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Effects of ambient temperature on avian incubation behavior

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Ambient temperature is commonly thought to influence avian incubation behavior. However, results of empirical studies examining correlations between ambient temperature and bout duration are equivocal. We propose that these equivocal results can be partly explained by developing a conceptual understanding of how we should expect temperature to influence incubation. We demonstrate why linear correlation analyses across a wide range of temperatures can be inappropriate based on development of an incubation model for small birds that incorporates how ambient temperature influences both embryonic development and adult metabolism. We found support for predictions of the model using incubation data from orange-crowned warblers (*Vermivora celata*) in Arizona. Both off- and on-bout duration were positively correlated with ambient temperature between 9° and 26°C, but unrelated to ambient temperature <9° and 26–40°C. Bout durations declined as ambient temperature approached or exceeded 40°C. Incubating orange-crowned warblers appeared to avoid bouts off the nest <7 min and bouts on the nest <20 min. Time of day, duration of the previous bout, and variation among nests all explained variation in both on- and off-bout duration. Although we found support for the general shape of the incubation model, temperature still explained only a small portion of the overall variation in on- and off-bout duration. Results of previous studies were generally consistent with the model for off-bout duration; most studies in colder environments reported positive correlations with temperature, and the one negative correlation reported was from a hot environment. However, the relationships between on-bout duration and temperature reported in previous studies were less consistent with our model and our data. Although some discrepancies could be explained by considering our model, some studies reported negative correlations in cold environments. The effect of ambient temperature on duration of on-bouts probably differs among species based on the amount of fat reserves females typically carry during incubation and the extent of male incubation feeding. Additional studies of the effects of temperature on avian incubation will help improve the general model and ultimately aid our understanding of energetic and ecological constraints on avian incubation. *Key words:* ambient temperature, foraging, incubation behavior, incubation model, incubation rhythm, nest attentiveness, on-bout duration, off-bout duration. *[Behav Ecol 11:178–188 (2000)]*

Ambient temperature is commonly thought to influence avian incubation behavior (Baerands, 1959; Drent, 1970; Haftorn, 1988; Lombardo et al., 1995; Weathers and Sullivan, 1989; Weeden, 1966; White and Kinney, 1974; Zerba and Morton, 1983). Incubating parents must balance the thermal needs of the developing embryos with their own energetic needs by leaving the nest to forage. Effective resolution of this trade-off between embryos and parent is particularly important in species with unassisted, single-sex incubation (Williams, 1991). Empirical studies have reported negative, positive, and no correlation between ambient temperature and on- and off-bout durations (Appendix). Where significant correlations exist, temperature typically explains only a small proportion of the variation in bout length. The equivocal or minor relationship between temperature and incubation behavior among empirical studies is contrary to experimental studies in which decreased nest or egg temperature increases nest attentiveness and decreases off-bout duration (Biebach, 1979; Davis et al., 1984; Drent et al., 1970; Haftorn, 1984; Vleck, 1981a; von Haartmann, 1956; White and Kinney, 1974). The inconsistent relationships between ambient temperature and incubation behavior in field studies are an enigma given the obvious importance of temperature to embryo development (Webb, 1987) and the female's response to experimentally altered temperature.

In an attempt to resolve this enigma, we propose a conceptual model that relates on- and off-bout duration to ambient temperature in small-bodied birds with single-sex incubation (species in which incubating females periodically leave the nest to forage in order to balance their energy budgets over the course of each day). The model is appropriate for species that are time limited during incubation; the amount of food consumed during typical off-bouts is below limits imposed by rates of digestion and assimilation. Our model incorporates the influence of ambient temperature on both embryonic development and adult metabolism. We show that searching for linear correlations between bout duration and ambient temperature across wide ranges of temperature is misguided. Our model provides a conceptual framework of how ambient temperature should influence incubation behavior, attempts to explain the equivocal results of previous studies, and provides guidance for future studies. To explain the development of this model, we (1) consider how temperature should affect bout duration through its effects on embryonic development, (2) consider how temperature should affect bout duration through its effects on adult metabolism, and (3) present our conceptual model by simultaneously considering trade-offs between embryo thermal needs and adult energetic needs.

Temperature and embryonic development

Thermal tolerance of domestic chicken embryos is frequently used as a model of temperature influences on embryonic de-

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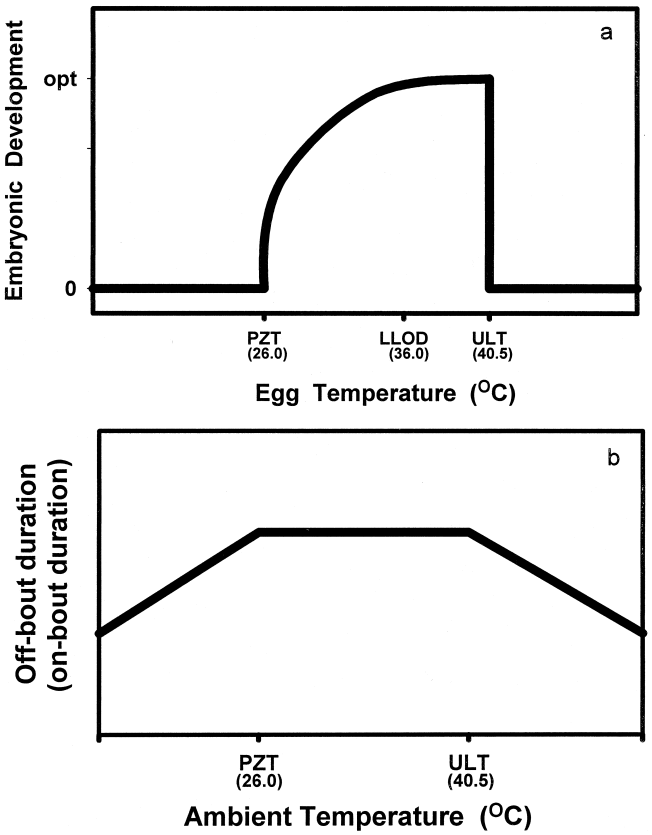

Figure 1
(a) Assumed general relationship between avian embryonic development and egg temperature (Lundy, 1969). PZT, physiological zero temperature; LLOD, lower limit of optimal development; ULT, upper lethal temperature. (b) Predicted general relationship between ambient temperature and off- and on-bout duration for birds with single-sex incubation, considering relationship in panel a.

