed eggs and yolk or dead, injured chicks were found in the nest, and hoof prints were visible in and around the nest. When the eggs were cold during a number of subsequent nest visits or dead chicks were encountered, we assumed nest abandonment, caused, for example, by the death of the female through predation (Donald et al. 2002). Failure, hatching, and fledging (when not observed) were assumed to have happened at the midpoint between the 2 last visits (Mayfield 1961).

Correlates of Dung Pavement Size

Building large pavements requires considerable time (Moiseev 1980), and significant energy investment is likely needed to carry the large amount of dung found in many pavements to the nest. Therefore, we first identified correlates of pavement size to develop hypotheses of potential benefits of pavements.

For each nest, we recorded dung pavement size (estimated in square centimeters to the nearest 50 cm² for large pavements, and to the nearest 10 cm² for pavements consisting only of single dung pieces) and the number of dung pieces in the pavement. We also recorded whether the nest had been placed in an existing dung pile or in an area of scattered dung pieces, or whether the pavement was assembled by the female. Pavements largely or wholly built by females were easily distinguished because the dung pieces looked clearly arranged, often placed side-by-side on top of vegetation or bare soil near the nest. To estimate dung availability and grazer density at the breeding sites, we counted the number of horse and cattle dung piles along a 50 m strip transect of 2 m width with a random bearing, centered on each nest. Dung is known to be a good correlate of grazer density (Laing et al. 2003). We assumed similar rates of dung production per animal in different habitats because the plants selected by the livestock are unlikely to differ between habitats (grasses such as *Stipa* and *Festuca* are positively selected on the steppe). We also assumed no differences in dung availability for detection by habitat because dung decomposition is slow due to the arid climate and low microbial activity (dung piles often do not decay until the following winter).

We calculated a background dung density around each nest by dividing the number of dung piles counted by the strip transect area. This figure was then multiplied by 15 because horse dung piles contained on average 15 pieces (J. Kamp personal observation), and cattle dung piles were of similar size to those of horses. We then calculated the minimum distance each female needed to travel to collect enough horse dung pieces to build their respective pavement as the radius of a circle that contained the required number of dung pieces, given the estimated background dung density. We controlled for the fact that only 60% of all horse dung pieces are of suitable size to be used by the larks (see Results).

Because nest survival is likely to vary with the vegetation structure at the nest, we also recorded the maximum vegetation height at each nest with a ruler and “modal” vegetation height as a proxy for vegetation density with a wooden disk sliding on a folding ruler. Because the 2 were correlated (Spearman's $\rho = 0.54$, $p < 0.001$), and models containing either of the variables yielded similar results, we present only analyses that use maximum vegetation height. We also included mean temperature 3 days prior to the first egg date (i.e. the time when the dung pavements are built) as a covariate to assess whether females build larger pavements in periods of colder weather. Local weather data are collected by KazGiproZem (2014) but were unexpectedly not made available to us. We therefore used data from Astana, a location ~120 km northeast of our study area, which is the nearest weather station with data available for

both study years (KazGiproZem 2014). Data were downloaded for April, May, and June at 3-hour resolution.

We used generalized linear models (GLMs) in R 3.0.2 (R Development Core Team 2014) with a negative binomial error distribution and a log link to model pavement area (in cm²) as a function of background dung density, year, and habitat (a 3-level factor of “abandoned farmland,” “sown grassland,” or “pristine steppe”). Models containing all possible combinations of variables were compared using Akaike's Information Criterion for small sample sizes (AIC_c, Burnham and Anderson 2002). Models with $\Delta\text{AIC}_c < 2$ from the model with the lowest AIC_c were considered equally informative and as receiving substantial support (Burnham and Anderson 2002). Because more than one model had $\Delta\text{AIC}_c < 2$, we averaged parameter estimates of all models following the approach of Burnham and Anderson (2002). We used function `model.avg` in R package `MuMIn` (Bartoń 2014) and calculated standard errors as the square-root of the unconditional variance estimator. Relative variable importance $w_+(j)$ was calculated as the sum of Akaike weights (w_i) over all models including the explanatory variable (Burnham and Anderson 2002). All continuous variables were z -transformed.

Nest Survival Analysis

Nest survival often varies with nest age or stage; hence, first egg dates were estimated in several ways. When the hatching date was known (hatching of chicks was observed), the mean length of the incubation and laying periods (10.8 + 3 days in 2011, 11.6 + 3 days in 2013) were subtracted from this date. The same was done for nests that hatched between 2 successive nest visits, assuming hatching to have occurred at the midpoint between these visits. When nests were found that contained chicks, chick age was estimated from morphological features. In 2011, when chick biometrics were taken, chick age was estimated from a regression of mass and tarsus length against time since hatching, the latter based on 123 measurements of 49 chicks of known age ($R^2 = 0.895/0.918$; Appendix Figure 6). When the age estimates differed, the mean of those from the tarsus regression and the mass regression were used. Hatching date was then back-calculated and first egg dates estimated as described above. For nests failing at the egg stage, first egg dates were calculated using a linear regression of egg density on age from a number of nests of known age ($R^2 = 0.693$; Appendix Figure 6).

