

Active Warming of Open Cup Nests Reveals Contrasting Effects of Temperature on
Development and Size in Wild Songbirds

by

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Abstract

Temperatures during development can affect bird physiology and morphology. As the climate changes, understanding these impacts across diverse sets of species in natural systems is increasingly important. Previous studies of the relationship between temperature and bird development have largely relied on field experiments using nest boxes, or have warmed eggs *ex situ* in an incubator. Fewer studies have tried to manipulate the temperature of open cup nests, largely limiting experiments to cavity-nesting species that are willing to nest in nest boxes. We developed an active warming device that consistently and accurately warms nests to a specified level above the ambient temperature and maintains this elevated temperature throughout the incubation period. We then used this method to warm the nests of three North American passerines—gray catbirds (*Dumetella carolinensis*), American robins (*Turdus migratorius*), and northern cardinals (*Cardinalis cardinalis*)—2°C above ambient temperature throughout the incubation and nestling period, and to quantify the impacts of warming on developmental rate and size. We find contrasting effects of the experimental warming across species, with warming resulting in faster development and smaller size in catbirds and slower development and larger size in robins. These contrasting responses may be explained by differences in the relationships between the ambient temperature at the study site and the optimum developmental temperature for each species. Our results show that large scale comparative analyses of warming-mediated developmental plasticity are needed in order to better-understand observed impacts of global warming on birds.

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Introduction

Across the tree of life, increasing temperatures due to climate change tend to be associated with consistent shifts in morphology (Gardner et al. 2011, Ryding et al. 2021). In ectothermic vertebrates, higher temperatures during development tend to result in smaller body size, and this relationship is widely thought to be driven by temperature-mediated developmental plasticity (Daufresne et al. 2009, Sheridan and Bickford 2011). In endothermic vertebrates, such as birds, the relationship between temperature and changes in morphology has long been attributed to natural selection (McKechnie and Wolf 2010, Speakman and Król 2010) since endotherms are able to regulate their body temperature through metabolic processes. However, there is increasing evidence that developmental plasticity may similarly underlie warming-driven morphological change in endotherms (Weeks et al. n.d.). As such, many of the broadly-consistent declines in size in birds that are driven by warming temperatures (Weeks et al. 2020, Jirinec et al. 2021) may be the result of phenotypic plasticity, in which temperatures during development alter the expression of the underlying genotype.

While prevailing temperatures in avian nests- can alter nestling development, and ultimately adult physiology and morphology, the form of these relationships is uncertain. Results from experiments examining morphological changes in nestling birds in response to experimentally elevated temperatures are variable across species, with some birds increasing in size (Dawson et al. 2005, Ton and Martin 2017) while others getting smaller (Londoño et al. 2008, Ardia et al. 2009, Wada et al. 2015, Rodríguez and Barba 2016, Rodríguez et al. 2016, Andrew et al. 2017, Andreasson et al. 2018, Ospina et al. 2018). Similarly, elevated temperatures can result in changes in body shape, for example shifts in relative wing length

(Dawson et al. 2005, Vedder 2012, Bleu et al. 2017). These experimental results are broadly consistent with trends in observational data (Weeks et al. 2020, Jirinec et al. 2021), however there remains unexplained variation in bird morphological responses to warming across systems (Sheridan and Bickford 2011, Ryding et al. 2021).

To empirically test the relationship between temperature and nestling development on morphology, prior studies have either directly warmed nest boxes, cavity nests, or open-cup nests, or have temporarily removed eggs from nests to be warmed in incubators (Strausberger 1998, Wingfield et al. 2003, Nord and Nilsson 2011, Wada et al. 2015, 2018, Berntsen and Bech 2016, Andrew et al. 2017, Ospina et al. 2018, Merrill et al. 2020). Nest boxes and cavity nests for nestling songbirds have been warmed mainly using heating pads or mats (Reid et al. 2000, Dawson et al. 2005, Álvarez and Barba 2014, Rodríguez and Barba 2016, Rodríguez et al. 2016, Andreasson et al. 2018, Castaño-Vázquez et al. 2018), but researchers have also used hand warmers (Bleu et al. 2017, Vaugoyeau et al. 2017), resistive film heaters (Mueller et al. 2019), heat sensors attached to aluminum plates (Vedder 2012), or thermoelectric heaters (Ardia et al. 2009).

When focusing on incubator and nest box studies, similarly diverse effects of heating are evident, with some studies reporting nestlings increasing in body size (Dawson et al. 2005), some decreasing (Ardia et al. 2009, Wada et al. 2015, Rodríguez and Barba 2016, Rodríguez et al. 2016, Andrew et al. 2017, Andreasson et al. 2018, Ospina et al. 2018), and some not significantly impacted (Reid et al. 2000, Wingfield et al. 2003, Nord and Nilsson 2011, Vedder 2012, Álvarez and Barba 2014, Vaugoyeau et al. 2017, Castaño-Vázquez et al. 2018, Wada et al. 2018). The relationship between tarsus length-perhaps the best metric of intra-specific differences in bird size-and temperature is also mixed, with increased

temperatures reducing tarsus length in some nestlings (Andrew et al. 2017, Ospina et al. 2018) or having no effect (Dawson et al. 2005, Nord and Nilsson 2011, Álvarez and Barba 2014, Rodríguez et al. 2016, Bleu et al. 2017, Vaugoyeau et al. 2017, Mueller et al. 2019). Hatching success in these experiments either decreased with increases in temperature (Strausberger 1998, Nord and Nilsson 2011, Wada et al. 2015) or was not impacted by (Reid et al. 2000, Vedder 2012, Álvarez and Barba 2014, Berntsen and Bech 2016, Bleu et al. 2017, Vaugoyeau et al. 2017, Mueller et al. 2019). The impacts of warming on fledging success was similarly variable, with decreases in fledging success (Rodríguez et al. 2016, Ospina et al. 2018, Mueller et al. 2019), increases in fledging success (Reid et al. 2000, Dawson et al. 2005, Andreasson et al. 2018, Castaño-Vázquez et al. 2018), or no effect (Vedder 2012, Álvarez and Barba 2014, Berntsen and Bech 2016, Rodríguez and Barba 2016, Bleu et al. 2017, Vaugoyeau et al. 2017). The degree of warming has varied between studies, with the majority having a temperature increase of 5°C or greater. Only one study, to our knowledge, increased nest box temperature within 1-2°C above the ambient temperature (Mueller et al. 2019), which is the projected mean increase for global temperature in the next century (IPCC 2022). The unexplained variety of responses to warming treatments highlights the need for broad comparative experiments in natural settings.

