Running Head: TEMPERATURE-SENSITIVE YAWNING IN BUDGERIGARS

The direction and range of ambient temperature change influences yawning in budgerigars (*Melopsittacus undulatus*)

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Abstract

Comparative research suggests that yawning is a thermoregulatory behavior in endotherms. Our previous experiments revealed that yawning increased in budgerigars (*Melopsittacus undulatus*) as ambient temperature was raised towards body temperature ($22 \rightarrow 34^{o}C$). In this study we identify the range of temperatures that trigger yawning to rule out the possible effect of changing temperature in any range. To corroborate its thermoregulatory function, we also related the incidence of yawning to other avian thermoregulatory behaviors in budgerigars (e.g., panting, wing venting). In a repeated measures design, 16 budgerigars were exposed to four separate 10-minute periods of changing temperatures: (i) low-increasing ($23 \rightarrow 27^{o}C$), (ii) high-increasing ($27 \rightarrow 33^{o}C$), (iii) high-decreasing ($34 \rightarrow 28^{o}C$), and (iv) low-decreasing ($28 \rightarrow 24^{o}C$). Birds yawned significantly more during the high increasing temperature range, and yawning was positively correlated with ambient temperature across trials. Yawning was also positively correlated with other thermoregulatory behaviors. This research clarifies the previously demonstrated relationship between yawning rate and temperature by providing evidence that, the physiological trigger for yawning is related to increasing body temperatures rather than the detection of changing external temperatures.

Keywords: yawning, ambient temperature, brain cooling, thermoregulation, *Melopsittacus undulates*

The direction and range of ambient temperature change influences yawning in budgerigars (*Melopsittacus undulatus*)

Yawning is phylogenetically old and has been documented in all five classes of vertebrates (Baenninger, 1987), suggesting important basic functions. Although the mere occurrence of yawning across species is not evidence that it is an evolved adaptation, the spontaneous and involuntary nature of yawning lends support for its adaptive significance. There is, however, little current consensus on the biological importance of yawning (Provine, 2005). One of the more widespread theories states that yawning stimulates or facilitates arousal during state change. In support of this theory, yawning has been shown to occur in anticipation of important events and during behavioral transitions or changes in activity levels across taxa (reviewed by Baenninger, 1997).

Recent research suggests/supports one adaptive hypothesis--that yawning is a thermoregulatory behavior (Gallup & Gallup, 2007, 2008; Gallup, Miller, & Clark, 2009). According to this hypothesis, yawning helps to maintain brain and/or body in thermal homeostasis, promoting arousal and mental efficiency. Brain temperature is determined by a number of variables, including the temperature of arterial blood going to the brain, rate of blood flow, and rate of metabolic heat production (Cabanac, 1986), and the physiological consequences of a yawn are in accord with those that would be necessary for cerebral cooling (Gallup & Gallup 2007, 2008). For instance, yawning causes acceleration in heart rate (Greco & Baenninger, 1991; Guggisberg, Mathis, Herrmann, & Hess, 2007; Heusner, 1946), and also raises blood pressure (Askenasy & Askenasy, 1996). More specifically, the constriction and relaxation of facial muscles during yawning increases facial blood flow and these changes are thought to increase cerebral blood flow (Askenasy, 1989; Baenninger, 1997; Zajonc, 1985), and this may act like a car radiator by removing hyperthermic blood from specific areas while introducing cooler blood from the lungs and extremities. The deep inhalation of air taken into the lungs could then alter the temperature of the blood traveling to the brain through convection. In support of this hypothesis, nasal breathing and forehead cooling reduce brain temperature in humans (Harris, Andrews, & Murray, 2007; Zenker & Kubik, 1996), and research has shown that nasal breathing and forehead cooling diminish the incidence of yawning (Gallup & Gallup, 2007).

