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Night-brooding behaviour in provisioning cavity-nesting birds is a trade-off between adult predation risk and nestling thermoregulation needs

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Night-brooding of nestlings in cavity-nesting avian species carries predation risks to parents. Anecdotally, several species are known to shift from constant adult night-brooding behaviour to leaving nestlings unattended at night during offspring development but the timing, speed of change and sex-specific differences between parents, and the factors shaping this behaviour have rarely been described. Moreover, the location and nature of night roosts used by adults whilst provisioning nestlings has received little research attention. We studied breeding Common Starlings (*Sturnus vulgaris*) and hypothesised that, in such a cavity-nesting species, 1) nestlings would only be night-brooded until they achieved thermal independence, 2) since the species is frequently polygynous, female parents would most likely exclusively night-brood offspring despite provisioning by both sexes and 3) night-brooding would be more likely during nights with lowest temperatures. Nightly video recordings throughout the nestling phase at eight Starling nests together with data from 18 Starlings fitted with GPS-loggers during 26 nights provided support for hypotheses 1) and 2), while we found no support for hypothesis 3). All tagged male Starlings always roosted far from the nesting site (up to 8 km) independent of nestling age; all females brooded nestlings, usually up to the first seven-nine days after hatching (when the nestlings achieve thermoregulation), but roosted with males after day 10, when all tagged Starlings from the same nesting 'colony' roosted together. These results confirm differential sex-related parental effort in provisioning Starlings, suggesting females only night-brood until young achieve homeothermy.

1. Introduction

Nestlings of altricial species have little or no capacity to maintain core body temperature immediately post-hatching, since they are dependent on parental heat until they have reached the stage of development where they can achieve thermoregulation (Andreasson *et al.* 2016). Physiological development of endothermy (metabolic heat generation to self-maintain body temperature) in passerine nestlings is closely correlated with increases in body mass and accompanying decreases in surface-area-to-volume ratio and age, but tends not to be correlated with plumage development (*e.g.*, Andreasson *et al.* 2016, Pereyra & Morton 2001). This implies that small nestlings are completely dependent upon parental care for warmth, food, and protection from the elements (Pereyra & Morton 2001, Wegrzyn 2013), until they attain homeothermy (when they can maintain a stable internal body temperature despite external influence, Andreasson *et al.* 2016).

The developmental pattern of thermoregulation has been studied experimentally by testing how well single nestlings at different ages can thermoregulate at ambient temperatures (Dunn 1976, Pereyra & Morton 2001). The onset of endothermy is species specific, dependent upon length of the nestling period, brood size, nest type and nest location (Clark 1982, Dunn 1975, Morton & Carey 1971). In reality, growing nestlings often benefit from heat provided by other brood members, enabling homeothermy in full broods earlier than would be the case with a single offspring. Clark (1985) showed that parent Common Starlings (*Sturnus vulgaris)* (hereafter Starling) altered their daytime brooding in relation to the average homeothermic capacity within broods and also showed dramatic increases in nest cup temperature 30 seconds after a parent entered the nest box during daytime, suggesting comparable benefits will accrue to offspring during night-brooding and the coldest part of the daily temperature cycle. This begs the question, given the increasing predation risk of being confined to a nest cavity with an ever more noisy brood of nestlings emitting strong olfactory signals accessible to nocturnal predators such as Mustelids (Feare 1984), how do night-brooding parents trade off their own predation risk through incubation with the diminishing need to brood young acquiring endothermy? In this study, we investigate how adult behaviour changes with the development of thermoregulatory abilities in nestlings by studying the degree of night-brooding among adult Starlings, to determine whether there are changes during the nestling rearing phase.

Adult passerine energy expenditure during incubation differs negligibly from that while only resting in a non-incubating posture above an air temperature of 15 °C (Haftorn & Reinertsen 1985). Hence adult birds would have expended much of the heat, which they impart to their young, in their own temperature regulation even if they were not brooding. This means maintenance of nestling endothermy by brooding is trivial energetically compared to, for example, the energy costs of intensive feeding (Wegrzyn 2013). Rather than leave the nest box, brooding adult Starlings may also benefit from staying overnight in a nest cavity with nestlings in cold environments, by accepting an increased risk of predation as a trade-off to reduce their own energetic costs of thermoregulation (Nilsson & Nord 2017). Several species are known, anecdotally, to show changes in adult brooding behaviour during nestling development, particularly shifting from initial constant adult brooding behaviour to later leaving nestlings on their own at night during the development of offspring (Katzenberger *et al.* 2015). However, details of the timing, the speed of the changes and parental sex-related differences, and the factors shaping this behaviour have rarely been described. Moreover, knowledge about the night roosts used by adults whilst provisioning nestlings has received little research attention.