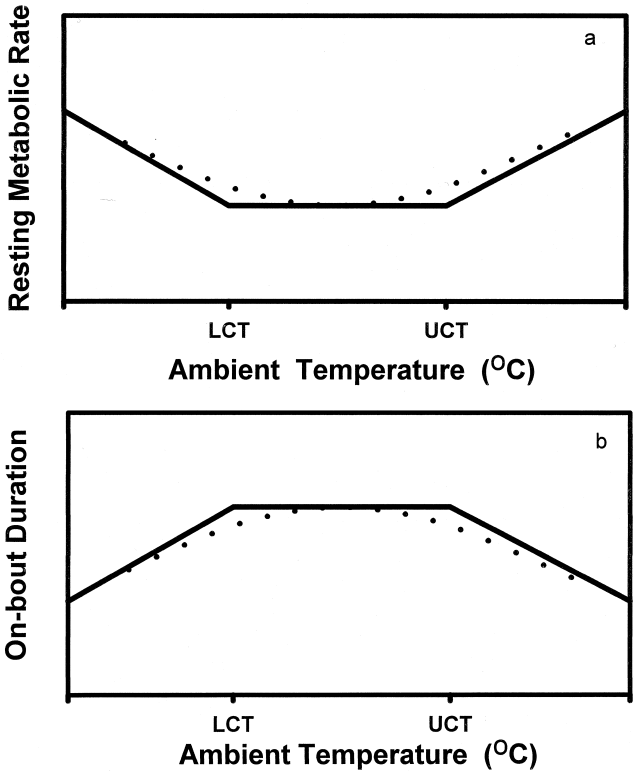

Figure 2
(a) Assumed general relationship between adult resting metabolic rate and ambient temperature. LCT, lower critical temperature; UCT, upper critical temperature. (b) Predicted general relationship between on-bout duration and ambient temperature considering relationship in 2a. Dotted line indicates possible relationship between incubation metabolic rate and ambient temperature.

velopment in wild birds (Drent, 1970; Haftorn, 1984; White and Kinney, 1974). Chicken embryo development is suspended below 26°C [physiological zero temperature (PZT); Lundy, 1969], and many authors have assumed that PZT is 26°C in all birds (Drent, 1975; Haftorn, 1984; Webb, 1987; White and Kinney, 1974). Between 26°C (PZT) and 36°C (lower limit of optimal development; LLOD), development is slowed but not impaired, but prolonged exposure can cause developmental abnormalities (Lundy, 1969; Webb, 1987). Optimal development occurs between 36°C and 40.5°C in chickens (Lundy, 1969), and optimal temperatures are often assumed to be the same across species (Huggins, 1941; Webb, 1987; White and Kinney, 1974). Above 40.5°C (upper lethal temperature; ULT), malformations develop, and death occurs with prolonged exposure (Lundy, 1969). Hence, embryonic development varies nonlinearly with temperature (Figure 1a).

Incubating females are commonly thought to limit off-bout duration such that egg temperatures seldom fall below PZT (Haftorn, 1984; Løfaldli, 1985; Vleck, 1981b, Weathers and Sullivan, 1989). If this assumption is correct, off-bout duration should decline as ambient temperature drops below 26°C because unattended eggs should cool at a faster rate as temperature declines. Hence, we would expect a positive correlation between off-bout duration and ambient temperature below 26°C (Figure 1b). Because single-sex incubators are often limited in time available for foraging (Mertens, 1977), females should take more off-bouts as bout duration declines, leading to shorter on-bouts. Consequently, on-bout duration should also be positively correlated with ambient temperature below 26°C (Figure 1b). Similarly, as temperature rises above 40.5°C, birds should be forced to take shorter off-bouts to prevent eggs from overheating to lethal temperatures during their absence (Figure 1b). At ambient temperatures 26°–40.5°C, eggs will not cool below physiological zero or overheat above upper lethal temperatures during off-bouts. Hence, we expect bout length to be less correlated with ambient temperature in this range (Figure 1b). Indeed, brief periodic cooling to temperatures not lower than PZT during off-bouts may actually increase hatching success (Batt and Cornwell, 1972; Kendeigh and Baldwin, 1932; Landauer, 1967; Oppenheim and Levin, 1975; Westerskov, 1956). Thus, variation in ambient temperature can influence incubation behavior through its effect on embryonic development, but effects on behavior may differ depending on the range of temperatures experienced (Figure 1).

Temperature and adult metabolism

Variation in ambient temperature may also influence incubation behavior through its effect on adult metabolism. Resting metabolic rate of homeotherms is minimal across a range of temperatures (thermoneutral zone; TNZ) and increases at temperatures below (lower critical temperature; LCT) and above (upper critical temperature; UCT) this zone (Haftorn and Reinertsen, 1985; Schmidt-Nielson 1994; Figure 2a). Although the LCT and UCT may differ among species (Hayworth and Weathers, 1984), the general shape of the relation-

ship between temperature and metabolic rate (Figure 2a) is consistent among species. The width of the TNZ may be narrower in incubating females (Figure 2a) compared to resting birds, but the relationship should otherwise be similar. Indeed, the energy required during incubation increases greatly in small birds when the ambient temperature falls below LCT (Biebach, 1981, 1984; Haftorn and Reinertsen, 1985; Vleck, 1981a). Increasing metabolic needs of the incubating adult (below the LCT and above the UCT) should force birds to take shorter on-bouts because they are metabolizing available energy more quickly (especially in species that rely mostly on exogenous resources for reproduction). Consequently, on-bout duration should be positively correlated with ambient temperature at temperatures below the LCT and negatively correlated with ambient temperature at temperatures above the UCT (Figure 2b).

Energetic costs of rewarming cooled eggs are high relative to maintaining optimal egg temperature during incubation (Biebach, 1986; Vleck, 1981a). In cold environments, eggs cool much quicker after a female leaves the nest to forage than they rewarm when the female returns (Drent, 1975). Moreover, the rate of egg cooling declines throughout an off-bout as egg temperature approaches ambient temperature. Consequently, a bird trying to optimize available energy should minimize rewarming episodes by taking few long off-bouts rather than many short ones (Drent, 1975). At ambient temperatures within their TNZ, incubating birds should maximize on- and off-bout duration within limits imposed by their metabolic rate, foraging success during off-bouts, and the onset of developmental abnormalities (Figure 2b).