According to the thermoregulatory hypothesis, one would expect yawning to occur in a thermal window, or a narrow range of ambient temperatures (Gallup & Gallup, 2007, 2008). The model predicts that yawns should increase in frequency as ambient temperature approaches body temperature, but should cease when ambient temperatures reach or exceed body temperature because they would no longer result in cooling. It is assumed that during the rise in ambient temperature, the body is heating, stimulating thermoregulatory mechanisms to control temperatures within a normal range. Likewise when temperatures fall below a certain point, yawning would not be beneficial because sending a wave of unusually cool blood to the brain would be maladaptive. The first prediction was recently tested using budgerigars (*Melopsittacus undulatus*) as an avian model (Gallup et al., 2009). Budgerigars' yawning rates were significantly influenced by increasing ambient temperatures, providing the first documented evidence that yawning may be a temperature regulating mechanism in birds. More specifically, yawning frequency increased during rising ambient temperature, but when temperature approached body temperature, yawning began to diminish as other evaporative heat loss behaviors (i.e., gular fluttering/panting) became prevalent. This supports the view that yawning serves as a compensatory rather than primary cooling behavior (Gallup & Gallup, 2007).

Although the findings of Gallup et al. (2009) provided new insight into the influence of ambient temperature on yawning, it was unclear whether yawning was triggered by an increase in internal temperature associated with exposure to higher or increasing ambient temperature, or simply by the change in ambient temperature, irrespective of direction. In these previous experiments, ambient temperature was first increased and then held close to body temperature, and, as described above, yawning was associated with the period of increase to just below body temperature. In order to distinguish between these contexts, we manipulated the ambient temperature experienced by budgerigars in both directions across a similar temperature range, while recording yawning, stretching, wing venting, and panting. Stretching is commonly associated with yawning and arousal (Provine, Hamernik, & Curchack, 1987), while wing venting and panting are both thermoregulatory cooling behaviors in budgerigars (Byman, Wasserman, Schlinger, Battista, & Kunz, 1985). Wing venting, i.e., holding the wings out from the sleeked body, enhances heat loss by exposing bare skin to convection and reducing insulation around the body, while panting increases the rate of evaporative water loss from the mouth and lining of the throat, ultimately promoting evaporative cooling in birds experiencing heat stress (Bartholomew, Lasiewski, & Crawford, 1968).

The results of Gallup et al. (2009) also did not identify specific ranges over which the frequency of yawning was most significantly affected; therefore, in this study, the range over which temperature change occurred was parceled into small segments (multiple increasing and decreasing ranges). Overall, the present study sought to examine yawning frequency as a function of the direction and range of ambient temperature change, as well as in relation to other behaviors involved in heat loss. It was hypothesized that, if yawning is involved primarily in heat dissipation and stimulated by actual increased brain or body temperature, there would be more frequent yawning during times of high increasing temperature and potential heat stress; as a result, yawning should also be correlated with the behavioral cooling responses in this species.

Methods

Study Animals

The budgerigars in this study included nine males and seven females from a research population bred at and housed in Binghamton University, Binghamton, NY, U.S.A. These birds live outside in the spring and summer months and are brought indoors during the late autumn and winter. These experiments were conducted indoors during October-November 2008. During this time, birds were kept in an indoor aviary (1.8 × 1.8 × 1.8 m), with a room temperature of 23^{o}C and light:dark cycle of 11:13 h.

Experimental Conditions

All birds were caught with small nets from their group aviary 24 h before being tested, and all experiments occurred between 1330 and 1500 hours. Birds were tested in groups of four in a wire-mesh cage (0.4 × 0.3 × 0.3 m), which was then covered by a wooden box. The box (0.96 × 0.43 × 0.61 m) fully enclosed the cage, while still allowing for ventilation, and a set of small heat lamps within the box were used to adjust the ambient temperature. A window (0.28 × 0.30 m) covered with Plexiglas allowed viewing and filming of the birds inside the box. A Springfield PreciseTemp^{TM} digital thermometer positioned near the birds (0.5 m from heat lamps) in the upper ½ of the box and visible to the observer was used to monitor the ambient temperature. Temperature was recorded every two minutes to the nearest 0.1^{o}C.

