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Ecological drivers and fitness consequences of incubation period in *Ficedula albicollis* (Collared Flycatcher): Insights from a long-term data set

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ABSTRACT

Using a 37-year dataset of *Ficedula albicollis* (Collared Flycatcher) we examined how incubation duration is influenced by environmental conditions and female characteristics. In our study, we clearly demonstrated that the length of the incubation period exhibits variability and may be subject to selection. Our findings indicate that the duration of the incubation period tended to affect hatching success but played a more substantial role in recruitment, which is a key indicator of fitness. We found that incubation duration is significantly affected by laying date, clutch size, female body condition, and ambient temperature, including its variability. Interestingly, both low and high ambient temperatures are linked to shorter incubation periods. In turn, an increase in temperature variability is associated with shortening incubation periods. Further research is needed to explore the long-term impacts of these incubation strategies on population viability, particularly in the face of increasing climate variability.

Keywords: climate change, Collared Flycatcher, *Ficedula albicollis*, fitness, parental care, temperature

How to Cite

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LAY SUMMARY

- Using a 37-year dataset of *Ficedula albicollis* (Collared Flycatcher), we examined how environmental conditions and female characteristics influence incubation duration and its consequences for hatching success and recruitment of the offspring.
- Our study indicates that the duration of the incubation period has the potential to affect hatching success, but it apparently plays a crucial role in offspring recruitment, which is a key indicator of fitness.
- We found that clutch size, female body condition, and ambient temperature, including its variability, significantly affect incubation duration.
- Low and high temperatures are linked to shorter incubation periods, while an increase in temperature variability is associated with shortening incubation periods.
- These findings provide insights into how environmental conditions may influence incubation as a key avian reproductive trait, with potential implications for bird responses to climate change.

Ekologiczne uwarunkowania i znaczenie długości inkubacji dla dostosowania *Ficedula albicollis* (muchołówki białoszyjej): wnioski z danych długoterminowych

ABSTRAKT

W oparciu o 37-letni zbiór danych z populacji *Ficedula albicollis* przeanalizowano, w jaki sposób warunki środowiskowe oraz cechy fenotypowe samic wpływają na długość okresu inkubacji. Wyniki jednoznacznie wskazują, że czas trwania inkubacji wykazuje znaczną zmienność i może podlegać presji selekcyjnej. Zaobserwowano, że czas trwania inkubacji wpływa zarówno na sukces wyklucia, jak i na rekrutację potomstwa, będącą kluczowym komponentem dostosowania. Czas trwania inkubacji istotnie zależał od daty zniesienia pierwszego jaja, wielkości lęgu, kondycji ciała samicy oraz średniej temperatury otoczenia i jej zmienności. Zarówno niskie, jak i wysokie wartości temperatury wiązały się

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ze skróceniem okresu inkubacji, podobnie jak zwiększona zmienność temperatury. Dalsze badania są niezbędne, aby ocenić długoterminowe konsekwencje tych wzorców dla stabilności populacji w obliczu szybko postępujących zmian klimatu.

Słowa kluczowe: muchołówka białoszyja, opieka rodzicielska, zmiany klimatu, temperatura, dostosowanie, *Ficedula albicollis*

INTRODUCTION

Climate change, marked by shifts in temperature, altered precipitation patterns, and increased extreme weather events, directly and indirectly, impacts birds' reproductive success (Dunn and Winkler 2019). However, some bird species may mitigate the detrimental effects of climate change by adjusting key behaviors, such as parental care. Parental care is particularly crucial in birds, as the investment in raising offspring is essential for the survival and fitness of the next generation (Royle et al. 2012). Phenotypic plasticity in parental care enables birds to adjust their reproductive behaviors in response to changing environmental conditions, allowing them to maintain reproductive success despite climatic variability (DuRant et al. 2019).