Combining embryo thermal needs and adult energetic needs

Simultaneously considering embryo thermal needs and adult metabolic needs allows us to develop a conceptual model of the relationship between ambient temperature and both off- and on-bout duration (Figure 3). As ambient temperature drops below PZT, off- and on-bout duration should decline because an incubating female must take shorter but more frequent off-bouts to obtain needed energy while preventing egg temperatures from cooling below PZT during her absences. As temperature continues to drop below both PZT and LCT, length of off- and on-bouts should decline even faster with temperature because the adult's metabolic needs start to increase inversely with temperature. Consequently, the slope of the positive relationship between ambient temperature and off- and on-bout duration should become steeper at temperatures below either the PZT or LCT (whichever is lower) (Figure 3). Similarly, we also expect the slope of the negative relationship to become steeper at temperatures above either the ULT or UCT (whichever is higher) (Figure 3).

However, we expect lower bounds on off- and on-bout duration. For example, continued reduction in off-bout duration with decreasing temperature will become unprofitable when the average energy obtained in such a short off-bout no longer exceeds the energy expended in foraging and rewarming eggs. Hence, at very low temperatures, further reductions in off-bout duration become unprofitable, and we might expect incubating females to maintain some minimal off- and on-bout duration despite further declines in temperature (Figure 3). Similarly, we expect a threshold at some high temperature above which the female stops taking off-bouts altogether and stays on the nest, enduring a negative energy balance (Maclean, 1967; Vleck, 1981b; Walsberg and Voss-Roberts, 1983; Figure 3). Further increases in temperature above this threshold (or prolonged time at this temperature) may result in nest abandonment or adult emaciation.

In summary, our conceptual model does not predict a consistent linear relationship between ambient temperature and off- or on-bout duration across all temperatures (Figure 3). Tests of predictions and future refinement of this general model should enhance our understanding of how ambient temperature limits incubation strategies available to incubating females. We tested predictions of this conceptual model using data from orange-crowned warblers (*Vermivora celata*) on a study site in central Arizona. This is a good system to test model predictions because only female orange-crowned warblers incubate the eggs, females rely mostly on exogenous resources during incubation, male incubation feeding is rare, and incubating females experience a relatively wide range of ambient temperatures on our study site.

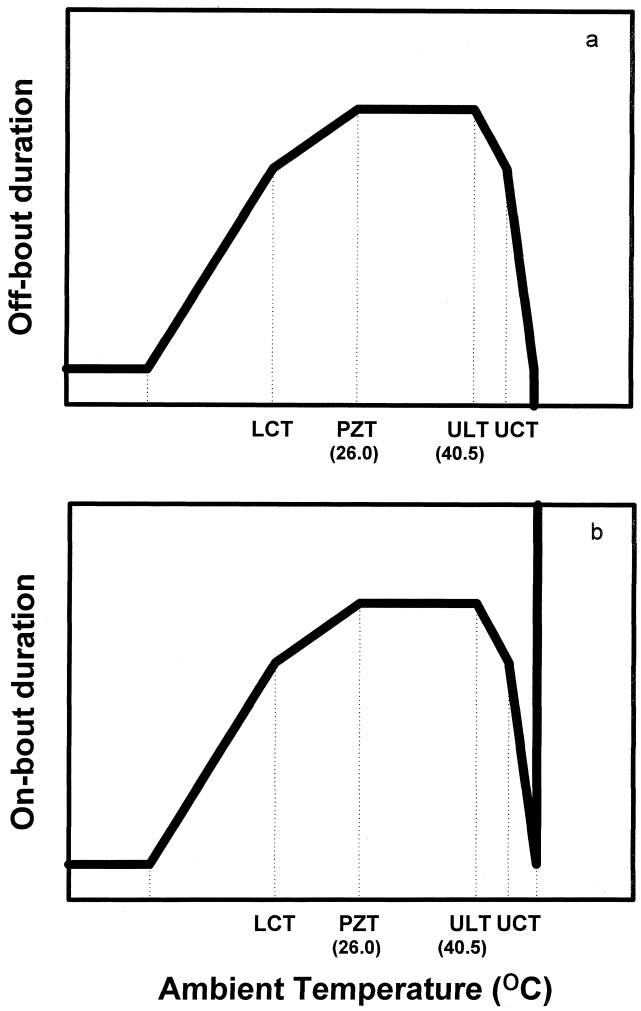

Figure 3
Proposed relationship between ambient temperature and both off-bout and on-bout duration in birds with single-sex incubation, based on relationships in Figures 1 and 2. LCT, lower critical temperature; UCT, upper critical temperature; PZT, physiological zero temperature; LLOD, lower limit of optimal development; ULT, upper lethal temperature.

METHODS

We collected data on length of on- and off-bouts at 34 orange-crowned warbler nests from 1991 to 1994 and in 1997 at our study site on the Mogollon Rim (2,600 m), Coconino National Forest, central Arizona, USA. Orange-crowned warblers on our study site produce only one brood per year. Although

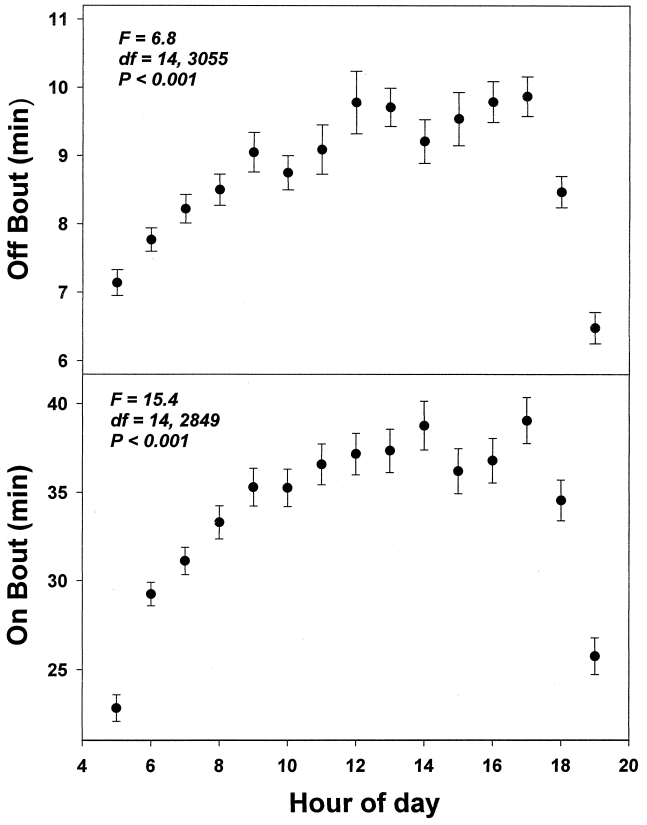

Figure 4
Mean (±1 SE) off- and on-bout duration of orange-crowned warblers during each hour of the active day.