We tested two separate thermal conditions, each 20 minutes in length. During each session, a researcher was present to monitor the birds and the ambient temperature while the trial was recorded using a Sony Hi-8 camcorder. Conditions included a rapidly increasing temperature range (23→33°C), and a rapidly decreasing temperature range (34→24°C). These conditions were further divided into four 10 minute intervals; including a (i) low-increasing range (23→27°C) followed by a (ii) high-increasing (27→33°C), and a (iii) high-decreasing (34→28°C) followed by a (iv) low-decreasing range (28→24°C). Prior to each trial, a 20 minute acclimation period occurred after the birds were positioned within the testing box. The temperature of the acclimation period was held constant and it represented the starting ambient temperature of each trial order (increasing: 23°C; decreasing: 34°C). A repeated measures design was used in which each testing session lasted 60 minutes and included both temperature conditions. The trials were counterbalanced with respect to the order of temperature changes: (i) increasing then decreasing (ID) or (ii) decreasing then increasing (DI).

Four groups of four birds each were tested. Birds were randomly assigned to groups and the trial orders were alternated between groups. The heat lamps were turned on at the beginning of the increasing condition in both the ID and DI trial orders, and prior to the acclimation period in the DI trial. Decreasing temperature was achieved by turning off the heat lamps and opening a hinged door in the top of the thermal box at the end opposite to the bird’s cage, allowing heat to rapidly dissipate. Ongoing research indicates no experimental evidence for contagious yawning in this species (Miller, Vicario, & Clark, 2008, in preparation), and thus it was unlikely that an individual’s yawns influenced yawning by others in its group.

Analyses

Two observers who were blind to the temperature condition scored video recordings using a 0.3 m Sony Trinitron monitor connected to a Sony Digital-8 Video Walkman (GV-D800 NTSC). Individual birds could be recognized on the tapes. Yawning, stretching, panting, and wing venting of each bird were recorded. Yawning was recognized as a wide opening of the beak and slight closing of the eyes, following by a brief pause (the acme state) with stretching of the neck. This can be distinguished from gaping, as gaping is a response to heat stress during flight, and it is described as an uninterrupted, and continuous opened beak (see Byman et al., 1985). Stretching consisted of an initial posterior-dorsal extension of one leg followed by further posterior extension of one or both wings. Panting was characterized as a rapid and continuous opening and closing of the beak that persisted longer than 10 sec. Wing venting was characterized as a simultaneous raising and slight extension of the wings that continued for at least 10 sec while the body feathers were sleeked. Wing venting is distinguished from stretching in that the wings are extended slightly laterally but not back, the wing movements persist and the behavior does not include an extension of the leg(s). As panting and wing venting are continuous behaviors, they were recorded as either occurring or not occurring within a particular bird during each two minute interval. The behaviors of each bird from each group were recorded for each 10-minute interval, and the distribution of behavioural observations was then paired with the appropriate temperature recordings. A repeated measures ANOVA was used to investigate differences between temperature ranges using SPSS version 16.0 (SPSS, Inc., Chicago, IL, U.S.A.). The relationship of ambient temperature across trials to each of the four recorded responses was tested with a Pearson correlation test. As a result of non-normal distributions, yawning, stretching, and wing venting were log-transformed prior to correlation analysis.

Ethical Note

The ambient temperature ranges experienced by the budgerigars did not exceed what they would typically experience in their natural habitat of mainland Australia or what these birds occasionally experience during summer in outdoor aviaries at Binghamton University. Following experimental procedures, all budgerigars were immediately returned to the aviary, and no birds showed signs of distress or dysfunction, resuming normal activities soon thereafter. All aspects of this experiment were approved by the Institutional Animal Care and Use Committee at Binghamton University (Protocol No. 610-07).