An essential aspect of avian parental care is egg incubation, which plays a key role in embryo development and survival (Deeming and Reynolds 2015). However, incubation is commonly a costly aspect of avian reproduction, requiring significant energy and time (DuRant et al. 2013, Deeming and Reynolds 2015, Nord and Williams 2015) because eggs must be kept at relatively high and stable temperature regimes for successful embryonic development (DuRant et al. 2013, Deeming and Reynolds 2015). Because incubation requires prolonged parental investment, it often comes at the expense of other essential activities, such as foraging and self-maintenance, creating a tradeoff (Conway and Martin 2000; Cooper and Voss 2013; Nord and Williams 2015). The tradeoff between incubation and self-maintenance is shaped by various environmental and ecological factors, including food availability (Nord and Cooper 2020, Ryeland et al. 2021), nest attentiveness (Heppner and Ouyang 2021), and predation risk (Yoon et al. 2017), with thermal conditions playing a particularly important role. Growing evidence suggests that temperature strongly influences incubation, making it a valuable model for studying how birds balance egg warming with their own energy demands (Deeming and Reynolds 2015, Lundblad and Conway 2021).

One of the key aspects of incubation is its duration, which varies within species as individuals adjust incubation length in response to environmental conditions (Higgott et al. 2020). In general, higher ambient temperatures are associated with shorter incubation periods, likely due to modifications in early incubation behavior that compensate for increased external heat (Ardia et al. 2006, Lord et al. 2011, García-Navas and Sanz 2011, Griffith et al. 2016, Diez-Méndez et al. 2021b, Temizyürek et al. 2022). However, the extent to which temperature influences incubation duration varies across individuals, populations, and species, as their responses are shaped by ecological context and parental conditions. For instance, *Tyrannus tyrannus* (Eastern Kingbird) exhibit shorter incubation periods in warmer conditions, whereas *Aegithalos caudatus* (Long-tailed Tit) prolong incubation under similar thermal conditions (Gillette et al. 2021, Higgott et al. 2020). Several studies suggest that increased nest attendance in response to warmer temperatures leads to shorter incubation periods (Hepp et al. 2006, Nord and Nilsson 2012, Coe et al. 2015, Diez-Méndez et al. 2021a). However, other studies do not find this relationship (Amininasab et al. 2016, Simmonds et al. 2017), indicating that the effects of temperature on incubation duration may be population-specific and influenced by broader ecological factors such as food availability and predation risk. A recent experimental study by Ton and Martin (2017) further highlights this variation, demonstrating that species incubating at colder natural temperatures exhibit stronger reductions in incubation duration when exposed to experimental warming, whereas species already near their physiological incubation temperature limits show minimal changes. These findings suggest that species-specific physiological constraints, rather than environmental conditions alone, play a crucial role in shaping incubation duration across taxa. While birds can adjust their incubation strategies to different thermal environments, the long-term consequences of these adjustments on offspring fitness and reproductive success remain poorly understood. Understanding how incubation patterns affect birds' fitness is particularly important as climate change continues to alter temperature regimes, potentially affecting avian reproductive success and population viability.

To get a better understanding of the significance of incubation duration, we used a 37-year dataset to study how incubation duration influences fitness-related traits in a migratory passerine, *Ficedula albicollis* (Collared Flycatcher). This study is among the first to leverage such extensive long-term data to examine the role of incubation duration in avian reproductive ecology. Specifically, we examined whether the duration of incubation affects the key reproductive outcomes, such as hatchability and subsequent recruitment of offspring. Moreover, we aimed to determine how ambient temperature and its variability during the incubation period, as well as laying date, clutch size, and the age and condition of the female, affect the length of the incubation period.

We hypothesized that shorter incubation periods would be positively associated with a higher number of hatched nestlings in a brood. This expectation is based on multiple mechanisms: (1) shorter incubation reduces exposure to predation and adverse environmental conditions, (2) stabilizes embryonic thermal conditions, (3) minimizes microbial infections on eggs, and (4) reflects optimized parental incubation investment (Ton and Martin 2017, Higgott et al. 2020, Ma et al. 2023). Moreover, we expected that ambient temperature during the incubation period would influence female incubation behavior. Indeed, our previous experimental study in the same *F. albicollis* population revealed that females in nests with elevated temperatures spent less time in the nest box during egg incubation and took more off-bouts than females in control nests (Arct et al. 2022). This suggests that under warmer ambient conditions, females may reduce their attentiveness without significantly disrupting embryonic development. Therefore, we predicted that higher ambient temperatures would be associated with shorter incubation periods, as females may take more frequent off-bouts without significantly disrupting embryonic development due to increased environmental heat. Although higher incubation effort is generally associated with higher embryonic temperatures within and among species, leading to shorter developmental periods, the effects of ambient temperature on parental attentiveness are not necessarily uniform. Warmer conditions could either increase or decrease incubation attentiveness, depending on species-specific life-history strategies, parental conditions, and ecological factors such as food availability. If attentiveness decreases with increasing ambient temperature, faster development would only occur if external heat provides an additive effect, maintaining higher egg temperatures even during parental off-bouts. In this scenario, warmer ambient conditions would not only buffer eggs against cooling when the female leaves the nest but could also elevate egg temperatures during on-bouts, reinforcing the acceleration of embryonic development (Arct et al. 2022).