Egg density was estimated as $(\text{length} \times \text{width}^2 \times 0.51) / \text{weight}$ (Hoyt 1979). A number of nests failed before the eggs were measured, but simply excluding these nests from age-specific nest-survival models would have positively biased nest survival rates. We therefore assumed that when first found, the eggs in these nests were the same age as the average age of eggs at time of first finding across known-age nests in the same year, and we used this year-specific

“time to find” estimate as the basis of estimating first egg date from subsequent observations. Daily nest survival was estimated using a maximum likelihood approach implemented in program MARK. We modeled a binary nest outcome (0 = success, 1 = failure) with exposure days fitted as the binomial denominator in a GLM with a binomial error distribution and logit-link (Rotella et al. 2004). Program MARK (White and Burnham 1999) was interfaced via the RMARK package (Laake and Rexstad 2008) in R 3.0.2 (R Core Development Team 2014). This modeling framework allows testing for time-dependent survival and seasonal patterns in survival. Because variation between years and habitats was large, we included year and habitat as fixed effects. The effect of dung pavement size on nest survival was evaluated by fitting the size of the pavement (in cm²) as a covariate. Vegetation height at the nest was also used as a covariate to assess whether nest survival varied with vegetation patterns at the nest. Additionally, we fitted the background dung density (number of dung piles along the 50 m transect) as a covariate to represent grazing pressure.

Models containing all possible combinations of variables, constrained to a maximum of 4 variables in the same model for reasons of parsimony, were compared using AIC_c (Burnham and Anderson 2002). An automated procedure implemented in R package MuMIn (Bartoń 2014) was used for this. Models within 2 AIC_c units of that with the smallest AIC_c were considered as receiving support from the data. Parameters of models within 2 Δ AIC_c units were averaged as described above. Relative variable importance $w_+(j)$ was calculated as the sum of Akaike weights over all models that included that explanatory variable.

Chick Growth

If dung pavements have a positive effect on nest temperatures, then females building larger pavements might be better able to exchange incubation for foraging, with consequent benefits for chick growth. We therefore collected data in the field on chick growth rates as measured by tarsus length and body mass. All chicks were weighed on an electronic high-precision balance to the nearest 0.1 g, and the tarsus measured on at least 2 occasions between the eggs hatching and the chicks leaving at around 11 days. Chicks were individually marked on the leg with an indelible marker pen to allow later recognition. For this analysis we used only data on the 49 chicks whose ages were known exactly (i.e. found on the day of hatching or the day after).

For analysis, we used nonlinear mixed effects models in package lme4 in R 3.0.2 to assess the influence of dung pavement size and hatching date on chick mass and tarsus growth rates, following the methods of Sofaer et al. (2013). Because chicks leave the nest before fledging and therefore

before the asymptotic mass or tarsus length is reached, we replaced the asymptotic term in the 3-parameter growth model with a constant reflecting the approximate adult mass or tarsus and fitted 2-parameter models in which only the growth rate constant and inflection point were estimated (Austin et al. 2011). We used these models to assess the influence of the size of the dung pavement and hatching date (days from 1 January) separately on chick growth rates, with a fixed asymptote. We fitted different random effects structures, allowing the random effects of nest, chick, or chick-within-nest on the inflection point, the growth constant, or both. These models contained the fixed effects of pavement size or hatching date, which were evaluated after the most appropriate random error terms were identified, following Zuur et al. (2009). The model with the best support was identified using AIC_c, and this was then compared to a model with the same random effects structure but without the covariates relating to the influence of pavement size or hatching date on growth constant and inflection point. Covariates were zero-centered by subtracting the mean from each value.

Nest Trampling and Microclimate Experiments

To assess whether dung pavements reduce nest trampling by livestock, we set up a field experiment in steppe habitat of the type used by Black Larks. We created a regular grid (90 × 90 m, 100 nodes resulting in an internode distance of 10 m) of artificial nest surrogates in an area regularly grazed by cattle, horses, and sheep. Dried clay disks of the diameter of a Black Lark nest, which would break if an animal stepped on it, were placed on each node of the grid, and cow dung was arranged at every second nest to resemble a medium-sized dung pavement around a Black Lark nest. We then drove a herd of 92 cattle into the grid, which remained there grazing for 1 hour. Cattle that attempted to leave the grid were gently driven back. After 1 hour, the numbers of broken and intact disks per dung category were counted. We repeated this experiment 6 times at 6 different sites with similar vegetation and levels of background dung.

We modeled the effect of dung on trampling probability in a generalized linear mixed effects model (GLMM) with a logit-link and binomial error distribution in package lme4 in R 3.0.2. The dependent variable in the model was the event of trampling (1 = trampled, 0 = not trampled). The presence or absence of dung was fitted as a fixed effect (2-level categorical variable). Because the outcome at each node was unlikely to be independent across trials, we fitted trial ID as random effect. The statistical significance of the fixed effect was used for statistical inference.

We used a second experiment to assess Moiseev's suggestion (1980) that dung pavements have a thermal effect on the nest and assessed the influence of dung pavement presence and size on inner nest cup tempera-

ture. Because field measurements from real nests were difficult to standardize due to varying vegetation patterns and topography at and around the nest, we used 36 artificial nests made from plastic cups with measurements corresponding to those of Black Lark nests (based on our own field measurements). These were placed in plastic trays ($50 \times 30 \times 6$ cm) filled with clay soil comparable to that at the field study area. Three different treatments were then created by adding varying amounts of horse dung to the nest: 12 nests were left without any dung, 12 nests were surrounded by a single ring of dung, and 12 nests were fitted with a double ring of dung. The dung pieces used were comparable in size to those placed around actual Black Lark nests. The first dung treatment corresponded to an average Black Lark nest pavement, whereas the treatment with a double ring corresponded to large pavements (Figure 1). The trays used in all treatments were devoid of vegetation. The trays with the nests were arranged in a random order with respect to the dung treatment on the roof of a building in Münster, Germany. We used temperature loggers (iButton DS1921G-F5, Maxim/Dallas Semiconductor Corporation, Sunnyvale, CA) to measure temperature at each nest at an interval of 2 minutes for 68 hours during the last week of August 2013, a period with similar ambient air temperatures to those experienced during the peak of the breeding season in Kazakhstan in the same year. Ambient temperature was measured by a separate data logger placed near the experimental setup. For analysis, we calculated the moving average over all nests and the entire duration of temperature measurements using time series analysis (function SMA in R package TTR; Ulrich et al. 2014). We compared measured maximum and minimum temperatures across treatments using a one-factor ANOVA, followed by a post-hoc Tukey test.