Results

A total of 57 yawns (37 by males, 20 by females) were observed during the four testing sessions. Of these, 12 occurred during the low-increasing range (mean per bird ± SE = 0.75 ± 0.23), 25 during the high-increasing range (1.56 ± 0.39), 11 during the high-decreasing range (0.69 ± 0.20), and nine during the low-decreasing range (0.56 ± 0.18). Figure 1 shows that average yawning frequencies differed significantly across ranges (i.e., high versus low), F (3, 42) = 3.50, $p < 0.05$, partial $\acute{\eta}^2 = 0.20$. Post hoc analyses indicate that the yawning rate in the high-increasing range was significantly higher than that during the low-decreasing range, $p < 0.05$. There was no significant difference in yawning rate between the high-increasing range and either the low-increasing, $p = 0.06$, or high-decreasing ranges, $p = 0.07$, although the absolute number of yawns was greatest in the high increasing range. All other comparisons showed no differences. Figure 2 shows that the average yawning frequency was significantly higher in the high temperature ranges (high-increasing and decreasing) when compared to the low temperature ranges (low-increasing and -decreasing) (F (1, 12) = 5.67, $p < 0.05$, partial $\acute{\eta}^2 = 0.30$). Figure 3 shows no statistical difference in average yawning frequency between increasing ranges (low-and high-increasing) and decreasing ranges (low- and high-decreasing), $F\ (1, 12) = 3.57$, $p = 0.08$, partial $\acute{\eta}^2 = 0.19$.

A test of between subjects effects revealed no difference in total yawning rates across the four groups tested ($F\ (1, 12) = 1.46$, $p = 0.28$, partial $\acute{\eta}^2 = 0.27$). A similar test also showed no difference in total yawning rates among trial orders ($F\ (1,14) = 1.060$, $p = 0.32$, partial $\acute{\eta}^2 = 0.07$). However, there was a significant interaction between temperature ranges and the trial order ($F\ (3,42) = 3.06$, $p < 0.05$, partial $\acute{\eta}^2 = 0.18$), the yawning rate in the low decreasing range being significantly higher during the DI trial ($t\ (14) = 2.966$, $p < 0.05$). All other comparisons were not significant. There was also no difference in yawning rates between males and females (4.11 ± 0.56 versus 2.86 ± 1.01, $t\ (14) = 1.15$, $\mathrm{p} = 0.27$).

The frequency of yawning within the group of birds tested was significantly affected by ambient temperature ($t\ (118) = 4.16$, $p < 0.01$). Similarly, the incidence of panting and wing venting within the group were also affected by ambient temperature, panting: ($t\ (118) = 10.47$, $p < .01$), wing venting ($t\ (118) = 2.72$, $p < 0.01$). Therefore, the incidence of yawning, panting and wing venting were all associated with higher ambient temperatures. Table 1 shows Pearson correlations between temperature and the four recorded behaviors. Ambient temperature was significantly correlated with all behaviors except for stretching. The incidence of yawning within the group was also positively correlated with the number of birds panting and wing venting within the group, but not with the frequency of stretching within the group ($p = 0.06$). Likewise, yawning within a group occurred significantly more frequently, indeed over twice as often, when at least one of the four birds was panting or wing venting than when no birds were panting or wing venting (with panting, 1.09 yawns ± 0.16 versus 0.49 ± 0.11 yawns without, t

(118) = 3.30, $p < .01$; with wing venting 1.36 ± 0.21 yawns versus 0.61 ± 0.10 yawns without, t (118) = 3.15, $p < .01$).

In all, 26 stretches (nine by males, 17 by females) were observed during the four testing sessions. Of these, 14 occurred during the low-increasing range (0.86 ± 0.41), six during the high-increasing range (0.38 ± 0.18), one during the high-decreasing range (0.06 ± 0.06), and five-occurred during the low decreasing range (0.31 ± 0.18). The average stretching frequency did not differ across conditions (F (3, 42) = 2.23, $p = 0.09$, partial $ή^2 = 0.14$). Stretching also did not differ between increasing ranges (low- and high-increasing) and decreasing ranges (low- and high-decreasing) (F (1, 14) = 2.54, $p = 0.13$, partial $ή^2 = 0.15$). In addition there was no difference in stretching between high temperature ranges (high-increasing and decreasing) and low temperature ranges (low-increasing and -decreasing) (F (1, 14) = 3.94, $p = 0.07$, partial $ή^2 = 0.22$).