Only a handful of studies have experimentally heated open cup nests *in situ*, presumably because of the higher fluctuations in daily temperatures and associated practical challenges (e.g., increased exposure to weather, predation, and difficulty manipulating the nests after they have been built). Those studies that have warmed open cup nests *in situ* have either used polyimide heaters (Ton and Martin 2017, Mitchell et al. 2020) or a light bulb in a cylindrical aluminum tube (Londoño et al. 2008). In these studies, egg mass decreased in

heated nests (Londoño et al. 2008), nestling growth rate increased in heated nests (Mitchell et al. 2020), and nestling hatching success and adult mass were unaffected by heat (Londoño et al. 2008, Ton and Martin 2017). More information on how both these and other developmental and survival metrics that have not been tested (e.g., tarsus length, fledging success) are being affected in nestlings by increasing temperatures is needed, particularly across a greater diversity of species. Furthermore, although the average degree of warming was within 1-2°C above ambient temperature in these studies, the temperature difference was only regulated constantly throughout the day and night in one of the three studies.

We use a novel method for warming open cup nests to test whether warmer temperatures during development lead to shifts in growth rates and body size in birds. We test our method on open cup nests of three migratory North American songbirds, gray catbirds (*Dumetella carolinensis*), American robins (*Turdus migratorius*), and northern cardinals (*Cardinalis cardinalis*), and use it to simulate climate change-driven changes in temperature. By experimentally heating eggs and nestlings we test the hypothesis that increased temperatures during development will result in increased nestling growth rates and smaller size at fledging.

Materials and Methods

The warming device

We developed an active warming device to warm open cup nests *in situ*. This device is an electrical circuit, consisting of a 5V polyimide heater, and breadboard with a series of 10 & 1 ohm resistors and a fuse (Fig. 1; Appendix S1: Table S1). All components were connected via an insulated copper wire (16 gauge, 2 m long). This device was connected to a 5V battery via a male USB terminal that was soldered to the copper wire. Male breadboard pins were soldered onto the end of the copper wire leading to and from the breadboard. All components of the warming device, except for the polyimide heater itself and its wires, were stored in a waterproof electrical box (Fig. 1, Appendix S1: Table S1). This box was placed at the base of the tree or shrub that held each nest.

Similar to the method used by Mitchell et al. (2020), the polyimide heater was placed directly underneath the cup of the nest, with a piece of aluminum foil underneath it to force heat upwards. To avoid conspicuousness, camouflage tape covered the aluminum foil (Fig. 1; Appendix S1: Fig. S1, S2 & S3). The warming device and wires were secured to the tree and nest using brown zip ties. For the warmed nests, the 5V batteries were changed every other day to maintain a constant energy supply to the warming devices. For the control nests, a warming device (polyimide heater, aluminum foil, tape, wires, zip ties) was attached to the nest, but not connected to a battery (Appendix S1: Fig. S3).

In order to maintain a difference of 1-2°C between the nest and ambient temperature, the heater was calibrated using a series of resistors and Bluetooth temperature loggers. Two temperature loggers were placed on top of polyimide heaters (one heated, one control) in outdoor conditions (not in direct sunlight) for over 24 hours to assess how much resistance

was needed to lower the heat output of the heater enough to only raise the ambient temperature by 2°C consistently. 12 ohms was determined to be the appropriate amount of resistance and all nests used 12 ohms.

Study site and species

The study was conducted from April to June 2021 at two University of Michigan temperate deciduous forest research sites located in southeast Michigan, USA: Saginaw Forest (42.27° N, 83.80° W), and Newcomb Tract (42.41° N, 83.90° W). The forests within these sites are closed canopy with dense understory trees and shrubs. This region is characterized by cold snowy winters and warm humid summers. The Köppen Climate Classification subtype in this region is Dfa (cold, without dry season, hot summer) (Peel et al. 2007). During April to June, the average temperature in these areas ranges from 3.9°C to 26.5°C and it rains approximately 8.66 cm (Southeast Michigan Climate Information 2021). We focused on three common passerine species at the sites: American robin (*Turdus migratorius*), gray catbird (*Dumetella carolinensis*), and northern cardinal (*Cardinalis cardinalis*). These species build open cup nests in trees and shrubs. We only considered nests that were less than two meters off the ground. A total of 11 robin and catbird nests with eggs were found and manipulated across both field sites. For the robins, six nests were heated and three nests were controls. For the catbirds, one nest was heated and one was a control. In addition, we also manipulated three cardinal nests to test the method but excluded these nests from the analysis of the effects of warming because the only cardinals eggs that hatched were in the two heated nests. In total, we considered 41 eggs in 11 nests (robins = 32, catbirds = 9). Of the 11 total

nests, only eight had at least one egg make it to hatching. The total number of nestlings across all nests was 28 (robins = 19, catbirds = 9).