The Starling is a cavity-nesting, widespread and numerous but declining breeding species associated with farmland and human settlements in western Europe (Feare 1984, Heldbjerg *et al.* 2019). The migration has been well studied throughout much of its breeding range (Fliege 1984), showing Danish breeding Starlings to be short distance migrants, mainly wintering in the British Isles and the Netherlands arriving early to the breeding sites, often in late winter, the majority in March (Bønløkke *et al.* 2006). They breed across the entire country with highest densities associated with large grassland areas and grazing dairy cattle (Heldbjerg *et al.* 2016, Vikstrøm &

Moshøj 2020). Typically, the species lays only one clutch but in years with early springs, two clutches are recorded in some areas. At the study site, the mean number of fledglings at the time of ringing (age 12–14 days) was 5.56 ± 1.01 SD (1971–2015: 857 clutches). The breeding period, which is highly synchronous has advanced by *ca.* 0.2 days year^{-1} during 1971–2015 with a mean first egg laying date in the most recent years at *ca.* 24 April and a corresponding fledgling date at *ca.* 30 May (Thellesen 2017). Starlings often breed in loose 'colonies' combining suitable nest sites with available feeding opportunities within a few hundred metres (Heldbjerg *et al.* 2017).

Cavity nest sites provide multiple benefits from environmental protection to avian parents over incubating and brooding in open nests (such as thermal insulation and protection from large predators that cannot access the cavity), yet confinement also brings risks (for instance from predation by species that can gain access to the nesting cavity). However, the chance of surviving a predator at night may still be better outside the nesting cavity than inside for adult birds. Starling nestlings in nest boxes are known to occasionally be predated by, for example, domestic cats (*Felis catus*), stone martens (*Martes foina*) and Magpies (*Pica pica*) but whether this is also a risk for the adults is unknown to us. If the predation risk is higher inside than outside the nest box, adult Starlings face a conflict between the need to maintain body heat in newly hatched nestlings that have yet to achieve effective homeothermy in the nest cavity *versus* the risk of their own predation from staying with nestlings at night (especially from mustelids, *e.g.*, Dunn 1977, Sorace *et al.* 2004). These factors shape our three hypotheses relating to night-brooding behaviours in Starlings for which we attempt to find support in this investigation.

Firstly, 1) Starling parents should night-brood offspring only as long as needed to maintain the body temperature of nestlings when ambient temperature falls at night, ceasing when the nestlings reach the age, weight and development to achieve effective homeothermy (generally seven to nine days after hatch, Clark 1982). In other words, the adult Starling behaviour should change in accordance to the nestling homeothermy. To test this, we assumed that our nestlings attained homeothermy at the same age as the Clark study (given this is metabolically determined) and examined whether night-brooding behaviour was dependent on offspring age, with an expectation that night-brooding declined after age seven days.

Secondly, Starlings are frequently polygynous (Merkel 1978, 1980); estimated at 20–60% of all males (Pinxten *et al.* 1989), and male birds in general tend to provide parental care when the fitness derived via offspring survival is greater than benefits of abandoning nestlings to seek out new mates (Balshine 2012). We therefore hypothesise that Starling males potentially divide parental investment between more than one brood, and hence 2) would be less likely to roost in nest boxes than females associated with a given brood. Males might rather benefit from association with local communal roosts (Feare 1984), to which we might expect females to resort once they ceased night-brooding homeothermic nestlings and we hypothesize that only females undertake brooding.

Finally, we hypothesized 3) that brooding would be more likely on cold nights, because regardless of the nestlings' own age and thermoregulatory abilities, nestlings would expend more energy in the absence of night-brooding by adults on cold compared to warmer nights, which would also be beneficial for the brooding adult.

2. Material and methods

Our studied colony comprised 15–17 Starling pairs breeding annually in nest boxes on a dairy farm with grazing cattle and mixed crops of spring barley, winter wheat, grass and fodder beet, owned by one of the authors (referenced as PVT from now on) in Hjortkær, near Esbjerg (55°32'N, 8°43'E) in southwest Denmark (Fig. 1), the subject of study since 1971 (Thellesen 2017). All breeding attempts were followed in detail in each nest box and the nestling age in each nest was recorded in days from day one (hatching date).

During the study of breeding Starlings over fifty years at the study site, PVT has observed that while female Starlings tended to brood newly-hatched nestlings in their nest boxes, nestlings over *ca.* one week old rarely had brooding adults in the nest box with them at night.