females will renest if a clutch is depredated early, most of our nests were first attempts, and we did not sample nests late in the season (initiation dates of the 34 nests were 4 May–27 June). The number of on-bouts (and off-bouts) we recorded per nest varied from 5 to 215 (mean = 85 bouts/nest) depending on stage of incubation, whether the nest was depredated, and number of concurrently active nests being monitored. We recorded bout duration by inserting a Copper-Constantan thermocouple through the wall of the nest among the eggs. At nine of the nests, we also inserted and glued a second thermocouple in the middle of one of the eggs of the clutch to measure egg temperature. The other ends of the thermocouple wires were attached to a Campbell Scientific CR10 datalogger, which recorded temperature at 30-s intervals. Another thermocouple was placed approximately 10 cm from each nest to measure ambient temperature at the nest site. The initiation and termination of each on-bout and off-bout was determined by examining nest temperature data. Sharp changes in temperature indicated when birds left the nest to forage and when birds returned to the nest to begin a new incubation bout.

We lack an empirical measure of lower critical temperature (LCT) for orange-crowned warblers, but LCT of a 10.5-g bird during the daytime can be estimated as 27°C using an allometric equation (Weathers and van Riper, 1982). Hence, for orange-crowned warblers, PZT and LCT are similar. Consequently, we examined four predictions of our conceptual model: (1) bout duration is positively correlated with temperature at ambient temperatures <26°C, (2) bout duration no longer declines with decreases in temperature below some lower threshold, (3) bout duration is not related to temperature between 26° and 40.5°C, and (4) bout duration declines with temperature >40.5°C.

Because bout duration differed according to time of day (Figure 4), we examined the relationship between bout duration and temperature for each of three time intervals (0500–0859, 0900–1659, and 1700–1959 h) based on similarities in the relationship observed in Figure 4. We also included hour of the day in ANCOVA analyses so that we could examine the relationship between temperature and bout duration independent of time of day. We did not include stage of incubation in our models because the incubation period of orange-crowned warblers is short (12–13 days), and bout duration did not differ among days of the incubation period ($F < 1.7$, $p > .19$; also see Davis, 1960; Ettinger and King, 1980; Kendeigh, 1952; Lawrence, 1953; Lombardo et al., 1995; Smith and Montgomerie, 1992; Sturm, 1945; Weeden, 1966). We used hierarchical ANCOVAs to examine the consistency of the linear relationship between on- or off-bout duration and ambient temperature. In each ANCOVA, on- or off-bout duration was the dependent variable, nest was a random factor, hour of the day was a fixed factor, and previous bout duration and ambient temperature were covariates. Including nest as the first factor in our hierarchical models allowed us to examine the relationship between temperature and bout duration after differences among individual nests were removed. We included previous bout duration in our models because the length of an on-bout should be influenced by the length of the previous off-bout (and vice versa) if birds are indeed attempting to balance their energy budgets over short time periods (an assumption of our model).

We divided the range of temperatures experienced on our study area into three temperature zones (<9°C, 9–26°C, and >26°C) and classified each observation into one of the three zones. We identified 9°C as a possible lower threshold based on initial analyses. We included the ambient temperature × temperature zone interaction as the final variable in each hierarchical ANCOVA analysis, allowing us to address the prediction that the slope of the relationship between temperature and bout duration differs with ambient temperature after the influence of all other factors was removed. We also present on- and off-bout duration as a function of temperature for one nest that exemplifies the range of variation in ambient temperature on our study site.

We also summarized results of previous studies that have examined the relationship between ambient temperature and incubation behavior. Although previous studies have used linear correlation analyses and do not present raw data, we wanted to address whether our model could explain some of the discrepancies. We focused on studies of small birds that must get off the nest periodically to forage in order to maintain daily energy balance. We also recorded the mean, minimum, and maximum daytime temperature during the period of study, where available. Because male incubation feeding can influence how females respond to changes in ambient temperature, we recorded the frequency of mate feeding for each species from the papers on incubation behavior and from Birds of North America accounts (Poole and Gill, 1992–1999). We found few quantitative estimates of actual rates of mate feeding but many qualitative descriptions, so we categorized the relative frequency of mate feeding for each species as seldom or never (0), infrequent (1), moderate (2), and frequent (3).

RESULTS

Overall, off-bouts averaged 8.7 min (SE = 0.1, $n = 3067$), and on-bouts averaged 34.1 min (SE = 0.3, $n = 2855$), but both off- and on-bout duration varied among nests (the factor

Table 1
ANCOVA results examining the influence of ambient temperature (°C) on length of on- and off-bouts (min) after controlling for variation among nests, time of day, and previous bout duration in orange-crowned warblers

		Off bout		On bout	
Time		F	p	F	p
All day	Nest	10.5	<.001	31.6	<.001
	Hour of day	14.5	<.001	13.7	<.001
	Previous bout	116.8	<.001	31.9	<.001
	Ambient temp	18.9	<.001	177.5	<.001
	Ambient temp × temp zone	0.4	.680	1.4	.251
		r^2 = .208		r^2 = .379	
0500–0859 h	Nest	4.3	<.001	9.7	<.001
	Hour of day	7.2	<.001	16.5	<.001
	Previous bout	32.2	<.001	4.4	.036
	Ambient temp	15.0	<.001	18.2	<.001
	Ambient temp × temp zone	1.4	.252	3.6	.028
		r^2 = .230		r^2 = .368	
0900–1659 h	Nest	6.6	<.001	20.0	<.001
	Hour of day	2.0	.048	1.4	.198
	Previous bout	48.8	<.001	9.4	.002
	Ambient temp	3.4	.067	129.8	<.001
	Ambient temp × temp zone	0.8	.435	2.8	.060
		r^2 = .174		r^2 = .397	
1700–1959 h	Nest	3.8	<.001	8.4	<.001
	Hour of day	60.8	<.001	29.1	<.001
	Previous bout	41.4	<.001	30.5	<.001
	Ambient temp.	9.2	.002	47.0	<.001
	Ambient temp × temp zone	0.9	.420	3.9	.048
		r^2 = .352		r^2 = .474	

We included the ambient temperature × temperature zone interaction to examine whether the relationship between ambient temperature and bout duration differs among temperature zones consistent with our model (Figure 3).