RESULTS

Characteristics of Dung Pavements

In total, we found and monitored 220 Black Lark nests. In 2011, 128 nests were found (56 on abandoned wheat fields, 31 on sown grassland, and 41 in pristine steppe). In 2013, 92 nests were found (38 on abandoned wheat fields, 23 on sown grassland, and 31 in pristine steppe). We found 98.6% of nests to have some dung around them; 37.3% of these nests were placed in existing dung piles (sometimes with some rearrangement of the dung) or areas of densely scattered dung pieces. At the remaining nests, the dung pieces had obviously been brought to the nest and were arranged in the form of a pavement, either surrounding the nest or in a half-circle opposite an existing grass tuft. Dung pavements consisted on average of 40.5 dung pieces (range: 0–134) and covered a mean area of 453 cm^2 (range: 0–2400 cm^2).

We observed nest construction behavior only in females during our study ($n = 27$ nests where females were seen building the scrape, carrying lining or dung or arranging the lining). We found 32 nests during the building stage (12 in 2011, 20 in 2013), on average 2.59 days before the observed or estimated first egg date. Four nests were found during the first day of building (when the scrape was formed by the female), and the first egg appeared in these nests 5 (1 nest) or 6 days (3 nests) later. After the scrape was excavated, lining (usually dry grass) was added. The females constructed the dung pavements over a period of 1–3 days ($n = 3$ nests with direct observation) during or after completing nest lining. Females were observed repeatedly collecting dung pieces within 50 m of the nest, which they then carried back on foot and arranged around the nest. Dung was also carried to the nest in flight, dropped over the nest and later rearranged into the pavement. No dung was added to or removed from the nest after the first egg was laid. In an earlier study, Moiseev (1980) observed a nest-building female that collected dung within 20–50 m from the nest over the course of 3 hours and added dung pieces to the nest every 1–5 minutes.

In 2013, we studied the contribution of different animal dung to the pavements at 92 nests in more detail: 99% had some cover of horse dung at the nest, 30% had some cattle dung also arranged, and only 3.6% contained single sheep droppings. At 3.7% and 3.8% of the nests, respectively, woody dwarf shrub roots and dry earth clumps had been integrated into the pavements. Horse dung was thus by far the most common material in dung pavements.

Dung pieces in pavements were not selected randomly from what was available nearby. Instead, smaller size classes were preferred (means for pieces in pavements: length $40.0 \text{ mm} \pm 8.0 \text{ SD}$, width: $30.0 \text{ mm} \pm 6.2 \text{ SD}$, weight: $3.8 \text{ g} \pm 2.0 \text{ SD}$, $n = 50$ pieces at 10 pavements; means for pieces in randomly selected dung piles: length $49.6 \text{ mm} \pm 12.2 \text{ SD}$, width: $36.8 \text{ mm} \pm 7.8 \text{ SD}$, weight: $8.1 \text{ g} \pm 6.7 \text{ SD}$, $n = 50$ pieces at 10 piles; dependent 2-group Wilcoxon Signed Rank Test, $p < 0.001$ for length, width, and weight). An average collected dung piece therefore equates to 9% of the female's body mass of 42 g (Korelov 1970). Pavements can contain >100 pieces of dung, with a total mass of >9 times that of the female (Fig. 1).

Correlates of Pavement Size

The amount of horse dung available within a 50 m radius around the nest was a significant predictor of nest dung pavement size (area in cm^2) in a univariate negative binomial GLM ($\beta = 0.018 \pm 0.007 \text{ SE}$, $p < 0.01$, $n = 220$; Figure 2A). This was not the case for the amount of cattle dung available (negative binomial GLM: $\beta = -0.01 \pm 0.01 \text{ SE}$, $p = 0.12$, $n = 220$). Neither dung pavement size nor dung availability differed between habitats, but pavements were significantly smaller in 2013 compared to 2011

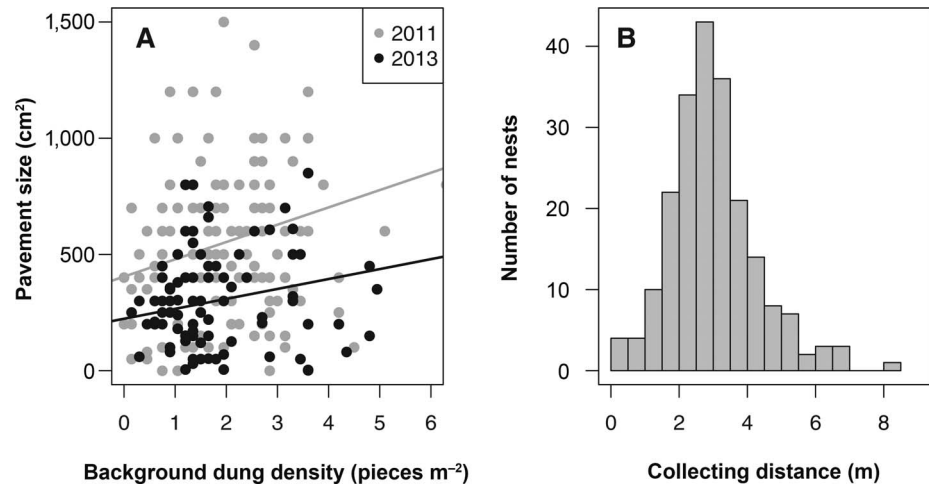


FIGURE 2. (A) Correlation between pavement size at Black Lark nests and background dung density (horse and cattle combined), separated between years (linear regressions, 2011: $p < 0.01$, adj. $R^2 = 0.041$, $n = 128$; 2013: $p < 0.001$, adj. $R^2 = 0.144$, $n = 92$). (B) Histogram of the radius of circles centered on each nest that contained the amount of dung recorded in the pavement of that nest, corrected for the availability of dung piece size classes that were selected by females. Most females could collect sufficient dung for their pavements within 3 m of the nest.