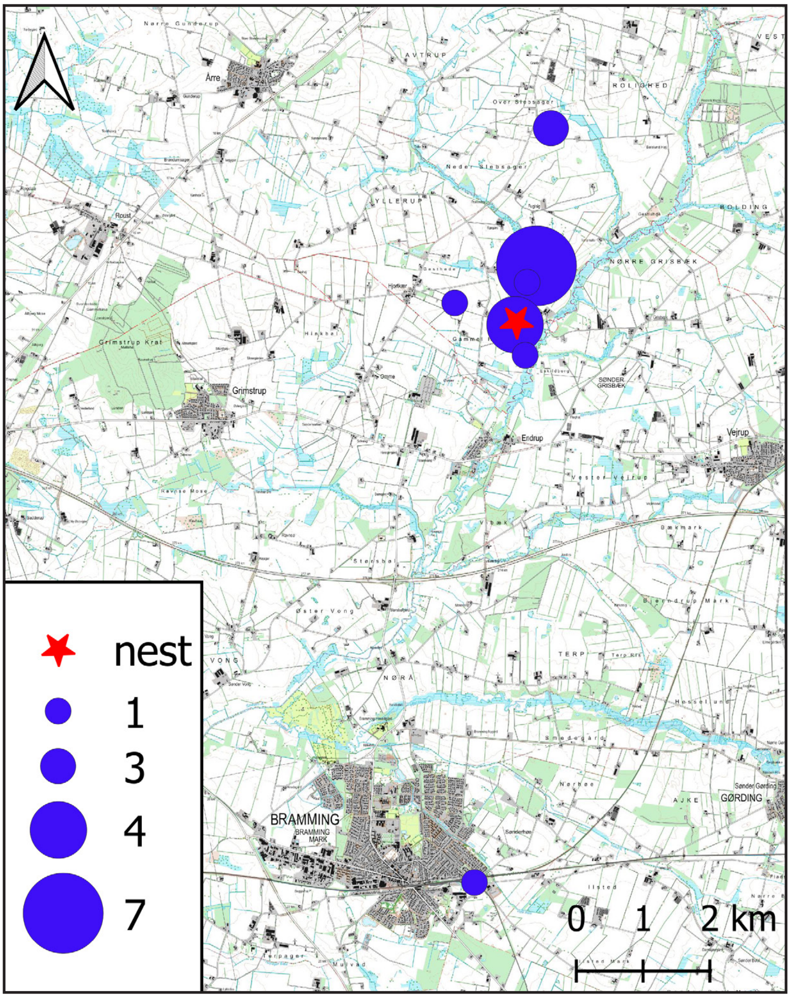

Fig. 1. Map of different overnight roosting sites used by parental provisioning Starlings (*Sturnus vulgaris*) (blue dots) breeding at the study dairy farm (red star). Increasing size of the symbols indicate the number of Starlings (one-seven) at each site. The Coordinate system is WGS84, UTM zone 32N (EPSG:25832). The map source is DTK25 – Danmarks Topografiske Kortværk 1:25 000 (www.kortforsyningen.dk)

2.1. Video surveillance

We used video surveillance of the entrance to nest boxes containing Starling nestlings of known age to determine the presence of a night-brooding adult and to relate presence/absence to ambient temperature and brood age, without disturbing the birds by our presence. Four video cameras were mounted 50 cm from, and focused upon, nest box entrances during the 2015–2017 breeding seasons to continuously monitor arrival and departure of birds throughout the provisioning period. Cameras were set to be triggered to record every movement, including parent birds entering and leaving nest boxes. Cameras were linked to a Digital Network Video Recorder (Handykam, Xvision XR960 HD DVR) which enabled storage of files for later analysis of activities. Activities recorded at eight (ultimately successful) Starling nest boxes are included in this study. Starling nightly presence/absence in a given nest box was registered by checking the last and first movements each day from hatching date (day one) to day 14. Starlings were never observed moving during darkness (recordings of night-active birds and other taxa at Starling nest boxes confirmed that movements were also registered and stored in absolute darkness). Out of the potential 112 camera-nights, 11 camera-nights were lost due to technical difficulties (hard disk capacity exceeded). The final outward movement from a nest box on a given day confirmed the bird was roosting elsewhere, while a final movement into the nest box indicated it was brooding nestlings inside. Similarly, movements were scored for the first movements in the morning (first in constituted roosting elsewhere, first out equated to night-brooding). The primary information from this source were "complete night records", where a given bird was confirmed coming to the nest box both at night and departing the following morning. Of the 101 complete night records, 79 confirmed the presence of an adult at night and morning while 22 were contradictory either as a result of movements potentially not being detected by the video or because visits by other adult Starlings to the nest boxes obscured our interpretation of whether a bird was present overnight or not. This equated to 78.2% of video recordings confirmed brooding on both occasions from all-night camera monitoring (see Supplementary Material Table S1 for details). We included additional data from the nights when the system independently recorded either last ("evening only") or first ("morning only") records only, in a subsequent analysis to assess their effect despite the lack of corroborative recordings.

2.2. Bird tracking protocol

We also tagged provisioning parent Starlings with GPS-loggers to describe their foraging movements and habitat preferences during day-time (Heldbjerg *et al.* 2017). Here, we use data from the same devices to determine sex-based differences in roosting site behaviour of adults, which was not always possible from identification of colour rings (see below) on the night-brooding adults on the video recordings.

Eighteen breeding Starlings provisioning offspring were caught during 5–14 May 2015 and 6–14 May 2016, either in nest boxes by a remote triggered closure of the entrance hole or in mist nets nearby. In a backpack attachment, we used battery powered Gypsy 5 GPS-loggers (Technosmart Europe srl., Rome, mass *ca.* 3.2 g including Teflon harness, *ca.* 3.5–4% of Starling body mass), which recorded with positional accuracy of 2–4 metres one fix per minute during daylight and one fix per hour at night, commencing one day after attachment to exclude behavioural effects of capture and handling (Heldbjerg *et al.* 2017). Tagged birds were recaptured after three–five days to retrieve loggers and data extracted via a cable connection. The recapture timing was chosen to be long enough to enable the full use of the battery capacity and short enough to be confident of recapturing the adults during the nestling phase, consistent with adults bearing loggers for the shortest possible period. All captured adults were sexed and ringed with a metal ring and three coloured rings to enable individual identification from distance and on video recordings. All procedures conformed with Aarhus University codes of research practice and were carried out with permission from the Danish Natural History Museum Ringing Centre.