Conversely, greater temperature variability might result in longer incubation periods, as females may need to adjust the frequency and duration of incubation bouts more often to maintain stable egg temperatures under fluctuating environmental conditions. In addition to environmental conditions, individual characteristics like condition and age can have an influence on female incubation behavior (Badyaev et al. 2003, Ardia et al. 2006, Soler et al. 2001) and male incubation feeding (Lifjeld et al. 1987, Siefferman and Hill 2005). For this reason, we predicted that females in better condition would have shorter incubation durations, as they might be more efficient at maintaining optimal incubation temperatures. Moreover, since younger females are less capable of keeping eggs warm, which may be due to physiological characteristics and/or energy constraints (Aldrich 1983, Yerkes 1998), we also predict that older females would have shorter incubation durations.

We also accounted for clutch size and laying date, as these factors have the potential to affect incubation duration. First, earlier egg-laying dates are typically associated with more favorable environmental conditions (e.g., Both and Visser 2005), which may influence incubation duration. While increasing temperatures have been shown to shorten the apparent incubation period (Both and Visser 2005), favorable conditions for early-laid clutches may sometimes lead to longer incubation periods, as birds do not need to begin full incubation before clutch completion (Veiga 1992, Stoleson and Beissinger 1999). Second, larger clutches usually require longer incubation periods due to increased energy demands on the incubating female (Thomson et al. 1998.), although this relationship may be modified by the laying date.

METHODS

The data on *F. albicolliss* analyzed in our study were collected on Gotland Island (53°N, 06°E) from 1981 to 2017. *Ficedula albicollis* is a single-brooded species (Wiggins et al. 1998); however, if a breeding attempt fails before fledging and sufficient time remains in the breeding season, pairs may initiate another attempt (Gustafsson 1985). However, in our studies, we focused only on the first broods. Nests are typically built in tree cavities or nest boxes and are composed of dry grass, leaves, bast, and pieces of bark (Cramp and Perrins 1993).

During each breeding season (April–June), all nesting attempts were systematically monitored, with ~95% of breeders being ringed and measured. From the end of April, nest boxes were inspected every 4 days to determine the laying date and clutch size. Starting from the laying of the fifth egg (assuming one egg was laid per day), nest checks were conducted every other day to determine the onset of incubation (incubation day 0). After 12 days of incubation, nests were checked every other day to determine the exact hatching date and the number of hatchlings. Following hatching (hatching day = day 0 of nestling life), nest visits were conducted on days 2 and 12 to obtain nestling measurements. Nestlings were ringed 12 days after hatching, allowing us to track individuals in subsequent years. By identifying ringed individuals upon their return and onset of breeding, recruitment at the brood level can be accurately quantified. The number of recruits at the brood level is defined as the number of offspring that survived to the subsequent breeding season and were observed breeding within the study population.

Whenever possible, adult birds were captured using cliptraps or mist nets and, if not already ringed, were marked with a numbered aluminum ring. Females were caught while incubating, whereas males were captured while feeding nestlings between days 6 and 12 post-hatching. Birds were aged based on a distinctive molt limit visible within the greater wing coverts, primary feather wear, and the coloration of the inside of the upper mandible. In most cases, their age was further verified using past ringing data. Sex was determined based on plumage characteristics (Svensson 1992). Wing length was measured as the maximum length of the flattened and straightened wing, following Svensson's (1992) methodology, to the nearest half millimeter. Wing length was measured using a wing ruler, while body mass was recorded using precision weighing scales. The number of observations for individual females varied as the availability of data differed across variables (Table S1).