"nest" was significant in ANCOVAs; Table 1). Hour of the day explained additional variation in the morning and evening time periods, but less so during the middle of the day (0900–1659 h; Table 1). Previous bout duration also explained variation in both off- and on-bout duration, even after removing differences among nests and time of day (Table 1). Indeed, on- and off-bouts were positively correlated within individuals (mean r = .247; 30 of 33 individuals had positive r values and 17 were significant; $p < .05$). Ambient temperature still explained substantial variation in both off- and on-bout duration after removing the effects of all other factors (Table 1).

As our conceptual model predicts, both on- and off-bout duration were positively correlated with ambient temperature between 9° and 26°C (Figures 5, 6). However, a positive relationship between ambient temperature and bout duration is not as apparent at temperatures <9°C and >26°C (Figures 5, 6). Indeed, off- and on-bout durations appear to decline (negative relationship) as ambient temperature exceeds UCT (Figures 5, 6). As Figures 5 and 6 suggest, the slope of the relationship between on-bout duration and ambient temperature differs among the three ranges of temperature (significant ambient temperature × temperature zone interaction; Table 1). The relationship between off-bout duration and ambient temperature (Figures 5, 6) also appears to support the general shape of our model (Figure 3), but the ambient temperature × temperature zone interaction term was not significant (Table 1). The general relationships between ambient temperature and off- and on-bout duration are similar when we examine our data for the one nest that best exemplifies the range of temperature variation (Figure 7). Hence, data from orange-crowned warblers generally support all four predictions of our conceptual model.

The reported relationship between ambient temperature and both off- and on-bout duration varied among previous studies (Table 2, Appendix). The majority of studies reported a positive correlation between temperature and off-bout duration (Table 2), but many suggested that the relationship was not linear across all temperatures sampled. Most previous studies were in colder, temperate climates (Appendix). The one study that reported a negative correlation between temperature and off-bout duration was in a very hot environment (Vleck, 1981b; Appendix). These results would be expected based on predictions of our model.

The reported relationship between temperature and on-bout duration was less consistent among studies (Table 2, Appendix). However, studies in the two coldest environments reported positive correlations (Norton, 1972; Zerba and Morton, 1983), and those in the two hottest environments reported negative correlations (Crook, 1960; Purdue, 1976). Still, some studies in cold environments reported a negative correlation between temperature and on-bout duration and Vleck (1981b) reported a positive correlation in a hot environment, opposite that predicted by our model.

DISCUSSION

Previous empirical studies examining the effects of temperature on avian incubation behavior have used linear correlation/regression analyses (Appendix). Yet our conceptual model predicts a nonlinear relationship between bout duration and temperature in small birds. Our incubation model suggests that the use of linear analyses across wide temperature ranges for examining the influence of temperature on

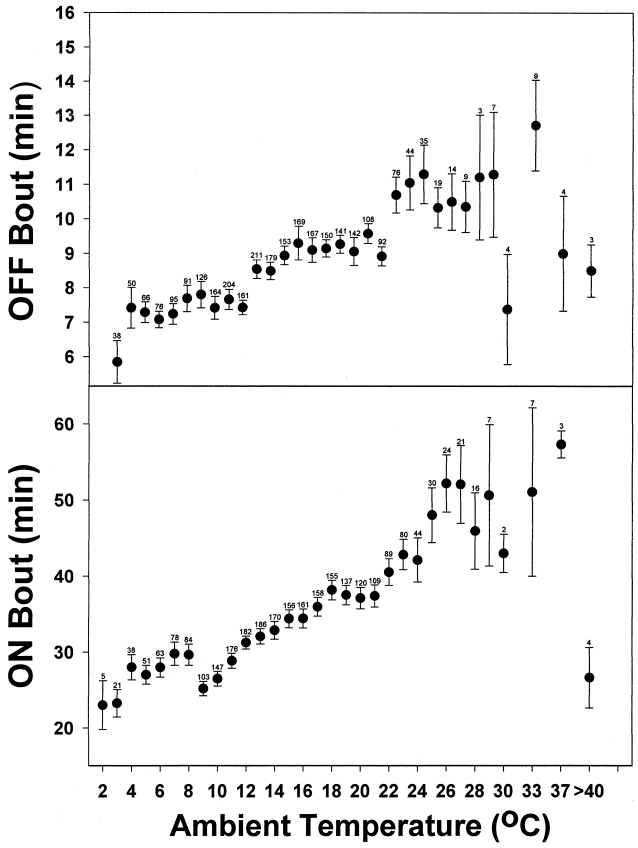

Figure 5
Mean (±1 SE) off- and on-bout duration of orange-crowned warblers at each ambient temperature.

incubation behavior may have caused previous investigators to overlook nonlinear relationships.

Data from orange-crowned warblers supported predictions of our conceptual model. Both off- and on-bout duration were positively correlated with ambient temperature between 9° and 26°C, even after controlling for time of day, previous bout duration, and differences among nests (Table 1, Figures 5–7). However, bout durations were not correlated with temperature >26°C (LCT and PZT) and appeared to decline as temperature exceeded UCT (Figures 5–7)—both patterns predicted by our model. Moreover, off- and on-bout duration were positively correlated within individuals.

Another prediction of our conceptual model is a lower threshold in both on- and off-bout duration. As our model predicts, orange-crowned warblers appeared to refrain from taking off-bouts shorter than 7 min and on-bouts shorter than 20 min; bout durations were less correlated with temperature <9°C (Figures 5–7). Indeed, we detected a significant temperature-dependent change in the slope of the relationship between ambient temperature and on-bout duration in ANCOVA analyses (Table 1). The relationship between off-bout duration and ambient temperature (Figures 5–7) also appeared to support the general shape of our model, even though our ANCOVAs failed to detect a significant ambient temperature × temperature zone interaction (Table 1). Skutch (1962) also observed that the relationship between temperature and incubation behavior breaks down in extremely cool weather.

Lower thresholds in bout duration may represent a minimally efficient incubation strategy. For example, on-bouts consistently shorter than 20 min on our study area may not adequately provide for the thermal needs of the developing embryos because some portion of that time will be required simply to rewarm eggs to optimal incubation temperature. These minimally efficient bout durations undoubtedly vary among species, populations, individuals, and even among days based on food abundance, foraging efficiency, individual quality, and thermal conductance of the bird, nest, and nest site.