(univariate negative binomial GLM, $p < 0.001$, $n = 220$), corresponding to an overall lower background dung density in 2013 across habitats (negative binomial GLM, $p < 0.001$, $n = 220$). A multivariate model containing year, background density of horse dung, and habitat received the greatest support, and variable importance was high for year and background horse dung density (Table 1). For temperature, variable importance was low and the

averaged regression coefficient indicated a rather weak effect (Table 1).

The strong effect of the background density of horse dung on pavement size was not the result of significant limitation in the availability of dung to nest-building larks. At all nests, background dung levels were sufficient to allow the female to collect the amount of dung necessary to build its pavement within 1–8 m radius of the nest,

TABLE 1. Competing negative binomial GLMs explaining variation in dung pavement size. The models whose w_i sum up to 0.95 and an intercept-only model are given. Models incorporate effects of year, habitat, background dung density (= grazer density), and temperature during the nest-building stage. Interaction terms of horse dung density and habitat, and horse dung density and year were also included. Variable importance $w_+(j)$ after Burnham and Anderson (2002) and model-averaged parameter estimates for covariates are also given.

Model	Intercept	Year	Background horse dung density	Habitat	Horse dung density–year interaction	Mean temperature during nest building	Background cattle dung density	Horse dung density–habitat interaction	df	ΔAIC_c	w_i
1	6.302	+	0.152	+					6	0.000	0.220
2	6.313	+	0.16						4	0.430	0.170
3	6.3	+	0.223	+	+				7	1.510	0.100
4	6.227	+	0.156	+		0.009			7	1.910	0.080
5	6.315	+	0.227		+				5	1.970	0.080
6	6.3	+	0.154	+			–0.006		7	2.120	0.070
7	6.236	+	0.163			0.009			5	2.290	0.070
8	6.311	+	0.16				–0.005		5	2.520	0.060
9	6.224	+	0.238		+	0.011			6	3.750	0.030
10	6.302	+	0.148	+				+	8	3.890	0.030
11	6.316	+	0.228		+		0.005		6	4.080	0.030
12	6.122								2	27.680	0.000
$w_+(j)$		1.00	0.98	0.52	0.24	0.21	0.2	0.03			
model-averaged parameter (SE)			0.176 (0.078)			0.009 (0.020)	–0.003 (0.059)				

TABLE 2. Competing models of nest survival. The models with w_i sum up to 0.95 and an intercept-only model are given. Variable importance $w+(j)$ after Burnham and Anderson (2002) and model-averaged parameter estimates for covariates are also given.

Model	Intercept	Habitat	Year	Nest Age	Maximum vegetation height	Season	Dung pavement size	Background horse dung density	df	ΔAIC_c	w_i
1	2.298	+	+	0.036					5	0.000	0.210
2	2.146	+	+	0.038		−0.008			6	0.690	0.150
3	2.224	+	+	0.036	0.11				6	0.900	0.130
4	2.292	+	+	0.036				−0.078	6	1.250	0.110
5	2.283	+	+	0.036			0.042		6	1.880	0.080
6	2.692	+	+						4	3.400	0.040
7	2.622	+	+		0.108				5	4.350	0.020
8	1.977	+		0.04	0.22				5	4.390	0.020
9	2.68	+	+					−0.086	5	4.510	0.020
10	2.594	+	+			−0.006			5	4.620	0.020
11	1.857	+		0.042	0.178	−0.009			6	4.850	0.020
12	1.98	+		0.04	0.217			−0.098	6	5.190	0.020
13	1.974	+		0.041	0.204		0.111		6	5.290	0.010
14	2.686	+	+				0.024		5	5.360	0.010
15	2.609	+	+		0.109			−0.086	6	5.450	0.010
16	1.847	+		0.044		−0.012			5	5.910	0.010
17	2.56	+	+		0.09	−0.005			6	5.960	0.010
18	2.599	+	+			−0.005		−0.075	6	5.980	0.010
19	2.617	+	+		0.108		0.023		6	6.320	0.010
20	2.665	+	+				0.051	−0.096	6	6.320	0.010
21	1.851	+		0.045		−0.011	0.121		6	6.600	0.010
22	2.737								1	27.560	0.000
$w+(j)$		1.00	0.87	0.81	0.27	0.25	0.2	0.16			
model-averaged parameter (SE)				0.037 (0.016)	0.138 (0.115)	−0.008 (0.007)	0.058 (0.118)	−0.084 (0.089)			

assuming every dung piece of suitable size was found and taken (Figure 2B). Field observations from 3 birds suggested that in fact females collected dung from locations up to 50 m away from the nest, much farther than even the upper limit of this minimum radius. Despite significant differences between years in pavement size, the relationship between pavement size and local dung density was constant. Females therefore built pavements of a size that consistently reflected, but was not limited by, the background dung density.