Female *F. albicollis* are solely responsible for incubating the eggs. The incubation period typically ranges from 10 to 17 days, with an average of 13.2 days (Table S2). Following previous studies (Cresswell and McCleery 2003, Bueno-Enciso et al. 2017, Higgott et al. 2020), we measured the apparent incubation period as the number of days between clutch completion and hatching. Specifically, incubation duration was defined as the number of days between the laying date of the last egg and the hatching date of the first egg (i.e., incubation duration = observed hatching date—last laying the date when the last egg was laid).

Climatic Factors

Daily temperature records were obtained from the meteorological station at Hoburgen (56.92°N, 18.15°E; ~10 km from the main study areas). The data were accessed via the website of the Swedish Meteorological and Hydrological Institute (http://opendata-download-metobs.smhi.se/explore/?parameter=3). We calculated the average daily temperature and their variability for the incubation period as the number of days between clutch completion and hatching for each female separately.

Statistical Analyses

To determine relationships between the duration of the incubation period (a dependent variable) and a set of explanatory variables, we fitted a generalized additive mixed model (GAMM) with a Gaussian error distribution and identity link function. In this model, female age was entered as a categorical variable (levels: young and old), whereas laying date, clutch size, female body condition, average ambient temperature, and ambient temperature variability were introduced as covariates. Female body condition was expressed as the scaled mass index and calculated from body mass and linear measurement of body size (wing length in our case), following the protocol proposed by Peig and Green (2009). Moreover, a GAMM with a Poisson error distribution and log link function was fitted to analyze the relationship between the number of hatched nestlings at the brood level (a dependent variable) and the duration of the incubation period with control for laying date and clutch size (all explanatory variables were treated as covariates). In turn, another GAMM with a Poisson error distribution and logit link function was fitted to examine the relationship between the number of recruits at brood level (a dependent variable) and incubation duration with control for hatching date and hatchling number entered into this model as a covariate. In all GAMMs, penalized thin regression splines (with a number of knots set to 5) for all covariates were used to model potential nonlinear relationships between dependent and explanatory continuous variables. All covariates were centered and scaled across years with a mean equal to zero and a standard deviation equal to one. Female identity, study plot, and year of study were introduced to all GAMMs as random factors to control for nonindependence of data within the same females, study plots, and years. We checked the assumptions for all models through visual inspection of the residual plots and also tested for concurvity of smooth terms. We found no problem with the concurvity among splines (the worst value detected by the concurvity test did not exceed 0.26). There were also no signs of overdispersion or zero inflation in the count data from GAMMs analyzing the number of hatched nestlings and recruited offspring. Statistical analyses were performed using packages *gamm4* (version 0.2-6), *mgcv* (version 1.9-1), and *mgcViz* (version 0.1.11; Wood 2017, Fasiolo et al. 2020, Wood and Scheipl 2020), and *DHARMa* (version 0.4.7; Hartig 2022), all implemented in the R environment ver. 4.4.2 (R Core Team 2025). All statistical tests were 2-tailed, and the significance level was set at $P < 0.05$. (To get insight into descriptive statistics of all analyzed variables based on raw data, Table S2 for details.).

RESULTS

We found that the number of hatched nestlings per brood was nonlinearly but positively related to clutch size (effective degrees of freedom [edf] = 2.88, $P < 0.001$; Table S3 and Figure S1), indicating that larger clutches generally produced more hatchlings. Moreover, the number of hatched nestlings per brood tended to be associated with incubation duration with the highest hatchling numbers at intermediate incubation durations (edf = 2.23, $P = 0.055$; Table S3 and Figure S2). No effect of laying date on hatchling number was detected (Table S3). However, we found that the number of recruited offspring at the brood level was nonlinearly predicted by the number of hatched nestlings (edf = 3.04, $P < 0.001$; Table S4 and Figure S3) and linearly related to hatching date and incubation duration (both terms with edf = 1.00, $P < 0.001$; Table S4). Both the hatching date and the duration of incubation periods were negatively associated with the recruit number (Figure 1 and Supplementary Material, respectively). Furthermore, we found that the duration of incubation is significantly influenced by several factors, including the average ambient temperature and its variability during incubation, laying date, clutch size, and female body condition (Table 1). Specifically, both low and high average ambient temperatures were associated with shorter incubation periods, with longer duration of incubation observed at intermediate temperatures (Figure 2). Moreover, greater temperature variability was related to shorter incubation periods, while low and moderate levels of temperature variability corresponded to longer incubation durations (Figure 3). Incubation duration successively nonlinearly decreased with the advance of the breeding initiation date until late breeding events, which were not related to incubation duration anymore (and even slightly increased incubation periods; Figure S5). In turn, we observed that incubation periods decreased when clutches became larger but only to the point when clutches were close to the average number of laid eggs (Figure S6). We also showed a