On- and off-bouts were shortest and least correlated with temperature during the first four morning hours (Figure 6). After fasting overnight, incubating females are emaciated and appear to incubate their eggs in a way that maximizes foraging time regardless of air temperature (also see Nolan, 1978; Weathers and Sullivan, 1989). Hence, females may be forced to make many short trips off the nest to replenish energy reserves while still providing for the embryos' thermal needs. As the previous nights' energy debt is replenished, bout duration becomes more correlated with ambient temperature (Figure 6). On- and off-bout duration were correlated with hour of the day early in the morning and late in the evening, but much less so during the middle of the day (0900–1659 h; Table 1). During the 3 h before darkness, on- and off-bouts once again become shorter (Figure 6). Taking shorter on-bouts increases the number of foraging bouts as the nighttime approaches (Figure 6).

Long on-bouts are preceded by long off-bouts, and vice-versa (Table 1). Long off-bouts allow females to obtain more food and hence to stay on the nest longer during the next on-bout. Similarly, a relatively long on-bout depletes the female's energy reserves, forcing her to forage longer during the next off-bout (Table 1). These results support one key assumption of our model: incubating warblers appear to be making behavioral decisions that allow them to balance their energy budgets over short time frames. Most previous studies examining the effects of temperature on incubation behavior have failed to control for time of day and previous bout duration. Future studies should consider these important factors.

Length of on- and off-bouts differed among nests (Table 1). Variation in incubation behavior among nests limits the ability to detect the true relationship between temperature and bout duration in studies that fail to account for such variation (ours did). One individual averaged 37.0 min on and 10.5 min off, while another individual averaged 21.6 min on and 4.9 min off. This difference in incubation behavior results in an 80% increase in nest activity between these two individuals (2.5 versus 4.5 nest trips/h). Such large intraspecific variation in incubation behavior may reflect variation in territory or individual quality because frequent nest trips are energetically inefficient (Drent, 1975) and may increase the risk of nest predation (Conway and Martin, in press; Martin, 1996; Prescott, 1964; Skutch, 1949). Variation in individual or territory quality and variation among species or populations in risk of nest predation would be expected to influence the typical length of on- and off-bouts, but not the general relationship with ambient temperature predicted by our model.

Although we found support for our model of the effects of temperature on incubation behavior, we were able to explain only 17–47% of the variation in on- and off-bout duration (Table 1). Bout duration is obviously influenced by other factors (e.g., predation risk, male behavior) in addition to those considered here, and future research should attempt to evaluate the relative importance of these factors. Indeed, analyses across species suggest that risk of nest predation influences incubation behavior (Conway and Martin, in press).

Our model helps explain some, but not all, of the conflicting results from previous studies (Appendix). In agreement with our model, most previous studies have been conducted in colder temperate environments and have reported a positive correlation between temperature and off-bout duration

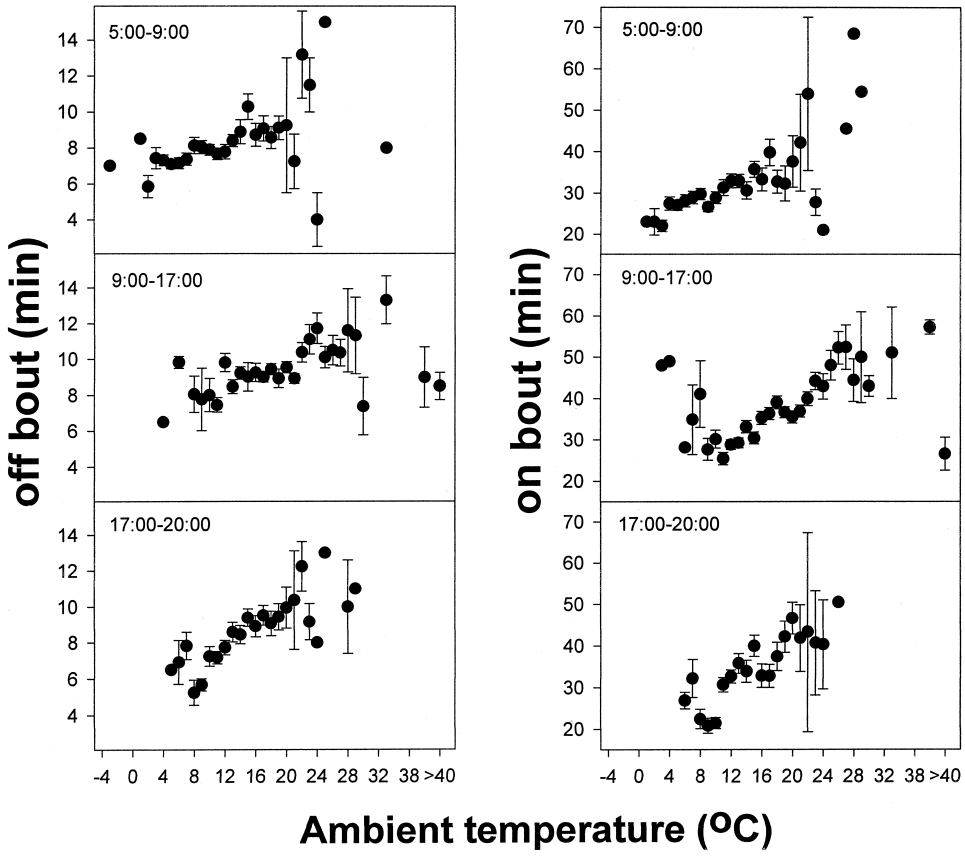

Figure 6
Mean (±1 SE) off- and on-bout duration at each ambient temperature within three time periods of the active day.

(Table 2, Appendix). Moreover, several studies with large sample sizes reported that the nature of the relationship changed with ambient temperature (Davis et al., 1963; Haftorn, 1979; Kendeigh, 1952; Kluijver, 1950; Norton, 1972; Zerba and Morton, 1983). The only reported negative correlation between off-bout duration and ambient temperature was a study of Costa's hummingbirds in a hot climate (Vleck 1981b); a thermal environment in which our model predicts a negative correlation [although Vleck (1981b) also reports a positive correlation with on-bout duration, opposite that predicted by our model]. The studies that failed to detect a correlation between off-bout duration and ambient temperature may have used inadequate sample sizes, failed to account for differences among nests, and/or worked in environments with moderate (or more variable) temperatures. Because temperature is only one factor influencing incubation behavior, one needs a large amount of data to quantify the relationship between ambient temperature and bout duration (Skutch, 1962). Failure to report raw data and failure to control for time of day and variation among nests limits our ability to interpret the lack of correlation reported in some studies. However, the results from previous studies on the relationship between off-bout duration and ambient temperature generally support our model, and our model helps explain conflicting results.