Nest Survival and Causes of Nest Failure

Daily nest survival for both years combined was 0.939 (± 0.005 SE, confidence level [CL]: 0.928–0.948), equivalent to a mean probability of a clutch surviving the entire nesting period of 0.209 (CL: 0.155–0.268), using the mean observed incubation period length of 11 days (+3 days for laying) and a mean observed age of 11 days at which chicks leave the nest. The size of the dung pavement had low variable importance, and its effect size averaged over all models was small. This finding, and the relatively high overall predation rate, yielded no evidence that building large pavements leads to decreased predation rates because of a camouflaging effect of the dung or deters predators from the nest. Nest survival increased with increasing age of the nest, but there was little support for a seasonal trend

in nest survival (Table 2). Nest survival was significantly lower in 2013 compared to 2011 and in agricultural habitat compared to pristine steppe. Models containing vegetation height, a seasonal survival trend, size of the dung pavement, and background dung density as additional covariates were competitive with respect to the best model (i.e. within 2 AIC_c units of that with the smallest AIC_c); however, effect sizes were small and variable importance low (Table 2).

Even in areas with high densities of grazing animals, trampling of nests was rare. The main cause of nest failure was predation, accounting for 97.1% of nest failures in 2011 and 84.5% in 2013. Only 2 nests were trampled in 2011 and none in 2013, but 9 nests were deserted in 2013. At 3 of these, remains of depredated females were found, corresponding to higher nest predation rates in this year (Figure 3).

In the trampling experiment, the mean number across the 6 replicates of artificial nests situated in dung piles that were trampled was 3.6 ± 1.8 SD, and the mean number of artificial nests trampled not situated in dung was 5.7 ± 3.3 SD. The presence of dung at an artificial nest was not a significant predictor of trampling outcome in a GLMM ($\beta = -0.479 \pm 0.287$ SE, $p = 0.094$), although the difference in means was in the direction of nests with dung being less likely to be trampled than those without dung.

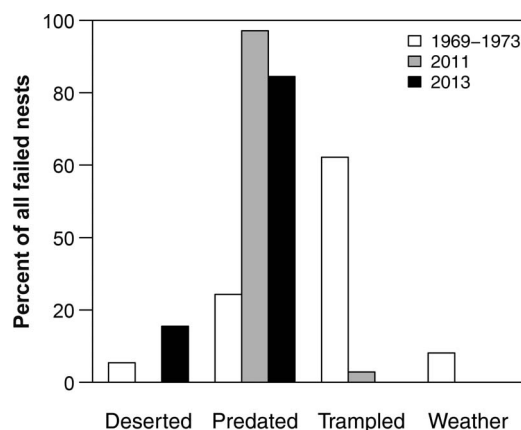


FIGURE 3. Causes of nest failure in Black Larks nests in 2011 and 2013 and from 1969–1973 (from Moiseev 1980). Sample sizes of failed nests were $n = 37$ in 1969–1973, $n = 70$ in 2011, and $n = 58$ in 2013.

The Effect of Dung on Chick Growth Rates and Nest Microclimate

Between 1 and 4 measurements of mass and tarsus were available for each of 49 chicks of known age in 17 nests (total $n = 123$ measurements). The best supported models of both mass and tarsus growth that included dung pavement size as a predictor were those including a random effect of both nest and nestling on inflection point and growth constant (mass: $\Delta AIC_c = 2.4$ from next best model; tarsus $\Delta AIC_c = 3.0$). Removing the effect of dung pavement size from these models resulted in a model within 2 AIC_c units, the increase in AIC with the removal of dung pavement size from the model suggesting equivocal support for a positive effect of dung pavement size on tarsus growth rates (mass: $\Delta AIC_c = -1.8$; tarsus: $\Delta AIC_c = 1.5$).

In the artificial nest experiment, minimum and maximum temperature differed significantly across the 3 treatments (ANOVA, $F = 6.007$, $df = 2$ and 30 , $p < 0.01$; Figure 4). Differences were most pronounced at the daily minima and maxima temperatures (Figure 4). The mean minimum temperature was on average 0.33°C higher in nests with a single ring of dung and 0.50°C higher in those fitted with a double ring. The mean maximum temperature was on average 0.25°C lower in nests with a single ring of dung and 1.88°C lower in those fitted with a double ring.

DISCUSSION

Our results provide little evidence that the large dung pavements built by female Black Lark around their nests serve as anti-predator devices because nests with more dung were not more likely to survive. We suggest that the pavements are more likely to serve a different function: they could reduce the risk of nests being trampled by

livestock and/or they might buffer inner nest temperature extremes.

Dung pavement size was positively correlated with local horse dung density but not limited by dung availability. Although pavement size varied significantly between years, the relationship between pavement size and local dung density was consistent across years and habitats, the size of the average pavement reflecting the number of dung pieces within 2–4 m of the nest. Because females were seen to collect dung from up to 50 m from the nest, the size of the pavement was clearly not limited by the availability of dung, even in areas with the fewest grazers. This finding suggests that female Black Larks might deliberately scale their pavements to their perception of the local density of dung and, by extension, to the local density of grazing animals and hence trampling risk. Nest survival rates were independent of dung pavement size and of local dung/grazer density, and trampling rates were extremely low. In our trampling experiment, the presence of a dung pile did not significantly reduce trampling risk, although the trend was in the predicted direction. The scaling of pavements to local dung densities might serve to protect nests from trampling without increasing predation risk because a large pavement of dung around a nest in an area of low dung density is more likely to attract the attention of predators than a pavement whose size reflects local dung densities. Alternatively, trampling risk might currently not be a threat to Black Lark nests in our study system, or trampling is effectively reduced by placing pavements around the nests. If dung pavements reduced overall trampling risk (trampling rates were no higher in areas of high grazing pressure than in areas of low or no grazing pressure) without attracting or deterring predators (predation rates were independent of pavement size), this would allow Black Larks to nest successfully even in areas with high densities of grazing animals.