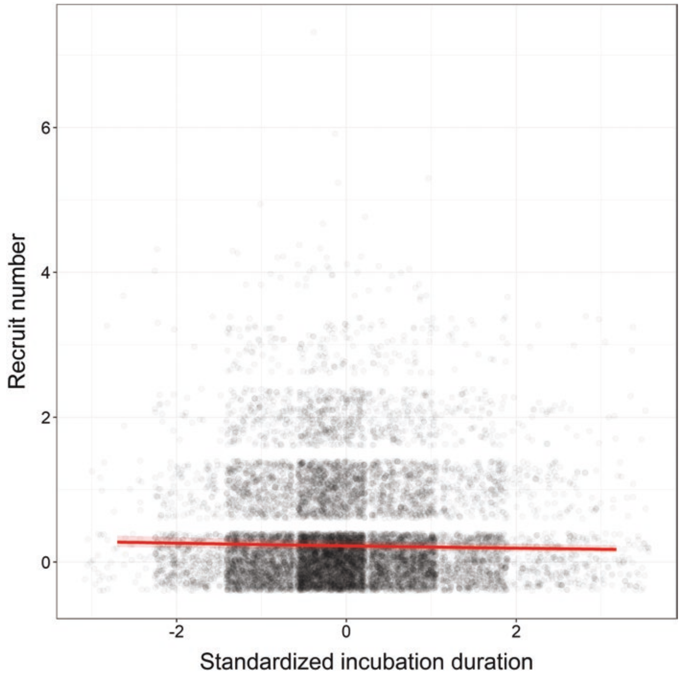

FIGURE 1. Relationship between the number of recruits at the brood level and the standardized incubation duration. A predicted line with a 95% CI and raw data points are shown.

TABLE 1. Results of a generalized additive mixed model with Gaussian error variance and identity link function that examined relationships between a set of explanatory variables and the duration of the incubation period. Female age was introduced to the model as a categorical variable (levels: young and old), whereas laying date, clutch size, female body condition, average ambient temperature, and ambient temperature variability were set as penalized thin regression splines (all with knot number set at 5). Female identity, study plot, and year of study were treated as random factors. Parameter estimates with SE in brackets for the intercept and categorical predictor and effective degrees of freedom (edf) for splines are given. An edf = 1 indicates linear relationships and edf > 1 indicates nonlinear relationships (i.e., quadratic if edf = 2, cubic if edf = 3, etc). Variance estimates for random factors are presented. The significance level for each explanatory variable is coded as *** ($P < 0.001$), ** ($P < 0.01$), and * ($P < 0.05$).

	Response variable
Explanatory variables	**Incubation duration (number of days) (*n* = 11,426 clutches of 8,074 females)**
Intercept	13.39 (0.11)***
Female age: young	0
Female age: old	−0.03 (0.02)
Laying date	edf = 3.90***
Clutch size	edf = 3.75***
Female body mass	edf = 3.14***
Average ambient temperature	edf = 3.66***
Ambient temperature variability	edf = 3.89***
Female identity $_{\text{random}}$	0.07
Study plot $_{\text{random}}$	0.02
Year of study $_{\text{random}}$	0.44