The relationship between on-bout duration and temperature varied even more among studies (Table 2). Our model helps explain some of this variation; studies in the two coldest environments reported positive correlations (Norton, 1972; Zerba and Morton, 1983), whereas those in the two hottest environments reported negative correlations (Crook, 1960; Purdue, 1976; Appendix). Moreover, eight studies reported that the relationship between on-bout duration and ambient temperature was nonlinear across the range of temperatures sampled. In several studies, on-bout duration was not correlated (or was even slightly negatively correlated) with temperature at very low ambient temperatures but was positively correlated with temperature at more moderate temperatures (Haftorn, 1978; Zerba and Morton, 1983); patterns that support our model. However, numerous studies conducted in generally cold environments reported a negative correlation between on-bout duration and temperature (Appendix). The fact that these females take longer, rather than shorter, on-bouts when ambient temperature declines raises the question as to why these females do not take longer bouts at more moderate temperatures because long bouts are beneficial (Drent, 1972, 1975; Morton and Pereyra, 1985; Skutch, 1949; Vleck, 1981b). Two possibilities are that as temperature declines, the frequency of male incubation feeding might increase (Skutch, 1957), or females may rely more on endogenous energy reserves.

Although our model does help explain some of the conflicting empirical results of the effects of temperature on incubation behavior, the nature of the relationship probably differs among populations that vary in their reliance on endogenous reserves and/or the extent of male incubation feeding. For example, some species might increase their use of endogenous fat reserves (rather than alter bout durations) during extreme temperatures to compensate for increased metabolic needs. Bout duration in populations that exhibit a temperature-dependent change in the use of endogenous versus exogenous energy sources during incubation would be expected to be less influenced by temperature (e.g., reduced slopes and/or thresholds at more extreme temperatures than those predicted by our model). Hence, we expect our model to be most appropriate for populations that rely predominantly on exogenous energy sources during incubation. Moreover, we expect the relationships between bout duration and ambient temperature presented in our model to be weaker in popu-

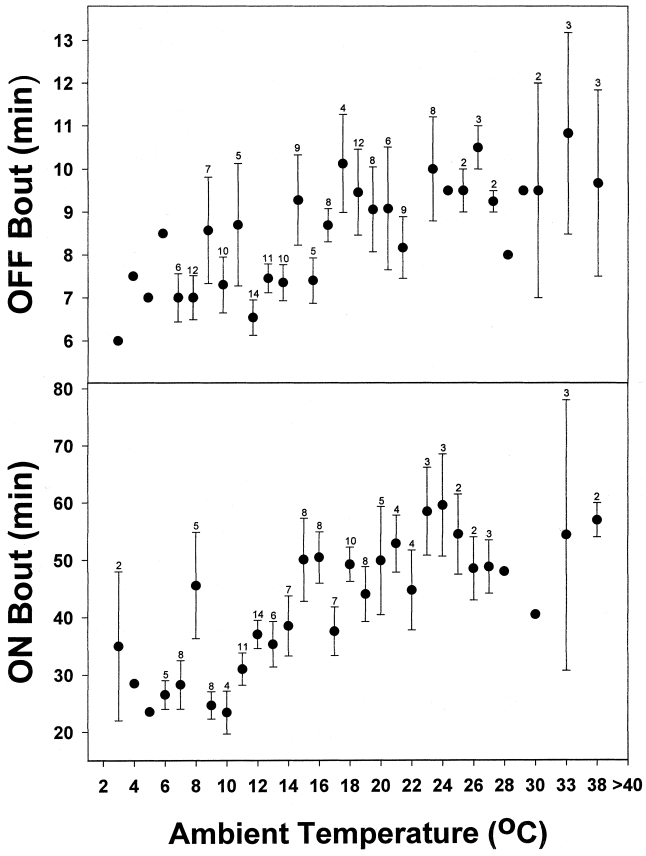

Figure 7
Mean (±1 SE) off- and on-bout duration of an individual orange-crowned warbler at each ambient temperature.

lations in which the frequency of male incubation feeding increases at extreme temperatures. An increase in male incubation feeding during extreme temperatures would help compensate for the increased metabolic rate of the incubating female and allow her to continue taking long on-bouts (Smith et al., 1989). Hence, we might expect species that rely mostly on exogenous energy sources during incubation and that do not exhibit mate feeding to fit our model best. Female orange-crowned warblers on our study site have no visible fat reserves during incubation, and males rarely feed incubating females (Conway and Martin, personal observations). Comparative data on the extent of reliance on fat reserves during incubation are not currently available for the species in the Appendix, and the extent of mate feeding does not help explain the variation in results among studies. However, temperature-dependent changes in mate-feeding frequency (rather than extent of mate feeding) would affect the relationship between bout duration and temperature most, and these data are also not currently available. Inflection points and thresholds predicted by our model may be at more extreme temperatures for species or populations in which males increasingly feed incubating females as ambient temperature declines.

Table 2
Number of studies reporting a negative correlation, positive correlation, and no correlation between ambient temperature and three components of avian incubation behavior

	Attentiveness	Off-bout duration	On-bout duration
Negative correlation	26	1	28
Positive correlation	7	30	12
No correlation	11	16	14

Our conceptual model presents only a general framework of the relationship between temperature and incubation behavior in small birds. Inflection points are probably not abrupt, and relationships between incubation behavior and ambient temperature will also vary among species exposed to the same range of temperatures because LCT, UCT, and embryo thermal tolerance may vary across species (Hayworth and Weathers, 1984; Williams and Ricklefs, 1984). The relationship between temperature and bout duration will also vary among taxa according to the temporal scale over which incubating birds balance their energy budgets. Such intra- and interspecific variation limits our ability to evaluate predictions of our model from previously published correlative studies; predictions could be best tested by experimentally manipulating temperature at nests in future studies.