Nest selection and temperature monitoring

Nests were located by either observing adult birds exhibiting nest building behavior or searching trees and shrubs for nests at each site from mid-April to early June. Accessible nests were primarily found in young trees and shrubs at forest edges with high to medium sunlight exposure. Once a nest was found, it was monitored every other day to track nest construction and egg-laying progress. After nest construction was completed and incubation started (the day the first egg in the clutch was laid), half of the nests for each species were randomly selected to be experimentally heated, and the other half acted as control nests.

To record ambient temperature throughout nest manipulation, a Bluetooth temperature logger ($\pm 0.5^{\circ}\text{C}$ accuracy; Appendix S1: Table S1) that took readings every minute was placed close to each nest in a location with similar sunlight exposure. We assessed the performance of the heating devices on our nests by placing an additional Bluetooth temperature logger inside the cup of the nest immediately after the nestlings fledged. Ambient and nest temperature were then recorded hourly for 24 hours. Six of the nests (5 robin, 1 catbird) disintegrated right after the nestlings fledged, and so we included three of the northern cardinal nests to supplement this analysis. Temperatures inside and outside of the nests were compared over a 24-hour period for each nest that was still intact post-fledging ($N = 5$). The average difference between ambient and inside-nest temperatures for control and heated nests was calculated (Fig. 2).

Nestling monitoring and morphological measurements

Following completion of egg laying, all nests were checked every other day. Nestlings were given a unique combination of nail polish colors on their toes to identify individuals. Each individual was weighed with an electronic scale to the nearest 0.1 g every other day beginning on the day after it hatched. Weighing ceased a few days before the nestlings fledged (*T. migratorius* = 10 days, *D. carolinensis* = 8 days) to avoid causing early fledging (Streby et al. 2013). Tarsus was measured with digital calipers to the nearest 0.1 mm on the last day of weighing. Eggs that failed to hatch and nestlings that didn't survive to fledge were also recorded for each nest. No nests were abandoned directly due to the warming or control device, but two robin nests were predated during the nestling stage.

Statistical analyses

Nestling growth rate was tracked by compiling individual mass data (g) through time. Growth trajectories were fit with a logistic growth function:

$$\text{Mass} = \frac{K}{1 + e^{\frac{\text{mid}-t}{\text{scal}}}}$$

where 'K' is the asymptote of the logistic curve, 'mid' is the inflection point of the curve, 'scal' is the scaling factor for time, and 't' is time. The logistic curve was parameterized using the SSlogis function in R (R Core Team 2020). We interpret K as the final mass, the inflection point as the time to reach the maximum growth rate, and the slope at the inflection point as the maximum growth rate.

Given that mass is variable through time, tarsus length is a preferable indicator of subtle differences in size within species (Senar and Pascual 1997). While it was not feasible to measure tarsus length throughout the nestling period due to the extremely small size of

very young nestlings, we were able to measure tarsus length at the time of fledgling (fledgling tarsus length) for all species. We then tested whether there were differences between fledgling tarsus length in the warmed and control nests. To do this, we used a linear model of fledgling tarsus length as a function of ambient temperature, experimental treatment (i.e., heated vs. control nest), species, and an interaction term between species and experimental treatment.

In addition to the model that included both robins and catbirds, we modelled the relationship between experimental treatment and fledgling tarsus length in separate models for robins and catbirds. This allowed us to explore more complex model structures within the robins, which had greater variation in nesting date (between April and June- 66 days). For robins, we used the dredge function from the MuMIn package (Bartoń 2020) in R to find the best linear model for fledgling tarsus length with ambient temperature, date, and experimental treatment as the possible predictors. Limited variation in nesting date prevented us from running a similar model for catbirds, so we examined fledgling tarsus length in the catbird-only model as a function of experimental treatment.

Results

Consistent warming through time

In our post-fledging nest analysis, we find that over a 24-hour period, the control nests, which included one robin, one cardinal, and one catbird nest, were on average 0.6°C ($\text{SD} = 0.59^{\circ}\text{C}$) cooler than ambient temperatures (Fig. 2). For the heated nests, which included two cardinal nests, the inside of the nest was on average 2.08°C ($\text{SD} = 0.48^{\circ}\text{C}$) above ambient temperature (Fig. 2).

Contrasting impacts of warming on nestling growth rates

The temperature treatment impacted growth rates differently for robins and catbirds. Robins in control nests (11 nestlings, 3 nests) were smaller, grew slower and reached their fastest growth rate earlier than robins in heated nests with a predicted final mass of 54.62 g, a maximum growth rate of 1.68 g/day, and they reached their maximum growth rate at 4.69 days (Fig. 3). Robins in heated nests (8 nestlings, 3 nests) had a predicted final mass of 66.81 g, their maximum growth rate was 2.01 g/day, and they reached their maximum growth rate at 6.15 days (Fig. 3). The effects of warming on catbirds were the opposite of the robins. Catbirds in control nests (4 nestlings, 1 nest) reached their maximum growth rate later, grew faster, and ultimately ended up being larger; they had a predicted final mass of 30.87 g, their maximum growth rate was 1.90 g/day, and they reached their maximum growth rate at 5.52 days (Fig. 4). In contrast, catbirds in heated nests (5 nestlings, 1 nest) had a predicted final mass of 24.36 g, their maximum growth rate was 1.52 g/day, and they reached their maximum growth rate at 3.70 days (Fig. 4).

Contrasting impacts of warming on fledgling tarsus length

The results of the linear model that included both species show that there is a significant interaction between species and experimental treatment ($P = < 0.01$, Table 1), indicating that the effect of the heating treatment on tarsus length differed between species. The overall effect of the treatment was positive for robins ($\beta = 1.66$) and negative for catbirds ($\beta = -1.22$). Ambient temperature during measurement had a significant negative relationship with tarsus length in both the catbird and robin models ($\beta = -0.42$, $P < 0.01$, Table 1), though this effect is likely not interpretable, as ambient temperature and laying date are highly correlated. The contrasting effects of the treatment are also reflected in the models run independently for each species.