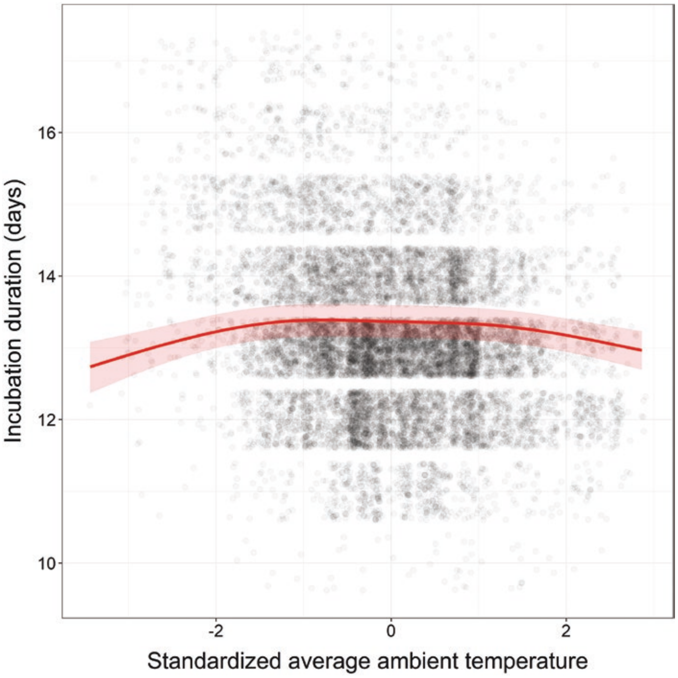

FIGURE 2. Relationship between the duration of incubation and the standardized average ambient temperature. A predicted line with a 95% CI and raw data points are shown. .

nonlinear relationship between female body condition and incubation duration. The observed pattern indicated that females at the extremes of body condition tended to have shorter incubation periods compared to those of intermediate body condition (Figure 4). We found no effect of female age on incubation duration (Table 1).

DISCUSSION

The results of this study provide important insights into how environmental factors and female intrinsic characteristics influence incubation duration, with further consequences for reproductive success in passerine birds. Our correlative findings are consistent with experimental studies showing that incubation duration is influenced by environmental temperature and parental traits, as demonstrated in controlled experimental manipulations (e.g., Ospina et al. 2018, Ton and Martin 2017). We found that incubation duration tended to be associated with the number of hatched nestlings per brood and was a significant predictor of offspring recruitment—a key indicator of fitness. Specifically, shorter incubation periods were associated with higher recruitment rates, a result that aligns

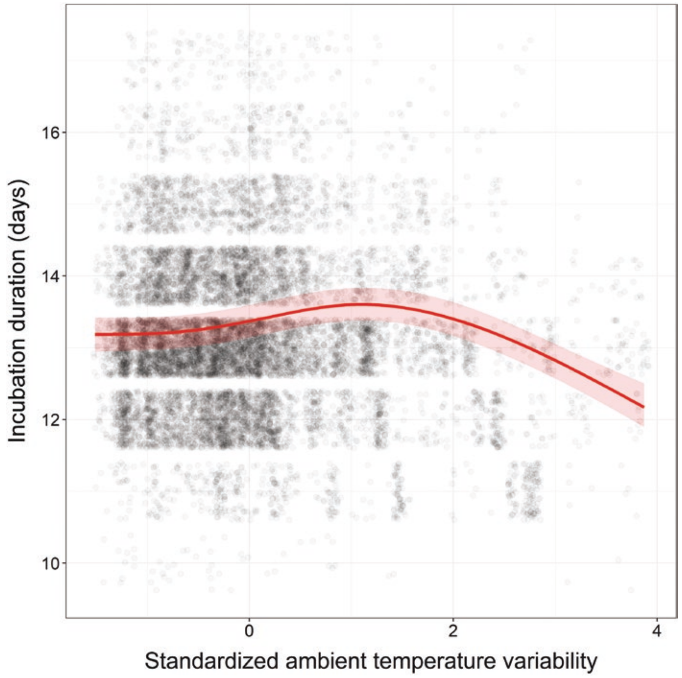

FIGURE 3. Relationship between the duration of the incubation period and the standardized ambient temperature variability. A predicted line with a 95% CI and raw data points are shown.