Each logger provided a data file (.txt) giving position, speed and precision information for every time-stamped fix until battery failure. We filtered data after Horizontal Dilution of Precision (HDOP), which is a good indicator of how accurate the positions are, using only a precision less than *ca.* 10 meters (HDOP > 2.5) to focus on the timing of movements to and from the night roost and its position, defined by the end point of the very last flight of the day to the roost site and by counting back to the first moving point along the first flight out early morning.

We predicted that adult Starlings may be more prone to stay in the nest box at night when the night temperatures are low. Therefore, we included the minimum daily temperatures in our model on the assumption that night temperature was an additional factor that affected decisions by brooding birds to stay or leave the nest box at night. For this purpose, we used temperature data from the nearest Danish Meteorological Institute observation site at Varde (20 km from the study site, accessed 21 August 2020 at https://www.dmi.dk). Sunset and sunrise at the study site for relevant days was obtained from the mobile application software 'Dusk and Dawn' (Stobbe 2016).

2.3. Statistical analysis

We used a generalized linear mixed model (GLMM) with a binomial distribution to test the qualitative response whether a Starling roosted in its nest box as recorded in the video surveillance, since presence/absence (probability) of Starlings in nest boxes at night follows a binomial distribution. We included individual as a random effect to account for the multiple observations gathered from each individual. The logistic regression tested follows this formula:

$$\text{Probability} = 1/(1+\exp(\beta*\text{day}+\text{intercept})) \quad (1)$$

The inflection point (*i.e.*, where the probability for spending the night at the nest box was 0.5) was therefore estimated as: –intercept/β (after isolating day in the equation 0.5=1/(1+exp(β*day+ intercept))). We tested the three different measures of presence: evening only, morning only and complete nights. In this analysis we aimed at estimating the inflection point and therefore omitted temperature from the model, as the inflection point then would be a function of both day and temperature.

In another logistic regression also based on video surveillance data, we tested the effect of temperature on the likelihood of spending the night in the nest box using a generalized linear model. Here, we included days since hatching and the lowest ambient night temperature in the area as fixed effects, and the individual starling as random effect using three different measures of presence: evening only, morning only and complete nights, which gave three models. We used proc glimmix in SAS version 9.4 (SAS Institute, Cary, NC) to run the models.

3. Results

Video recordings verified whether each Starling stayed in the nest box or roosted away from it on a given night in eight nest boxes, enabling us to establish at what age nestlings were left on their own at night. We found that days after hatching had a significant effect on the likelihood of presence/absence in the nest box at night (GLMM: $F_{1,70} = 15.22$, $P = 0.0002$, $\beta_{day} = 1.2726$, Intercept = –10.01). Based on all eight nest boxes, the inflection point when more than 50% of the adult (female) Starlings spent the night away from the nest was estimated to be 7.9 days after hatching (Fig. 2). Estimated values based on evening behaviour alone (7.7 days) and morning behaviour alone (7.1 days) provided confirmatory results (Table 1). As early as day five, the first female spent the night away and by day 10 all females stayed away from their nest boxes at night (Fig. 2). The lowest ambient temperature did not affect the likelihood of spending the night in the nest box (Table 2).

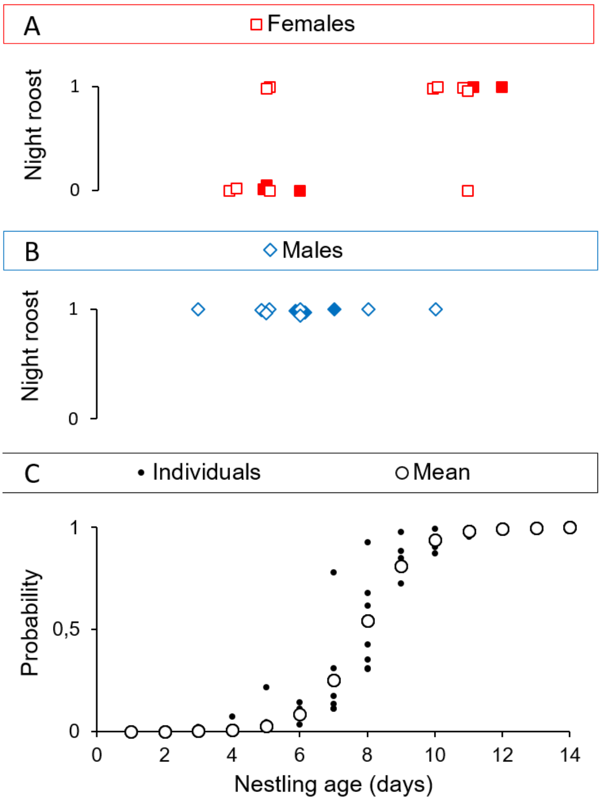

Fig. 2. Panel A shows presence (0) and absence (1) of GPS tagged female Starlings (*Sturnus vulgaris*) (red squares) night roosting in the colony with respect to nestling age; filled symbols indicate 2^{nd} nights of the same individuals. Panel B shows the same for males (blue diamonds). Panel C shows mean fitted logistic curve (open circles) based on the daily probability of presence/absence of night-brooding Starlings (from video recordings) derived from logistic regressions of data from eight individuals (shown by small filled circles from individual models). The inflection point is the nestling age when the probability of night-brooding is 0.5.