The best robin-only model, according to AIC, included the date of nesting and the experimental treatment. In this model, tarsus length was significantly positively associated with the heating treatment ($\beta = 0.76$, $P = 0.02$, Table 2). Consistent with this relationship, we find that heated robins had an average tarsus length of 27.93 mm and control robins had an average tarsus length of 23.77 mm (Fig. 5). The date of measurement negatively affected tarsus length in robins ($\beta = -0.25$, $P < 0.01$, Table 2), suggesting that robins that hatched later in the season tended to be smaller. In the catbird-only model, tarsus length was significantly negatively associated with the heating treatment ($\beta = -0.99$, $P < 0.01$, Table 3). Consistent with this relationship, heated catbirds had an average tarsus length of 16.19 mm and control catbirds had an average tarsus length of 20.73 mm (Fig. 6).

Survival

While we cannot quantitatively assess the impacts of heating on hatching success, given the limited number of nests, we see limited differences in hatching and fledging success between control and heated nests. Hatching success for control and heated robins was 50 and 80 percent, respectively. Hatching success for control and heated catbirds were both 100 percent. Fledging success for control and heated robins was 25 and 10 percent, respectively. Fledging success for control and heated catbirds were both 100 percent.

Discussion

We find that temperature during development affects nestling growth rate and size, but the direction of these effects differs among species. Experimental warming of robins during development resulted in a slower growth rate and larger final size (Figs. 3,5). In contrast, experimental warming of catbirds resulted in a higher growth rate and smaller final size (Figs. 4,6). These findings are consistent with a negative relationship between growth rate and final size, supporting the idea that plasticity in growth rates—long thought to underlie the negative relationship between size and temperature in ectotherms (Daufresne et al. 2009)—can similarly impact endotherms (Weeks et al. n.d.). Interestingly, our results are in contrast to a recent long-term observational study that found 40-year declines in size in both American robins and gray catbirds associated with increased temperatures (Weeks et al. 2020).

It is possible that temperature-driven declines found in observational data (Weeks et al. 2020) result from consistent selection for smaller body size, while our results reflect opposing impacts of developmental plasticity. However, differences in geographic range may provide a more parsimonious explanation. We speculate that the contrasting species-specific effects of the heating treatment may be the result of differences in the distributions and migratory strategies of the species. When species are breeding in temperatures that are sub-optimally cold, increasing temperatures during development may result in larger individuals; in contrast, when species are breeding in optimal, or higher-than-optimal, ambient temperatures, increases in temperature may drive size reductions (Weeks et al. n.d., Andreasson et al. 2020).

Southeastern Michigan is located in the middle of the breeding range for robins, and as a result, robins are year-round residents in the area, though some of them will migrate south for the winter (Brown and Miller 2016). The robins in this region frequently lay more than one clutch in a single breeding season (Young 1955). This potentially results in breeding in sub-optimally cold temperatures early in the spring, when we performed our experiment, in order to accommodate a second clutch later in the breeding season. Therefore, our heat treatment may have made the development temperature closer to the optimal temperature for development for these early breeders. While early breeders may benefit from warmer temperatures during development, if climate change were to warm this region, robin nestlings developing under sub-optimal temperatures (mid-April – early May, late June – early July) would benefit from the change but nestlings produced during the current optimum temperatures (late May- June) may experience a reduction in size. Further experiments that take advantage of double clutching species to explore the interaction between experimental warming and ambient temperatures are needed to test this explanation.

In contrast to robins, Southeastern Michigan is close to the northern breeding range limit for catbirds, and the individuals in Southeastern Michigan are migratory. As a result, while catbirds in the region do frequently double brood, they are not reliably able to do so (Scott et al. 1988). As a consequence, the breeding biology of these populations may be adapted to temperatures found early in the spring, as reproduction again later in the spring is uncertain. The majority of nestling catbirds in this experiment were developing in late May – June which falls in the early portion of the catbirds' reproductive window in this region, suggesting we were measuring development of the first clutch of these birds (Scott et al. 1988). As a result, the ambient temperatures may have been near the optimal temperature for

development for the catbirds, and our experimental increase in temperature may have moved the developmental above optimal, leading to the observed reduction in body size and tarsus length. If climate change were to warm this region, the impacts on catbirds are likely to be complex. On the one hand, warmer temperatures might be sub-optimal for their development, but on the other, a longer breeding window would allow for increased rates of double-clutching (Scott et al. 1988) that might actually make shift the optimal reproductive temperatures in these populations.

Our study has several limitations. As a result of the limited number of nests, we were unable to statistically control for differences in the relationship between our experimental treatment and final body size. Limitations to sample size also precluded manipulating temperatures across the full length of the breeding season or with a range of temperatures, both of which would speak directly to our hypothesized explanation of the contrasting impacts of warming across robins and catbirds. However, our results demonstrate the promise of expanded comparative work exploring the impacts of different degrees of warming across gradients of ambient temperatures, species ranges, and laying dates to understand the impacts of climate change on bird morphology.

In order to realize the promise of large scale comparative experimental warming experiments, a flexible and easy to implement method for actively warming developing birds *in situ* are necessary. Despite the challenges of warming cup nests *in situ*, we were able to consistently warm nests an average of 2.08°C above ambient temperature. In contrast, control nests were on average 0.6°C colder than the ambient temperature (Fig. 2). This complements a growing effort to manipulate nest temperatures in natural settings using active heating approaches, including previous attempts to warm nests that successfully heated nests to 1-

2°C warmer than ambient temperatures (Ton and Martin 2017, Mitchell et al. 2020). Our method offers a high degree of flexibility, as different amounts of resistance can be wired into the circuit to alter the heat output. In the future, in order to simulate a more realistic increase in nest temperature, the amount of warming generated by the heaters can be modified to account for natural differences between nests (nest material, sunlight exposure, parental incubation behavior, etc.) that can alter the relationship between internal nest temperatures and external ambient temperatures. The potential for this growing class of warming methods to improve understanding of biotic responses to warming is evidenced in the impacts we observe.