In an earlier study on Black Larks (Moiseev 1980), a lower proportion of nests had dung pavements (73% compared to nearly 100% in this study), and a high proportion (60%) of unsuccessful nests failed due to trampling by cattle and horses compared to $<1\%$ in our study (Figure 3). Livestock numbers in Kazakhstan increased from the 1950s until the late 1980s (Robinson and Milner-Gulland 2003, Kamp et al. 2011). At the time of Moiseev's study (1980), nearly every steppe grassland area with access to water was used as pasture with usually high stock densities. After the break-up of the Soviet Union in 1991, livestock numbers across Kazakhstan collapsed, and at the time of our study there were still more than 22 million fewer head of livestock in the steppe zone of Kazakhstan than in the late 1980s (Kazakhstan State Statistics Agency 2014). In addition, grazing patterns have changed significantly; because most livestock are now privately owned for subsistence, they are concentrated

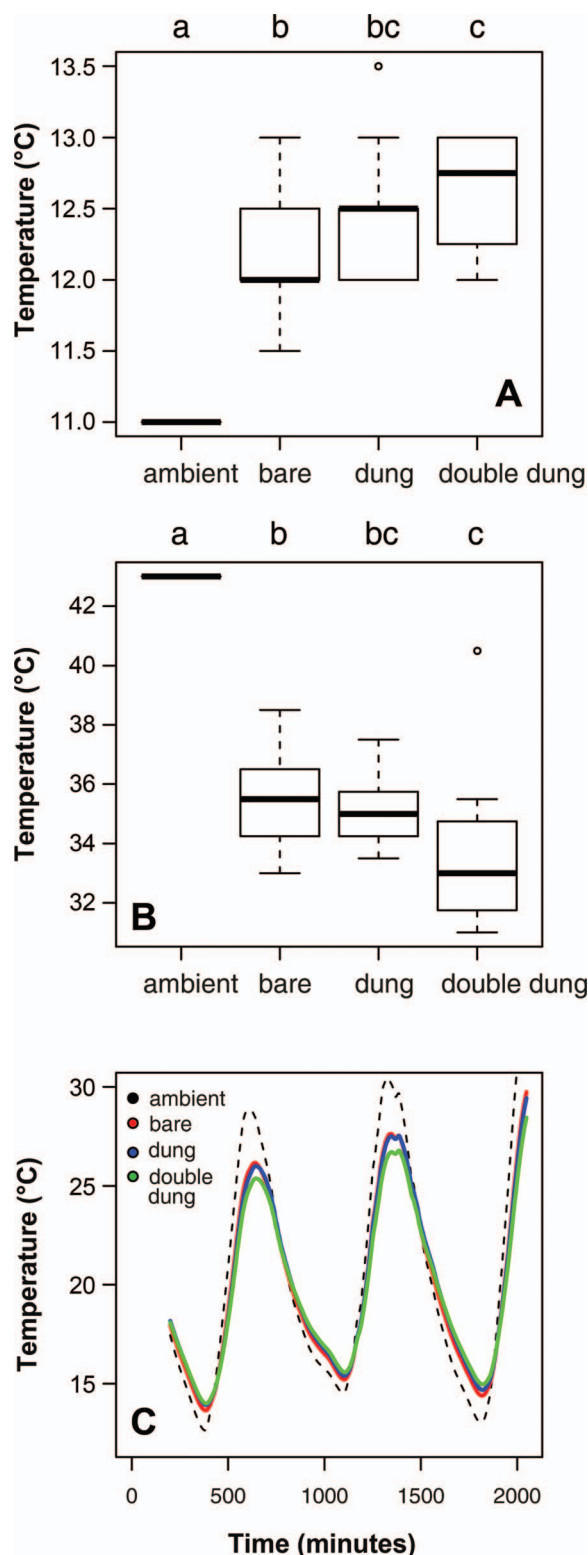


FIGURE 4. Minimum (A) and maximum (B) temperatures recorded in a randomized experiment with artificial nests and varying amounts of dung ($n = 12$ artificial nests per treatment, 1 additional data logger recording ambient temperature). Note the buffering effect of dung that results in an increase of

within a radius of 10–20 km around settlements, leading to overgrazing around human habitation and vast ungrazed areas farther away. Furthermore, more land is available for grazing livestock compared to Soviet times; by 2013 nearly 40% of the formerly used cropland (~14 million ha) was abandoned across the steppe zone compared to the 1990 area (Kazakhstan State Statistics Agency 2014).

Black Larks avoid overgrazed areas (Kamp et al. 2012) and are now found in habitats with moderate grazing pressure. The behavior of arranging dung around nests to reduce trampling risk might thus have evolved fairly recently, in a period when livestock densities were higher, and trampling risk was therefore greater than today but is still maintained, although current trampling risk is likely to be much lower. Our trampling experiment, which yielded a nonsignificant trend for an effect of dung as a deterrent to nest trampling, simulated grazing pressure far higher than that currently experienced by breeding Black Larks, so the low incidence of trampling recorded in real nests of the species does not necessarily invalidate trampling as an important past ecological pressure that required the evolution of an adaptive response. Delayed responses of organisms to formerly reliable cues have been suggested to occur widely (Schlaepfer et al. 2002). Furthermore, the lack of correlation between grazing pressure and nest survival indicates that even under today's reduced grazing pressure, dung pavements might serve an important anti-trampling function, or alternatively that trampling by grazers is currently not a threat but might have been in the past.