Table 1. Generalized mixed model testing the effect of day in relation to the likelihood of the female Starling spending the night in the nest box. β and intercept are parameter estimates and inflection point estimate is the night where 50% of the females did not attend the brood at night.

Dependent variable	df	*F*	*P*	β	Intercept	Inflection point
Combined	1, 70	15.22	0.0002	1.2726	–10.01	7.87
Evening away	1, 95	28.79	<0.0001	0.4569	–3.50	7.66
Morning away	1, 95	29.82	<0.0001	0.5247	–3.73	7.11

Table 2. Generalized linear model testing the effect of day and minimum ambient temperature as fixed factors in relation to likelihood of the female Starling spending the night in the eight nest boxes (N=79).

Variable	Combined			Evening away			Morning away		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Day	1, 69	10.94	0.0015	1, 94	23.59	<0.0001	1, 94	26.92	<0.0001
Temperature	1, 69	2.55	0.1147	1, 94	0.36	0.5506	1, 94	1.06	0.3058

We derived positions for 18 GPS-tagged Starlings from 26 nights. This included eight birds with data from two consecutive nights (Supplementary Material Table S2). All eight males (during 11 nights) consistently roosted away from the colony (Fig. 2, see Supplementary Material Table S3), the furthest *ca.* 8 km away in a group of coniferous trees at the edge of an urban area (Fig. 1). Four females (on seven nights in all) roosted in their nest boxes (Fig. 2). The remaining six females (eight nights) roosted 0.5–3 km from the nest (Fig. 1). Males roosted away from the colony independent of nestling age (day 3–11). The four females roosted (seven nights) in the colony with nestlings of day 4–11 (4–6 and one from day 11). The six other females that roosted (eight nights) away from the colony had nestlings of day 5–12 (10–12 and two at day five). All eight birds (five females, three males) with information on roosting site from two consecutive nights roosted at the same site.

Of nine birds tracked on the same night (7–8 May 2016, when all broods were five to seven days old), all six males roosted together in a willow thicket *ca.* one kilometer north of the colony, while all three females roosted in the colony. Two females (10–12 day old nestlings) also used the willow site on two consecutive nights (14–16 May 2016). The only pair with positions from the same night (10 day old nestlings) roosted together in a willow *ca.* three kilometers north of the colony.

Starlings arrived at roosts shortly before sunset (mean = 22.8 minutes ± 18.4 SD, n = 10) and departed again shortly before sunrise (mean 17.3 minutes ± 6.0 SD, n = 13) with no significant differences between the sexes in either arrival or departure.

4. Discussion

The video recording results confirmed that female Starlings always night-brooded nestlings in nest boxes at the beginning of brood rearing but this behaviour changed when the nestlings were *ca.* eight days, when they are downy and the flight feathers are about to emerge from the sheaths (Supplementary Material Fig. S1) and after ten days all females stayed away from the nest at night. Effective homeothermy was found in experiments to be attained at lower mean individual nestling weights in larger broods (Clark 1982), but at our study site and for Starlings in general, clutch sizes varied little, hence the variation between the nests were small and confirmation of the effect of brood size on night-brood cessation date must await larger samples with larger brood size variation. Starlings with GPS-loggers confirmed the pattern of a behavioural change in night-brooding. Data from loggers showed only females roosted at the colony, confirmed by the fact that no tagged males roosted at the colony (and hence never in nest boxes). The precision of the GPS positions is too low to identify the exact night roost (*i.e.*, whether or not in the nest box), especially because the positional precision is reduced when the GPS is located inside a nest box. However, despite the fact that we did not have irrefutable proof (*e.g.*, by observing a given female based on leg rings in the nest boxes on each given night), we are confident that Starlings night roosting in the colony were actually roosting in their nest boxes. This judgement is based on our observations of colour ringed females witnessed entering and leaving nest boxes when caught on the video recordings and on the extensive experience of PVT, which confirmed that Starlings were never found roosting in other nest boxes during the nestling phase nor at any other roost site away from their own nest box at the farm (*e.g.*, in buildings or trees in the immediate vicinity).

These observations support our hypotheses that 1) Starlings (specifically females) only brooded nestlings at night until *ca.* eight days of age and 2) that provisioning males never roosted in nest boxes (also confirmed by PVT from ringing studies). Hence, males were not tied to the nest site at night, but instead shared communal roosts with other males at different roost sites at night a significant distance away from the nests. We found no support for hypothesis 3) that the lowest ambient night temperature affected brooding in nest boxes.