Hatching and fledging success in this study were difficult to assess due to the limited sample size and high predation rates. From the information gathered, we find no evidence that heated nests had different hatching success than control nests. The additional heat may have increased hatching success because the eggs were kept warmed while the parent bird was off the nest. This would have been especially beneficial for the first broods of the season in robins when spring temperatures were more variable and colder relative to conditions later in the spring when they might lay a second clutch. Fledging success was lower or the same in heated individuals, which is consistent with other studies (Wada et al. 2015, Ospina et al. 2018), but additional data are needed to understand potential mechanisms underlying this trend in our system.

Conclusions

We find extreme differences in species-specific responses to warmer temperatures during development. Based on decades of research on developmental temperatures on bird size, particularly in poultry studies, we hypothesize that these species-specific differences may reflect different optimal temperatures for development (Weeks et al. n.d., Andreasson et al. 2020). This work suggests developmental plasticity may underlie widespread warming-driven size reductions in birds, but large comparative analyses are needed. Our method for warming nests is cheap, effective and flexible, opening the door for broader tests of hypothesized mechanisms linking temperature and size. There is increasing evidence that avian populations are adapting to climate change through shifts in phenology (Zimova et al. 2021), range (Socolar et al. 2017), and morphology (Wada et al. 2015, Andrew et al. 2017, Vaugoyeau et al. 2017, Weeks et al. 2020), and phenotypic plasticity may be driving some of these changes (Weeks et al. n.d.). Our study highlights the importance of understanding avian responses to climate change from a plasticity rather than selection perspective.

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Appendices

Appendix A. Tables

Table 1. Model output from the linear model showing the effects of ambient temperature, the experimental heat treatment, species, and an interaction term between species and experimental treatment on nestling tarsus length for both robins and catbirds.

Predictor variable	β	SE	t	P
Ambient temperature	-0.42	0.11	-3.80	< 0.01
Treatment	-1.22	0.25	-4.91	< 0.01
Species	0.27	0.25	1.09	0.29
Treatment*Species	2.88	0.43	6.68	< 0.01

Table 2. Model output from the linear model showing the effects of measurement date and the experimental heat treatment on nestling tarsus length for robins.

Predictor variable	β	SE	t	P
Measurement date	-0.25	0.067	-3.67	< 0.01
Treatment	0.76	0.26	2.92	0.022

Table 3. Model output from the linear model showing the effects of the experimental heat treatment on nestling tarsus length for catbirds.

Predictor variable	β	SE	t	P
Treatment	-0.99	0.23	-4.28	< 0.01

Appendix B. Figures

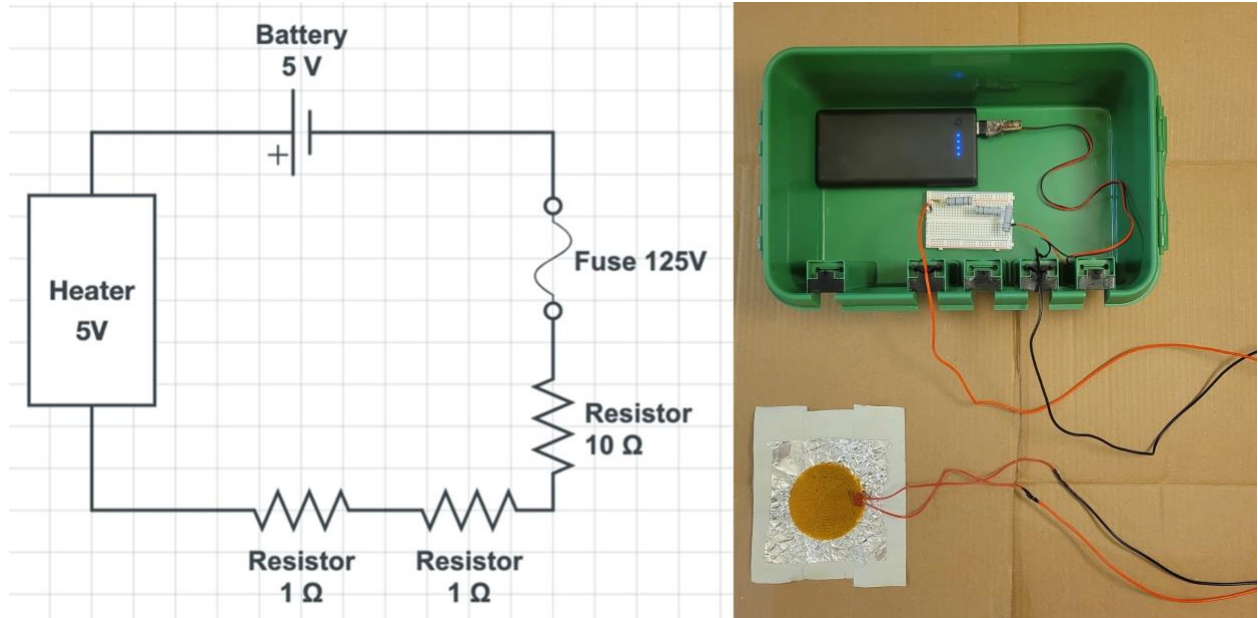


Fig. 1. *Left:* Schematic of warming device used to warm open-cup nests. The electrical circuit consists of a polymide heater attached to a breadboard containing 12 ohms of resistance (10 and 1 ohm resistors) and a fuse (125V). The circuit was completed and activated using a 5V battery. *Right:* Photo of warming device used to warm open-cup nests. All components of the device (battery, breadboard, resistors, fuse), except for the polymide heater, were contained in a waterproof electrical box. Aluminum foil and camoflage tape were placed underneath the heater to force heat upwards and avoid conspicuousness, respectively.