We also found experimental evidence for a temperature buffering effect of dung pavements and equivocal support for a positive relationship between pavement size and chick growth rates. In an experiment, increasing the amount of dung around artificial nests increased the buffering of more extreme temperatures, resulting in a higher nest temperature during the coldest time of the night and a lower maximum temperature during the warmest hours of the day. Incubating female Black Lark leave their nests for up to 3 hours during periods of intermediate air temperature (Appendix Figure 7), far longer than other larks such as the Skylark (*Alauda arvensis*), in which breaks in incubation generally last for only a few minutes (Donald 2004). The duration of these off-bouts is generally longer in birds of warmer climates because they face a lower risk that eggs and chicks cool to temperatures below the physical zero tolerance (Conway and Martin 2000). In addition, fewer but longer off-bouts

← minimum and a decrease of maximum temperatures with increasing dung cover at the nest. Treatments with the same superscript letters are not significantly different (Tukey post-hoc test, significance level $p < 0.05$). (C) Plot of the smoothed moving average of temperature over 3 days.

are an adaption to high predation risk because they reduce visible activity at the nest (Conway and Martin 2000). Recesses of several hours are rare in passerines and have so far been treated as outliers or exceptional events in periods of inclement weather that increased energy expenditure of females and thus required longer foraging trips (MacDonald et al. 2013). We also found a cooling effect of dung on the nest cup temperature during the hottest hours of the day, likely caused by evaporating moisture that was absorbed by the dung during the colder night hours. This effect might decrease the time needed by the female to shade the chicks and broaden the window of absence at the nest.

The buffering effect of dung on nest temperature might explain the routinely long absence from nests in Black Larks. During these long recesses the larks can forage without risking overheating (early morning trips) or cooling (evening trips) of eggs and chicks, and thereby even reduce predation risk. Additionally, longer foraging trips in the morning hours are important for larks to maintain their water balance because consumed seeds contain more absorbed moisture than during the day (Orr 1970). Additionally, more time could be spent collecting food for the nestlings, and we found some, albeit equivocal, evidence for a positive correlation between the size of the pavement and chick growth rate.

It is unclear how or when the unique dung pavements of Black Larks evolved. Structures akin to dung pavements, such as ramparts or pavings of pebble and small stones around the lip of the nest, have been described in other lark species (Beason 1995) and wheatears, but these tend to be small and rare (Donald 2004). Stone pavements at nests of the Rock Wren (*Salpinctes obsoletus*) have been shown to prevent water infiltration into nest cavities and might act as an “early warning system” of approaching predators because they changed the sound of a simulated predator approach (Warning and Benedict 2014). Stone carpets at Blackstart (*Cercamela melamira*) nests help to absorb heat and radiation during the day and radiate it back when temperatures drop in the evening and during the night (Yosef and Afik 1999), thereby buffering extreme temperatures, similarly to the dung pavements in our study species. Other breeding endemics of the Eurasian steppes such as Sociable Lapwing (*Vanellus gregarius*) and Black-winged Pratincole (*Glareola pratincola*) that prefer areas with high densities of domestic and wild grazers often place their clutches into existing horse dung piles but do not actively collect dung (Kamp et al. 2009a, 2009b). These colonial nesting species command a rich repertoire of anti-livestock displays such as distracting poses on the ground or sky-diving accompanied by alarm calls; therefore, there might not be a need to protect nests from trampling using added dung pavements.

Based on our data, it is not easy to assess whether trampling reduction or nest microclimate regulation is the main driver of the evolution of the behavior of constructing extensive dung pavements; however, comparable but far smaller structures seem to regulate microclimate in other related species, and it seems plausible that the extreme structures built by Black Larks represent an evolution of these. The environment of Black Larks consists of grass, grazers, dung, and little else, so it seems plausible that Black Larks or their ancestors initially used dung to fulfill the role of the stone ramparts of related species. The fortuitous anti-trampling effect stimulated the growth of these structures to the size seen today, when their flexibility in relation to background dung levels may allow them to minimize the effort needed in relation to the risk while limiting the extent to which they become conspicuous to predators. Manipulation experiments might shed further light on this possibility.