The nature of night roosts used by birds whilst breeding has received very little attention (see Jirinec *et al.* 2016). Those authors found that the nocturnal roosts of Wood Thrush (*Hylocichla mustelina*) males were on average 121.8 meters from their active nests in habitats with denser canopy, often outside the diurnal home ranges. Similarly, Hill and Cresswell (1997) found male Eurasian Blackbirds (*Turdus merula*) at a communal roost several hundred metres away from nests and were accompanied by females once the nestlings were 11 days old. However, night-roosting of male Starlings, unexpectedly up to eight km away from nests, while provisioning nestlings has hitherto been unreported. The fact that roosts were several kilometres away from the nest may imply that once the adults have decided to leave the nest, they seek the best quality night roost, and that the distance moved is negligible in terms of energy use in comparison to value of using such a site. Whether this is due to the communal benefits of roosting with other birds (*e.g.*, learning of alternative rich feeding opportunities or dilution of predation risk) remains unclear and warrants further investigation. The general trend for an overall decline in brooding behaviour during the course of the nestling phase is well known from several other avian species, such as pigeons (Saxena *et al.* 2008), hawks (Wreford *et al.* 2017), falcons (Rejt 2004), tits (Tinbergen & Dietz 1994) and swallows (Marsh 1980, Winkler *et al.* 2011) but in all cases, these studies lack detail on the nestling age when the change occurs and the variation in this behaviour.

4.1. Changing needs and behaviour during the nestling phase

Results showed that females brooded their offspring overnight during the period when the nestlings are considered to be unable to self-regulate their own temperature, but ceased to do so once they had reached an age when it is considered that they have attained homeothermy. This confirms that night-brooding only continues as long as necessary to protect nestlings against heat loss, a risk adults must trade off against their own risk of predation in the cavity at night. We have no data to compare the risk for the female to be predated in the cavity to being predated away from the nest but these results clearly demonstrate that after nestlings attain homeothermy, females choose to desert them at night in the cavity in favour of a collective roost with other adult conspecifics. It is however important to note that females showed some variation in when they left the nest box at night, but we have no data on factors that could cause this variation.

Another change that may be related to the achievement of homeothermy can be seen in the behaviour of the provisioning adults. Until the nestlings are ten days old, adult Starlings remove faecal sacs from the nest, but when nestlings are feathered, this activity ceases (Feare 1984). Faecal sacs remaining in the nest will potentially result in damp and colder nestlings but Feare (1984) suggested that after this developmental stage, it is less critical to the maintenance of the thermal insulation properties of nest cavities.

Clark (1982) showed that, in general, Starling brooding behaviour decreased in relation to the effective homeothermic capacity of nestlings within broods. Temperature loss in Starling nestlings is inversely correlated with brood mass and air temperature, *i.e.*, the lower the temperature and the smaller the brood size the greater the loss (Clark 1982). As brood age and weight increase, loss of body temperature declines until day seven-eight when homeothermy is attained for a given brood size and air temperature. By day eight (when our data confirms that females change their brooding behaviour) nestlings have attained body mass of *ca.* 50 g compared to *ca.* 6 g at hatching (Feare 1984). Our birds tended to have a mean clutch size of five, resulting in total brood mass at day eight of *ca.* 250 g, the brood weight at which Clark (1982) found that Starling nestlings were able to self-regulate their body temperature at air temperatures, which lay somewhere between 6.5 and 13 °C (the temperatures experienced at our study site in the nestling period).

In this case, it is difficult to differentiate between the effective homeothermy and individual endothermy of a brood (*i.e.*, nestlings in a large brood can be effectively homeothermic due to high thermal inertia while still failing individually to maintain body temperature in the face of cold ambient conditions, *e.g.*, Dunn 1976, 1979). However, in Starlings, the age of effective homeothermy and endothermy appear strongly correlated, at least at low ambient temperatures (Clark 1982), but the difference here is perhaps not significant, as seen from the perspective of the parent, the brood has attained the ability for individuals to regulate their body temperatures in situ. For this reason, we suggest that once their offspring attained homeothermy, our female Starlings ceased brooding nestlings in the colony and joined males at communal roosts. Unfortunately, we have no GPS recordings from females with nestlings at day seven to day nine, *i.e.*, around the time of inflection.

The videos were recorded from outside the nest boxes and hence gave no information about the actual behaviour of the female in the nest box (*i.e.*, whether it was actually brooding or not). Studies on tits by Nilsson and Nord (2017) have shown that females often spend the night in the nest box late during nestling development when nestlings are endothermic, sleeping at the rim of the nest-cup and with no contact to the nestlings. They interpret this as a behaviour that mainly functions as a thermoregulatory benefit to the female. However, this behaviour may be species specific since in a Starling nest, there is no rim of a nest-cup and no space for the adult female to avoid contact to the nestlings. Hence at the nestling age of *ca.* eight days (*i.e.*, the inflection point, when the clutch typically weighs 250 g and cover almost all nest box ground surface) she will functionally be night-brooding and we cannot exclude that leaving the nestlings on their own is simply a matter of limited space in the nest box when the nestlings have grown large. Recordings inside nest boxes would describe any variation in the female behaviour during the nestling phase.

4.2. Differential sexual parental investment

Video records rarely enabled us to sex the bird (based on coloured leg rings) entering or leaving the nest box due to rapid movements under difficult light conditions. Nevertheless, in the small sample of GPS-tagged birds all those identified were females, confirming the pattern from ringing data compiled during the 50 year long breeding bird studies, that males were never retrapped in nest boxes at night during the nestling phase. Following the statement by Feare (1984) that females exclusively incubate eggs at night, it seems reasonable that the same sex invests in the initial nocturnal brooding of young nestlings.