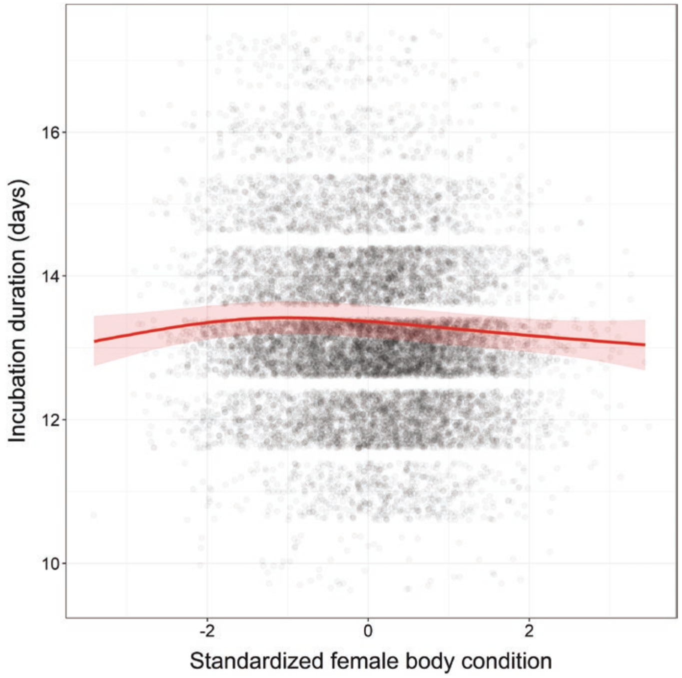

FIGURE 4. Relationship between the duration of the incubation period and the standardised female body condition. A predicted line with a 95% CI and raw data points are shown.

with studies showing that prolonged incubation may increase exposure to nest predation and expose eggs to adverse weather conditions (e.g., Martin et al. 2007, Hepp et al. 2006, Ardia et al. 2006, Higgott et al. 2020), which ultimately may decrease fitness. Similarly, DuRant et al. (2013) demonstrated that embryos of *Aix sponsa* (Wood Duck) experiencing longer developmental periods hatch with lower body mass and condition. These results underscore the importance of adequate incubation time in ensuring proper embryonic development and, consequently, offspring survival.

We also demonstrated that average temperature and its variability during the incubation period significantly influence the length of incubation. Ambient temperature plays a crucial role in energy expenditure during incubation, with lower temperatures requiring greater incubation effort to maintain suitable conditions for embryonic development (Vleck 1981, Haftorn and Reinertsen 1985, Reid et al. 1999, Tinbergen and Williams 2002, Cresswell et al. 2004, Coe et al. 2015, Amininasab et al. 2016). Specifically, lower temperatures cause eggs to cool more rapidly when left unattended, which can slow embryonic growth and decrease hatching success (Reid et al. 2000, Olson et al. 2006). Our study does not support these findings, showing that lower temperatures shorten the incubation period. This result stands in contrast to existing research on various species, where prolonged exposure to cold, even on the scale of hours to days, has been shown to lengthen incubation periods (Sealy 1984, Lyon and Montgomerie 1985, Olson et al., 2006). Similarly, high temperature has also been found to shorter incubation duration, potentially due to thermal stress affecting parental behavior and embryonic development (Nord and Nilsson 2016, Ton and Martin 2017, DuRant et al. 2013). In contrast, a study on *Parus major* (Great Tit) found that experimentally increasing nest temperature through a heating treatment did not significantly affect the incubation duration (Vaugoyeau et al. 2017). However, despite numerous experimental studies investigating the influence of environmental temperature on avian reproduction, the wide variety of heating protocols used in these experiments complicates the ability to generalize the effects of incubation temperature on avian reproductive outcomes (Reid et al. 2000, Cresswell et al. 2004, Olson et al. 2006, Ardia et al. 2010, Nord et al. 2010, Álvarez and Barba 2014, Nord and Nilsson 2016, Ton and Martin 2017).

Our study found that eggs exposed to highly fluctuating temperatures during incubation exhibited shorter incubation periods. This suggests that parents may adjust their incubation behavior in response to thermal variability, potentially enhancing incubation efficiency and ultimately shortening the incubation period. Incubating adults might increase nest attendance, modify brood patch contact, or alter egg-turning frequency to improve heat transfer and accelerate embryonic development (Turner 2002). By intensifying incubation effort under fluctuating thermal conditions, parents may compensate for temperature instability, effectively reducing overall incubation duration. This behavioral adjustment could serve as a strategic response to mitigate the risks associated with prolonged exposure to unpredictable or suboptimal thermal environments, thereby promoting offspring survival and fitness. Similarly, DuRant et al. (2013) demonstrated that fluctuating temperatures can destabilize the incubation environment, potentially prompting embryos to hatch sooner as an adaptive mechanism to minimize prolonged exposure to unfavorable thermal conditions.