Temperature Differences for Heated and Control Nests

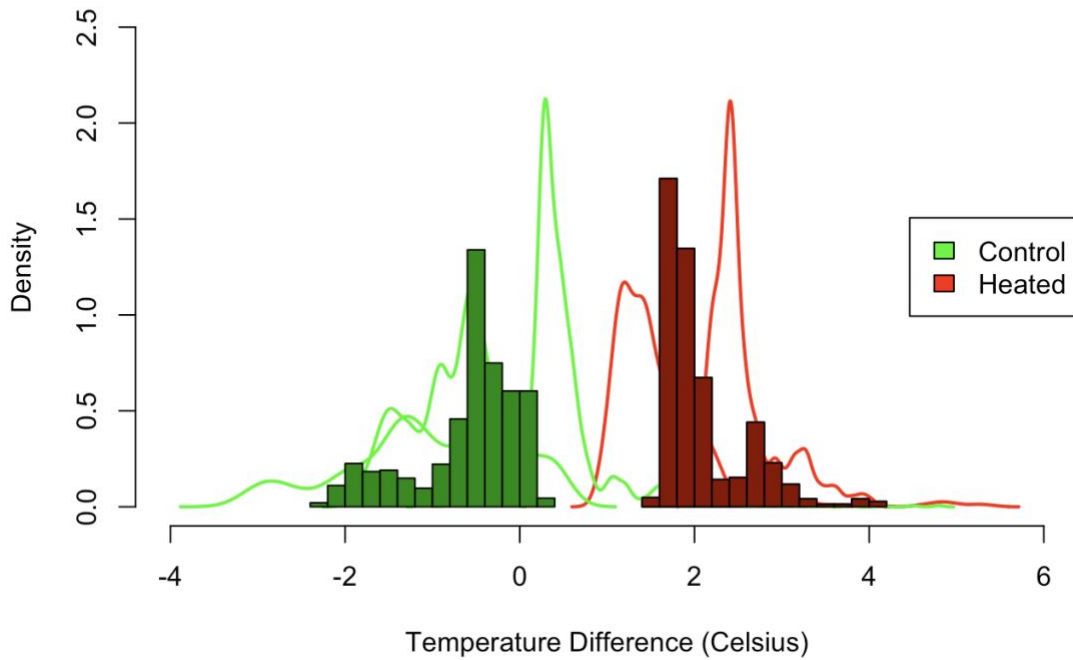


Fig. 2. Histogram showing the temperature differences between internal nest temperature and external ambient temperature between treatments. Bars represent the average difference between internal and external temperature for each treatment group and lines represent the same difference but for individual nests. Control nests were on average 0.6°C colder than the external ambient temperature (median = -0.49°C , standard deviation = 0.59°C). Heated nests were on average 2.08°C warmer than the external ambient temperature (median = 1.91°C , standard deviation = 0.48°C). Control nests had a sample size of three (one catbird, 1 cardinal, and 1 robin nest) and experimental nests had a sample size of two (two cardinal nests).

Nestling Growth Rate for Robins

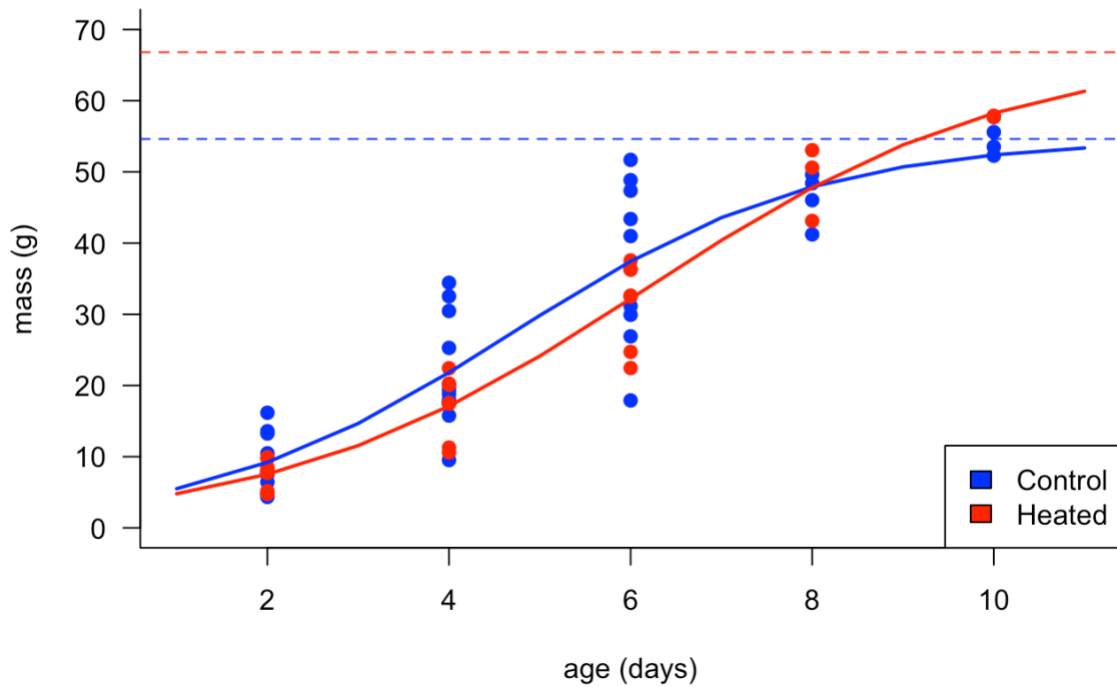


Fig. 3. Effects of the experimental treatment on growth and development rates for robins.