Our data support our hypothesis that males and females differentially invest in their offspring. Starlings are frequently polygynous, hence males are likely to simultaneously have nestlings in more than one nest while females attend only their own clutches (Feare 1984). We suggest this explains her acceptance of a greater risk from predation to enhance her offspring survival by keeping nestlings warm prior to the onset of their own thermogenesis. Equally, the results suggest a willingness to trade-off her own survival versus that of their offspring. It is unlikely that the daily risk of nest predation changes during the nestling phase, so the decision to leave the nestlings on their own with increasing age is likely related to their probability of thermogenesis, rather than any real change in predation risk.

Nattruvningsbeteende hos fåglar som häckar i håligheter är en avvägning mellan egen predationsrisk och ungarnas termoregleringsförmåga

Nattruvning ökar predationsrisken hos fåglar som häckar i håligheter. Det är känt att flera arter verkar byta från fullständig nattruvning till att helt övernatta utanför håligheten och lämna ungarna i boet obevakade över natten. Man vet dock mindre om tidpunkten då detta sker, hur snabbt det sker, samt om det finns könsspecifika skillnader i dessa beteenden mellan föräldrafåglarna. Även kunskapen om var de övernattar då de matar på dagarna är begränsad. Vi undersökte häckande starar Sturnus vulgaris och lade fram hypoteserna att 1) nattruvning av ungarna skulle bara fortlöpa tills ungarna kan termoreglera, 2) enbart honorna nattruvar trots att båda könen matar ungarna, eftersom staren är polygyn, och 3) nattruvning är vanligast under de kallaste nätterna. Vi fann stöd för hypoteserna 1) och 2) men inte för hypotes 3) med hjälp av data från nattlig videoinspelning under hela ungomvårdnadstiden och data från 18 starar med GPS-loggers under 26 nätter. Alla GPS-försedda hanstarar övernattade långt från häckningsplatsen (upp till 8 km) oberoende av ungarnas ålder medan alla GPS-försedda honor nattruvade sina ungar vanligtvis sju till nio dagar efter kläckning (då ungarna kan termoreglera), men övernattade med hanarna efter dag 10, då alla starar från samma ”koloni” övernattade tillsammans. Dessa resultat bekräftar att det finns könsspecifika skillnader i ungomvårdnad hos matande starar och att honorna bara nattruvar tills ungarna själv kan termoreglera.

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References

Andreasson, F., Nord, A. & Nilsson, J.-Å. 2016: Brood size constrains the development of endothermy in blue tits. — Journal of Experimental Biology 219(14): 2212–2219. https://doi.org/10.1242/jeb.135350

Balshine, S. 2012: Patterns of parental care in vertebrates. — In The Evolution of Parental Care (eds. N.J. Royle, P.T. Smiseth, & M. Kölliker): 62–80. Oxford University Press, Oxford.

Bønløkke, J., Madsen, J.J., Thorup, K., Pedersen, K.T., Bjerrum, M. & Rahbek, C. 2006: The Danish Bird Migration Atlas. — Forlaget Rhodos A/S & Zoologisk Museum, Københavns Universitet.

Clark, L. 1982: The development of effective homeothermy and endothermy by nestling starlings. — Comparative Biochemistry and Physiology – Part A: Physiology 73(2): 253–260. https://doi.org/10.1016/0300-9629(82)90066-4

Clark, L. 1985: Consequences of homeothermic capacity of nestlings on parental care in the european starling. — Oecologia 65(3): 387–393. https://doi.org/10.1007/BF00378914

Dunn, E. 1977: Predation by Weasels (*Mustela nivalis*) on Breeding Tits (*Parus* spp.) in Relation to the Density of Tits. — Journal of Animal Ecology 46(2): 633–652.

Dunn, E.H. 1975: The Timing of Endothermy in the Development of Altrical Birds. — The Condor 77(3): 288–293.

Dunn, E.H. 1976: The Relationship between Brood Size and Age of Effective Homeothermy in Nestling House Wrens. — Wilson Bulletin 88(3): 478–482.

Feare, C. 1984: The Starling. — Oxford University Press.

Fliege, G. 1984: Das Zugverhalten des Stars (*Sturnus vulgaris*) in Europa: Eine Analyse der Ringfunde. — Journal of Ornithology 125(4): 393–446. https://doi.org/10.1007/bf01640135

Heldbjerg, H., Fox, A.D., Levin, G. & Nyegaard, T. 2016: The decline of the Starling *Sturnus vulgaris* in Denmark is related to changes in grassland extent and intensity of cattle grazing. — Agriculture, Ecosystems and Environment 230: 24–31. https://doi.org/10.1016/j.agee.2016.05.025

Heldbjerg, H., Fox, A.D., Thellesen, P.V., Dalby, L. & Sunde, P. 2017: Common Starlings (*Sturnus vulgaris*) increasingly select for grazed areas with increasing distance-to-nest. — PLoS ONE 12(8). https://doi.org/10.1371/journal.pone.0182504

Heldbjerg, H., Fox, A.D., Lehikoinen, A., Sunde, P., Aunins, A., Balmer, D.E., Calvi, G., Chodkiewicz, T., Chylarecki, P., Escandell, V., Foppen, R., Gamero, A., Hristov, I., Husby, M., Jiguet, F., Kmecl, P., Kålås, J.A., Lewis, L.J., Lindström, Å., … Weiserbs, A. 2019: Contrasting population trends of common starlings (*Sturnus vulgaris*) across Europe. — Ornis Fennica 96(4): 153–168.