Our research also demonstrates that clutch size affects the incubation period. Consistent with other findings from our study, factors that deviate from average values significantly influence incubation time. Specifically, small clutches required longer incubation periods. Smaller clutches tend to cool more quickly and experience lower initial incubation temperatures compared to larger ones, which may contribute to prolonged incubation durations (Boulton and Cassey 2012). In contrast, larger clutches require greater heat energy for effective incubation, increasing parental energy investment (Tinbergen and Williams 2002). This higher energy expenditure may explain the extended incubation duration observed in larger clutches. Indeed, several studies have shown that incubating larger clutch sizes results in longer incubation periods (e.g., Dobbs et al. 2006, Leach et al. 2017). Additionally, while larger clutches may not inherently retain heat better due to thermal inertia, they may experience slower temperature declines due to parental adjustments in incubation effort or nest insulation effects (Boulton and Cassey 2012). However, embryonic temperatures still drop rapidly during parental off-bouts, regardless of clutch size (Martin et al. 2015), highlighting the importance of continuous incubation behavior in maintaining optimal egg temperatures.

Our study also revealed that female body condition, but not age, was associated with variation in incubation duration (Figure S5), potentially reflecting condition-dependent behavioral strategies during incubation. The nonlinear relationship observed between female body condition and incubation duration suggests energy tradeoffs inherent in incubation. Females in better condition may take more frequent off-bouts during incubation, leading to longer overall incubation periods, while females in poor condition may lack the energy reserves for efficient incubation, also leading to extended incubation durations. This is consistent with Hepp et al. (2006), who highlighted the critical role of body condition in incubation efficiency. In addition to environmental conditions, female age has been suggested to influence incubation behavior, as older females may be more efficient incubators. However, in our study population, we found no significant effect of female age on incubation duration. This contrasts with findings in some species where older females exhibit improved incubation efficiency, such as higher nest temperatures or shorter recess durations (Aldrich 1983, Yerkes 1998). Similar to our study, female age was not related to nest attentiveness in *Larus glaucescens* (Glaucous-winged Gull, Reid 1988). However, in *L. argentatus* (Herring Gull), female age did not correlate with egg temperature (Bogdanova et al. 2007), further illustrating that age-related incubation patterns can vary across species. Overall, there is limited evidence for consistent age-specific incubation strategies in birds, and more longitudinal studies are needed to determine whether and how female age affects incubation behavior.

Our findings provide valuable insights into how incubation duration varies with environmental conditions and how this variability may influence reproductive success. While our study does not directly assess long-term climate change effects, it highlights the potential consequences of both temperature fluctuations and rising temperatures on incubation patterns. The observed lengthening of the incubation period in response to low or highly variable temperatures suggests a flexible incubation strategy, demonstrating the plasticity of avian reproductive behaviors. This flexibility may allow birds to adjust incubation patterns to optimize hatching success, ultimately contributing to fitness under changing environmental conditions. However, further research is needed to determine the long-term implications of these responses and how they interact with other reproductive traits, such as nest-site selection and parental care strategies.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

The study uses the data that has been previously collected during the long-term study in a wild population of Collared Flycatchers. The data upon which this study is based has been obtained following the Swedish guidelines for work on natural populations and under licenses and permits from the Swedish Ringing Centre (license no. M716 to SMD) and Swedish National Board for Laboratory Animals, Stockholm (ID 9164-2021; ID 872-2017; 37-15-2015).

Conflict of interest statement

We declare we have no competing interests.

Author contributions

Aneta Arct: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing; Karolina Skorb: Investigation, Methodology Writing – review & editing; Lars Gustafsson: Funding acquisition, Project administration, Resources; Szymon M. Drobniak: Methodology, Conceptualization, Writing – review & editing; Rafał Martyka: Methodology, Conceptualization, Formal analysis, Validation, Writing – review & editing.

Data Availability

Analyses reported in this article can be reproduced using the data provided by Arct et al. (2025). DOI: https://doi.org/10.5061/dryad.fqz612k47.

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