The sample size for control robins was 11 nestlings, found across three nests. The sample size for heated robins was 8 nestlings, found across three nests. Dots represent individual nestling measurements and lines depict the fit of the data to a logistic growth function.

Dashed lines indicate the asymptote of the logistic curve. Control robins (blue) had a predicted final mass of 54.62 g, a maximum growth rate of 1.68 g/day, and reached their maximum growth rate at 4.69 days. Heated robins (red) had a predicted final mass of 66.81 g, a maximum growth rate of 2.01 g/day, and reached their maximum growth rate at 6.15 days.

Nestling Growth Rate for Catbirds

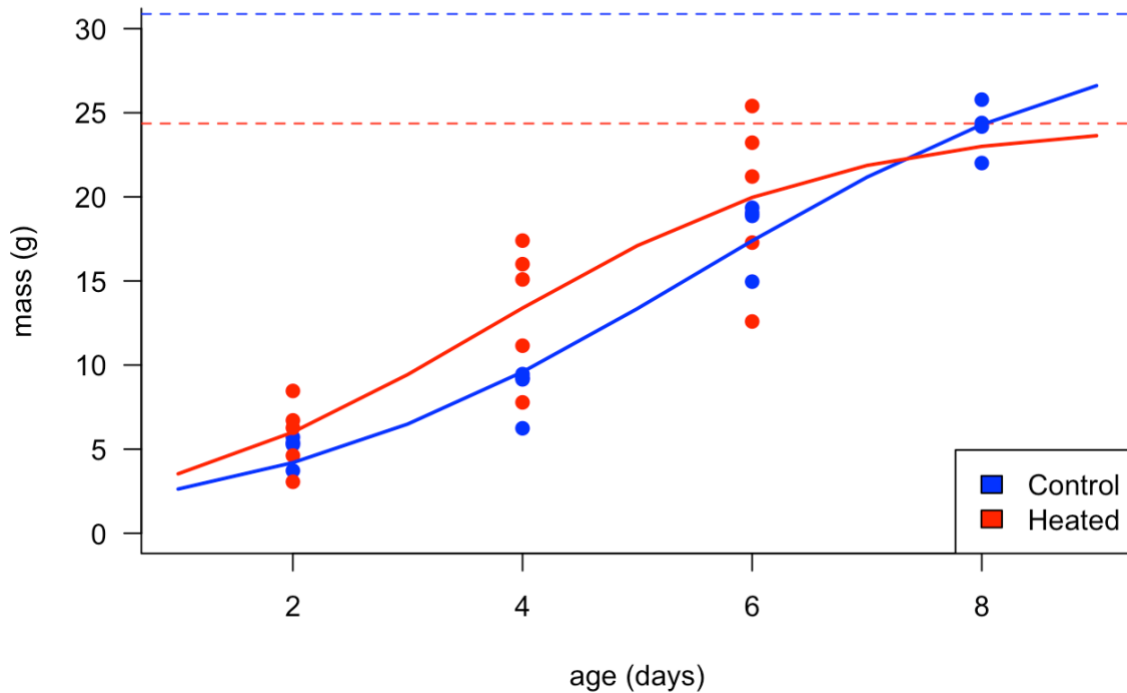


Fig. 4. Effects of the experimental treatment on growth and development rates for catbirds. The sample size for control catbirds was four nestlings, found in one nest. The sample size for heated catbirds was five nestlings, found in one nest. Dots represent individual nestling measurements and lines depict the fit of the data to a logistic growth function. Dashed lines indicate the asymptote of the logistic curve. Control catbirds (blue) had a predicted final mass of 30.87 g, a maximum growth rate of 1.90 g/day, and reached their maximum growth rate at 5.52 days. Heated catbirds (red) had a predicted final mass of 24.36 g, a maximum growth rate of 1.52 g/day, and reached their maximum growth rate at 3.70 days.