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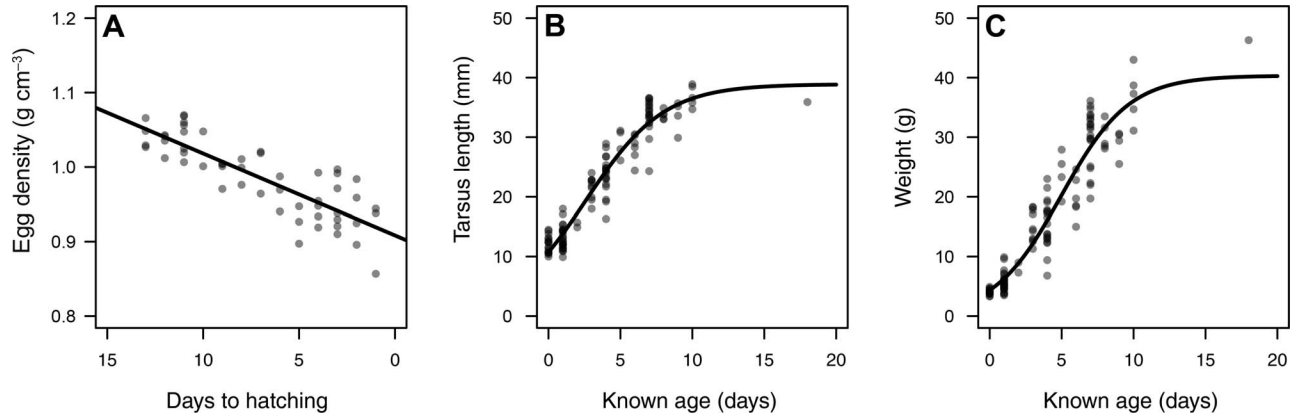
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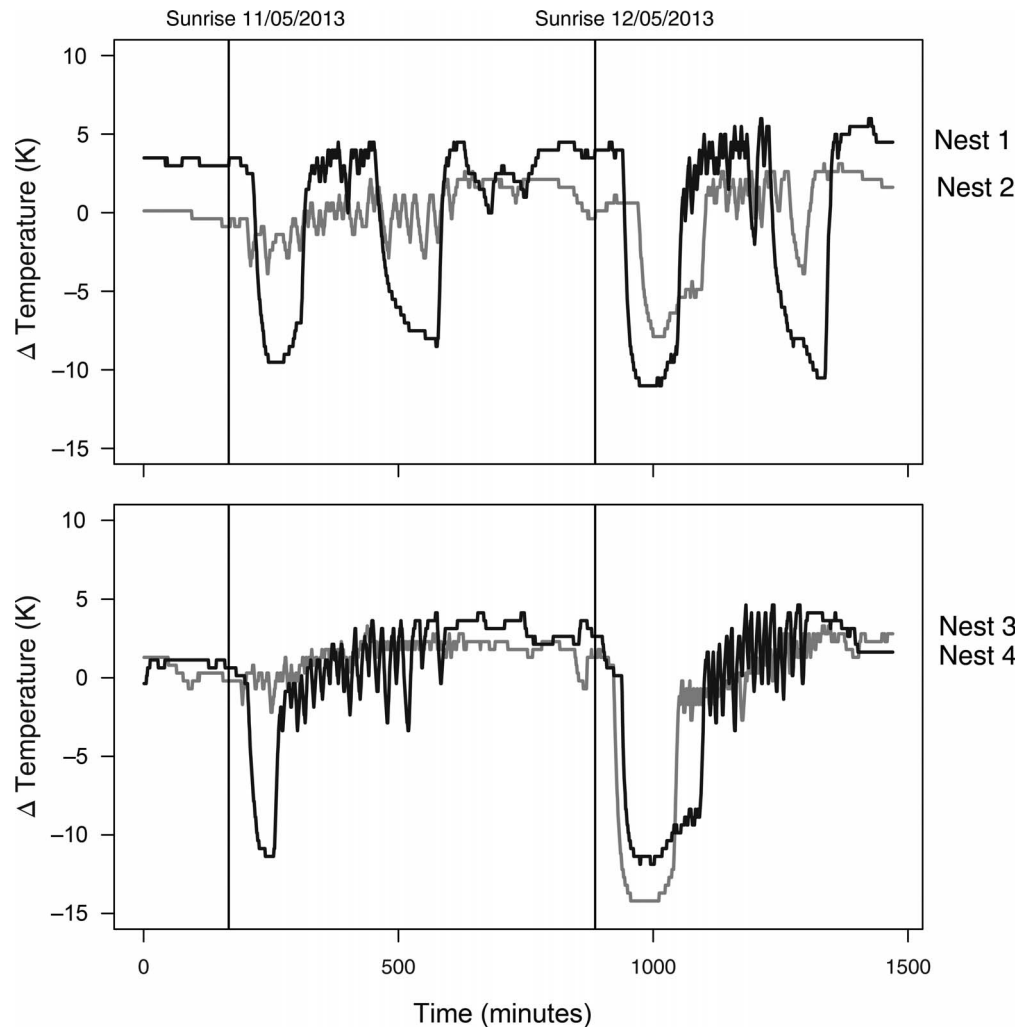
APPENDIX



APPENDIX FIGURE 5. Black Lark female on the nest. Note the large dung pieces that were collected by the female (observed in the field) and piled up at the nest entrance. Korgalzhyn, Kazakhstan, May 2011.



APPENDIX FIGURE 6. (A) Linear regression of egg density against time to hatching used for the back-calculation of first egg dates, year 2011 ($y = 0.011 \cdot x + 0.908$; $R^2_{\text{adj.}} = 0.687$, $p < 0.001$, means of $n = 53$ clutches of 3–5 eggs). Nonlinear regression of tarsus length (B) and mass (g) (C) against known chick age used for age estimation of chicks of unknown age, year 2011. The model was fitted by nonlinear least squares, and model parameters from a similar model for Eurasian Skylark *Alauda arvensis* (Donald et al. 2001) were used as starting values. The model was fitted to 123 measurements of 49 chicks from 17 nests found on the day of hatching or the day after (day 0 or 1 in the graph) and re-measured on 1 to 3 occasions until leaving the nest. Estimated parameters: tarsus $\sim 38.897 / (1 + \exp(0.964 - 0.369 \times \text{age}))$; mass $\sim 40.330 / (1 + \exp(2.112 - 0.425 \times \text{age}))$. In the graphs, darker point shading indicates repeated measurements.



APPENDIX FIGURE 7. Temperature curves over 48 hours from iButton data loggers placed into 4 Black Lark nests in May 2013 (zero-centered for all nests). Parallel observations with binoculars and video cameras confirmed that steep drops in nest cup temperature after sunset, and again during the afternoon, occurred when the females left the nest unattended. Individual variation in female incubation strategies is apparent, but external conditions also seem to trigger synchronous departure from nests in females (morning of day 2).