In summary, we found general support for a new conceptual model of temperature influences on avian incubation. As the model predicted, off- and on-bout duration were positively correlated with ambient temperature between 9° and 26°C. No correlations were observed at temperatures <9°C and >26°C (Figures 5, 6). Length of on-bouts declined as ambient temperatures approached the upper lethal temperature (Figures 5, 6). Hence, previous studies that have used linear correlation analyses across a wide range of temperatures may have overlooked, or simplified, important relationships. Our model provides testable predictions about the way temperature influences incubation strategies in small birds and should help increase our understanding of the energetic costs of incubation. Inflection points and slopes may vary across species and populations, but the general shape of our model should be consistent for species in which females rely primarily on exogenous energy sources for incubation and are rarely fed by their mates. A review of previous studies suggests that our model explains disparate results based on off-bout duration and some of the inconsistencies based on on-bout duration. This general model is a first step at improving our understanding of temperature effects on avian incubation by taking into account the combined effects of temperature on the thermal needs of the embryos and metabolic needs of the incubating adult; additional data on avian incubation across a wide range of taxa and thermal environments will undoubtedly allow model improvements.

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APPENDIX

Reported relationships (P, positive correlation; N, negative correlation; and nc, no correlation) between ambient temperature and three components of incubation behavior (attentiveness, on-bout duration, and off-bout duration). Mean, minimum, and maximum daytime temperature (°C) on the study area, and extent of male incubation feeding are also listed where available.

Species	Attentiveness	Off bout	On bout	Temperature			Male feeding	Source
				Mean	Minimum	Maximum		
Great snipe	N	P		10			0	Løfaldli, 1985
Dunlin	P			5			0[c]	Norton, 1972
Snowy plover	nc[a]		N[a]		16	45	0[c]	Purdue, 1976
Sandpipers (4 spp.)	nc[a]	P[a,b]	P[a]	5				Norton, 1972
Calliope hummingbird		nc	nc				0	Calder, 1971
Anna's hummingbird		P	P	15.1	4.0	26.9	0	Smith et al., 1974
Anna's hummingbird	nc	nc	nc	10.8	4	19.2	0	Vleck, 1981b
Black-chinned hummingbird	nc	nc	nc	15.2	12.9	16.3	0	Vleck, 1981b
Costa's hummingbird	P	N	P	27.9	17.2	39.1	0	Vleck, 1981b
Orange-breasted sunbird	N	P	P		7	20	0	Williams, 1993
Dusky flycatcher	P	nc	P	16	1	26	3	Morton and Pereyra, 1985
Western flycatcher	nc	P[a,b]	N[b]	20	13	29	2	Davis et al., 1963
Willow flycatcher	nc			17			0	Ettinger and King, 1980
Pied flycatcher		nc	N				3	von Haartmann, 1956
Eastern wood-pewee	P	nc	P	20.7	14.4	25	3	Kendeigh, 1952
Great-crested flycatcher			N	19.4	17	23	1	Kendeigh, 1952
Say's phoebe		nc	nc	24.4	20	27.2	1	Kendeigh, 1952
Purple martin			N	15.5	13.3	21.1	0	Kendeigh, 1952
Barn swallow	N	P	N	24.9	20	30	0[c]	Kendeigh, 1952
Barn swallow	N	P	P	18	14.8	21.7		DeBraey, 1946
Barn swallow	N	P	N		15	37	0[c]	Smith and Montgomerie, 1992
Tree swallow	N		nc				0	Lombardo et al., 1995
Great tit	N	P	N				3	Kluijver, 1950
Great tit	N	P	N	12.2	1	28	3	Haftorn, 1981
Coal tit	N	P	nc		−1	27	3	Haftorn, 1984
Willow tit	N	P[a]	N	12.5	2	23	3	Haftorn, 1979
Goldcrest	N	P	nc[a]		5	27	0	Haftorn, 1978
Carolina wren	N	P[b]	N	19	15	24	3	Nice and Thomas, 1948
Carolina wren			N	26	24	28	3	Laskey, 1946, 1948
House wren	N	P[a]	N	20.6	9	31	1	Kendeigh, 1952
European wren	N	P	N				1	Whitehouse and Armstrong, 1953
Eastern bluebird	N	P	N	20.9	16.1	26.1	1	Kendeigh, 1952
American robin	N	nc	N	18.3	11	29	2	Kendeigh, 1952
Wood thrush		nc	nc	21.4	18.3	23.9	1	Kendeigh, 1952
Veery			P	20	17	24	0	Annan, 1961
Gray catbird	N	nc	N[a]	21.1	16.1	26.7	1	Kendeigh, 1952
Meadow pipit			nc	15.3				Halupka, 1994
Cedar waxwing		nc	nc	26.5	23.3	30	3	Kendeigh, 1952
European starling	N	P[a]	N[a]		8	28	0[c]	Kluijver, 1950
European starling	N		N	13.5			0[c]	Delvingt, 1963
European starling	N	P	N		10	28	0[c]	Drent et al., 1985
Red-eyed vireo			nc	24	8.3	33	0	Southern, 1958
Red-eyed vireo	N	nc	N	23	17	30	0	Lawrence, 1953
Willow warbler	nc	P	N					Kuusisto, 1941
Prairie warbler		nc	nc	20	12.2	28.6	1	Nolan, 1978
Yellow warbler	P			15.2	11.1	22.8	3	Kendeigh, 1952
Spotted towhee	nc[b]			16	7	23	1	Davis, 1960
Savannah sparrow	N		N				0	Davis et al., 1984
Dead Sea sparrow	nc[a]				15	41	0	Yom-Tov et al., 1978
Song sparrow	nc	P	P	19	6.1	29	0	Kendeigh, 1952
Song sparrow		P	P	18.6	12.8	21.1	0	Nice, 1937, 1943
American tree sparrow		nc	nc	13			2	Weeden, 1966
White-crowned sparrow	nc[a]	P[a]	P[a]		−8	28	0	Zerba and Morton, 1983
White-crowned sparrow		P			−3	30	0	Webb and King, 1983
White-crowned sparrow	N	P	N[a]	14	2	25	0	Norment, 1995
Harris' sparrow		P	N[a]	16.4	2	25	0	Norment, 1995
Chipping sparrow	N	P	N	25.3	21.1	28.9	3	Kendeigh, 1952
Yellow-eyed junco	P	P	P	19.5	2	30	1	Weathers and Sullivan, 1989
Eastern meadowlark	N	P					0	Saunders, 1932
Yellow-headed blackbird		nc	nc	16.2	13	22	0	Fautin, 1941
Scarlet tanager	N		N	19.5	13	27	2	Prescott, 1964
American goldfinch	P			21.2	17.2	23.9	3	Kendeigh, 1952
Weaverbird		P	N	Hot			0	Crook, 1960
15 Species	N	nc[b]						von Haartmann, 1956

[a] Nonlinear; relationship changes with temperature.

[b] Nature of relationship varies among nests sampled.

[c] Male helps incubate eggs.

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