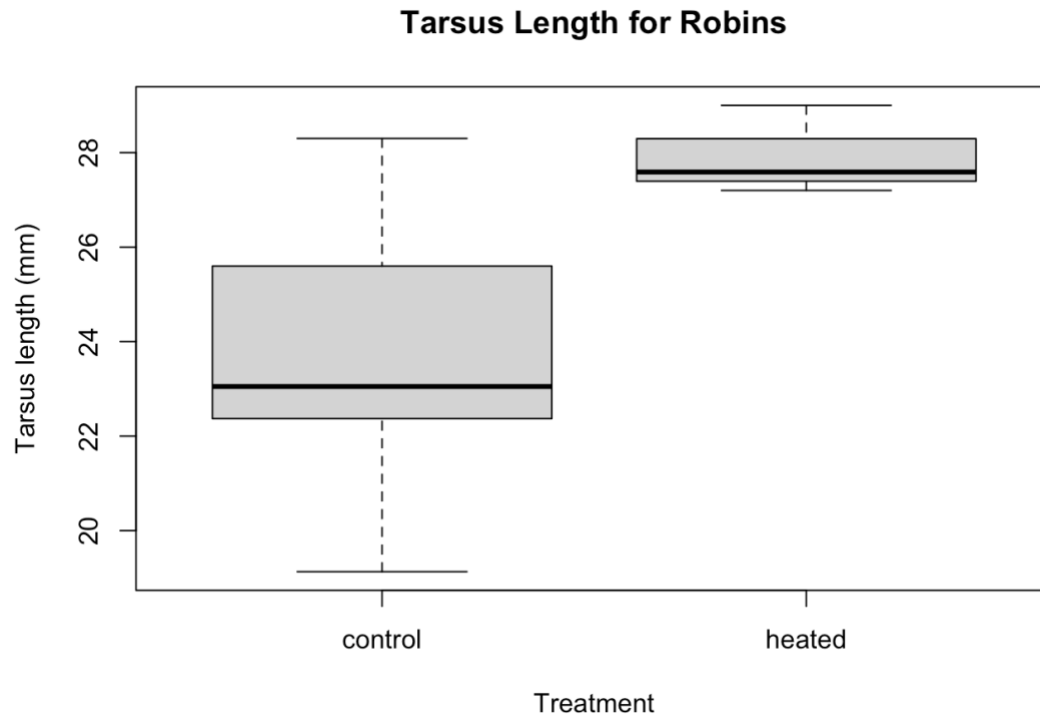


Fig. 5. Effects of the experimental treatment on tarsus length (body size) for robins. Analysis was performed using a two sample, equal variance t-test. The sample size for control robins was seven nestlings, found across two nests. The sample size for heated robins was three nestlings, found across two nests. Control robins resulted in an average tarsus length of 23.77 mm, whereas heated robins had an average tarsus length of 27.93 mm (t value = -2.2085, p = 0.05822).

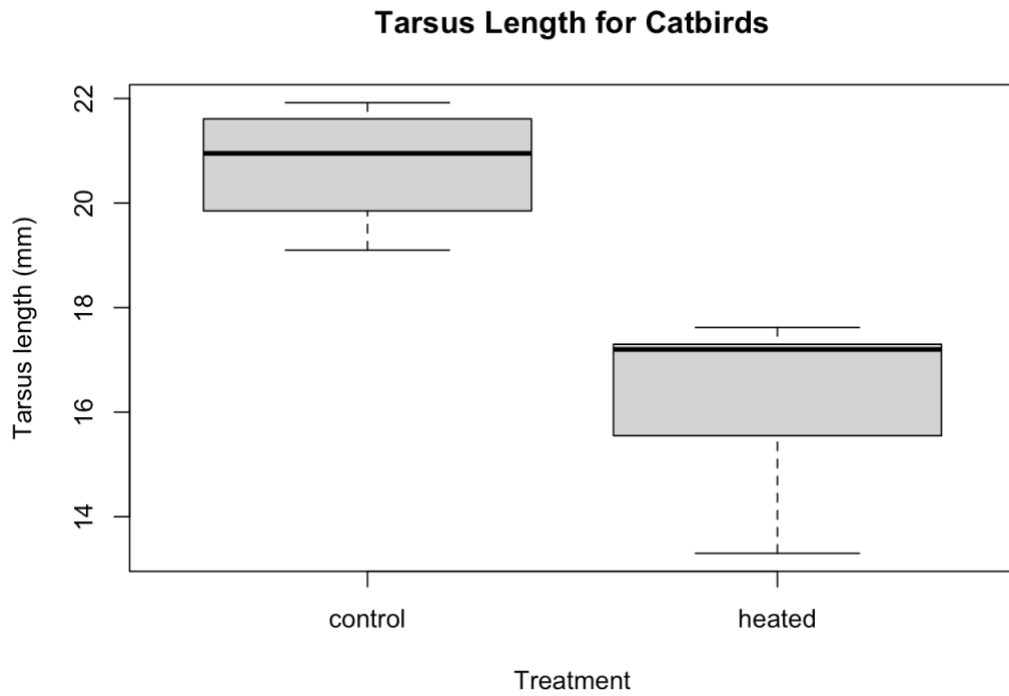


Fig. 6. Effects of the experimental treatment on tarsus length (body size) for catbirds.

Analysis was performed using a two sample, equal variance t-test. The sample size for control catbirds was four nestlings, found in one nest. The sample size for heated catbirds was five nestlings, found in one nest. Control catbirds resulted in an average tarsus length of 20.73 mm, whereas heated robins had an average tarsus length of 16.194 mm (t value = 4.2798, $p = 0.003656$).

Appendix C. Supplementary Material

Table S1. Additional information on the components of the warming device. Brand, part number, and defining characteristics are identified.

Part	Brand	Part Number	Characteristics
Polymide heater	Icstation	ASIN: B07P1H8N8H	70 mm diameter, 5V
Resistors	Uxcell	a19041800ux0035 & a19041800ux0002	10 & 1 ohm
Fuse	Littelfuse	0251001.MXL	125V, 1A
Battery	Lanluk	ASIN: B07TSHW85D	5V
Electrical box	SocketBoX	ASIN: B006EUHS96	33x22x12 cm
Bluetooth temperature logger	Onset HOBO	MX2201	+/- 0.5°C accuracy



Fig. S1. Photo of Heating Device

Example of a heating device set up in a spruce tree (*Picea sp.*) for an American robin nest.

The electrical box containing the battery, resistors, and fuse was placed at the base of the tree and powered the polyimide heater, which was attached to the base of the nest. Camouflage tape covered the heater and aluminium foil to avoid conspicuousness. The heater and wires were secured to the nest and tree using brown zip ties.



Fig. S2. Photo of Heating Device

Example of a heating device set up in a rose brush (*Rosa multiflora*) for a northern cardinal nest. The electrical box containing the battery, resistors, and fuse was placed at the base of the tree and powered the polyimide heater, which was attached to the base of the nest. Camouflage tape covered the heater and aluminium foil to avoid conspicuousness. The heater and wires were secured to the nest and tree using brown zip ties.



Fig. S3. Photo of Control Device

Example of a control device set up for an American robin nest. Control nests only contained components of the warming device that were directly attached to the nest (polymide heater, aluminium foil, camoflague tape). The camoflague tape covered the heater and aluminium foil to avoid conspicuousness. The heater was placed at the base of the nest and was secured using brown zip ties.