Hill, I. F. & Cresswell, B. 1997: The use of a communal summer roost by radio-tagged Blackbirds *Turdus merula*. — Bird Study 44(1): 114–116. https://doi.org/10.1080/00063659709461044

Jirinec, V., Varian, C. P., Smith, C. J., & Leu, M. 2016: Mismatch between diurnal home ranges and roosting areas in the Wood Thrush (*Hylocichla mustelina*): Possible role of habitat and breeding stage. — Auk 133(1): 1–12. https://doi.org/10.1642/AUK-15-76.1

Katzenberger, J., Tate, G., Koeslag, A. & Amar, A. 2015: Black Sparrowhawk brooding behaviour in relation to chick age and weather variation in the recently colonised Cape Peninsula, South Africa. — In Journal of Ornithology 156(4): 903–913. https://doi.org/10.1007/s10336-015-1199-0

Marsh, R.L. 1980: Development of Temperature Regulation in Nestling Tree Swallows. — The Condor 82(4): 461–463.

Merkel, F.W. 1978: Sozialverhalten von individuell markierten Staren *Sturnus vulgaris* in einer kleinen Nistkastenkolonie 1. Mitteilung: Gruppenbild urn einem Staren mann. — Luscinia 43: 163–181.

Merkel, F.W. 1980: Sozialverhalten von individuell markierten Staren *Sturnus vulgaris* in einer kleinen Nistkasten-kolonie. III. Die Rolle der Polygyny. — Luscinia 44: 133–158.

Morton, M. L. & Carey, C. 1971: Growth and the Development of Endothermy in the Mountain White-Crowned Sparrow (*Zonotrichia leucophrys oriantha*). — Physiological Zoology 44(3): 177–189.

Nilsson, J.-Å. & Nord, A. 2017: The use of the nest for parental roosting and thermal consequences of the nest for nestlings and parents. — Behavioral Ecology and Sociobiology 71(12). https://doi.org/10.1007/s00265-017-2400-7

Pereyra, M.E. & Morton, M.L. 2001: Nestling growth and thermoregulatory development in subalpine Dusky Flycatchers. — The Auk 118(1): 116–136.

Pinxten, R., Eens, M. & Verheyen., R.F. 1989: Polygyny in the European Starling. — Behaviour 111(1): 234–256.

Rejt, L. 2004: Nocturnal Behaviour of Adult Peregrines at the Nest during Nestling Period. — Vestnik Zoologii 38(3): 87–90.

Saxena, V.L., Pandey, E., Agarwal, S. & Saxena, A.K. 2008: Execution of breeding and nidification behaviour in Pigeon (*Columba livia*) and Dove (*Streptopelia chinensis*). — Asian Journal of Experimental Science 22(3): 405–410.

Sorace, A., Petrassi, F. & Consiglio, C. 2004: Long-distance relocation of nestboxes reduces nest predation by Pine Marten *Martes martes*. — Bird Study 51(2): 119–124. https://doi.org/10.1080/00063650409461343

Stobbe, K. 2016: Dusk and Dawn (Version 1.8) [Mobile application software]. — Retrieved from https://apps.apple.com/us/app/dusk-and-dawn/id492122434

Thellesen, P.V. 2017: Common Starling *Sturnus vulgaris* clutch size, brood size and timing of breeding during 1971-2015 in Southwest Jutland, Denmark. — Dansk Ornitologisk Forenings Tidsskrift 111: 87–95. (In Danish with English summary)

Tinbergen, J.M. & Dietz, M.W. 1994: Parental Energy Expenditure During Brood Rearing in the Great Tit (*Parus major*) in Relation to Body Mass, Temperature, Food Availability and Clutch Size. — Functional Ecology 8(5): 563–572. https://doi.org/10.2307/2389916

Vikstrøm, T. & Moshøj, C.M. 2020: Fugleatlas – De danske ynglefugles udbredelse. — Dansk Ornitologisk Forening & Lindhardt og Ringhof.

Wegrzyn, E. 2013: Resource allocation between growth and endothermy allows rapid nestling development at low feeding rates in a species under high nest predation. — Journal of Avian Biology 44(4): 383–389. https://doi.org/10.1111/j.1600-048X.2013.05846.x

Winkler, D.W., Hallinger, K.K., Ardia, D.R. & Robertson, R.J. Stutchbury, B.J. Cohen, R.R. 2011: Tree Swallow (*Tachycineta bicolor*). — In The Birds of North America (ed. Poole, A.). Cornell Lab of Ornithology, Ithaca. https://birdsoftheworld.org/bow/species/treswa/cur/introduction

Wreford, E.P., Hart, L.A., Brown, M., & Downs, C.T. 2017: Black Sparrowhawk *Accipiter melanoleucus* breeding behaviour and reproductive success in KwaZulu-Natal, South Africa. — Ostrich 88(3): 287–290. https://doi.org/10.2989/00306525.2017.1307875

Online supplementary material

Supplementary material available in the online version of the article includes Tables S1–S3 and Fig. S1.