A test of between subjects effects revealed a strong significant difference between stretching frequency across groups (F (3, 12) = 8.49, $p < 0.01$, partial $ή^2 = 0.68$). The fourth group tested stretched a total of 18 times, and post hoc analyses revealed this difference to be significant when comparing this group to all others ($p > 0.05$). There was also a significant interaction of stretching across ranges and groups tested (F (9, 36) = 6.23, $p < 0.01$, partial $ή^2 = 0.61$). Post hoc analyses show that stretching occurred significantly more during low-increasing range of the fourth group compared to all other ranges ($p < 0.01$). As a result, there were also significant differences between individual birds within groups in the distribution of stretching across trial order (F (1, 14) = 10.21, $p < 0.01$, partial $ή^2 = 0.42$), with stretching occurring significantly more often during the DI trial order. There was however, no interaction between temperature ranges and trial order for stretching (F(3, 42) = 1.68, $p = 0.19$, partial $ή^2 = 0.11$).

There were also no differences in stretching rates between males and females (1.00 ± 0.67 versus 2.29 ± 0.87, *t* (14) = 1.20, *p* = 0.25).

Discussion

Yawning frequency was influenced by the direction and range of ambient temperature change, occurring over twice as often during high-increasing ambient temperature range, as it did during other periods. This difference was only significant when compared to the low-decreasing range, but approached significance when compared to either the low-increasing or the high-decreasing ranges. Yawning also occurred significantly more often during the two high temperature ranges than during the two low temperature ranges across trials. These findings are consistent with the notion that yawning is temperature-sensitive, not simply a response to temperature change. Yawning as well as the two thermoregulatory behaviors, panting and wing venting, were all positively correlated with ambient temperature. The frequency of yawning was also correlated with the number of birds engaging in either of these behaviors. In addition, yawning was significantly more frequent in a group when at least one of the four birds was displaying either of these two heat-dissipating behaviors. Stretching, on the other hand, was not affected by ambient temperature change, and also was not correlated with yawning or panting. These data suggest that, like panting and wing venting, yawning is a thermoregulatory behavior in budgerigars.

Thus we propose that yawning may be an initial response to loss of thermal homeostasis. Endothermy involves an active relationship between internal heat production and heat loss to the external environment. Ambient air temperature provides an accurate index to the rate of heat loss or heat gain within a particular environment. Homeothermic species preserve a relatively constant body temperature as ambient temperature fluctuates, using a combination of autonomic and behavioral mechanisms controlled by the central nervous system (reviewed by Bicego, Barros, & Branco, 2007). In this experiment, yawning occurred over twice as often during the high-increasing temperature range, a range which was likely to produce highest amounts of heat stress. Likewise, yawning was significantly more frequent during the highest temperature ranges, suggesting that yawning is sensitive to high temperature change. Also, our other behavioral findings are consistent with the view that yawning is triggered in combination with other thermoregulatory responses, as it occurred over twice as often when at least one of the four birds was either panting or wing venting.

Scholander, Hock, Walters, Johnson, and Irving's (1950) model of endothermy, a foundation model in avian physiology, provides a way of understanding the dynamics of temperature regulation among avian species. Their model assumes that birds expend the least amount of energy on temperature regulation in the thermoneutral zone, which is the ambient temperature range where respiration rates do not change with temperature. Within this zone, heat loss is generated with little direct energy expenditure, typically through varying rates of venous blood flow or by altering body posture. Outside of this zone however, temperature regulation requires increases in metabolism through shivering or panting. When ambient temperature rises above the upper critical temperature, non-evaporative mechanisms are progressively reduced, while more effective evaporative heat loss is increased (Scholander et al. 1950).

We suggest that a yawn provides a metabolically inexpensive means of cooling by increasing venous blood flow while cooling blood traveling to the brain through convection. In addition, we propose that yawning serves as a compensatory rather than primary cooling behavior, which is trumped by more effective, but possibly more costly evaporative cooling behaviors when temperature rises above some upper critical temperature. Gallup et al. (2009) supported this proposition by demonstrating a reduction in yawning as panting became more prevalent at higher temperatures (i.e., 34→38^{o}C). As an arid zone bird, budgerigars are under pressure to conserve water which would be lost during evaporative cooling through panting. Thus, yawning may act as an adaptive response to early signs of thermal stress. In addition, the relationship between yawning and rising ambient temperature replicates the findings of Gallup et al. (2009).

Stretching on the other hand, which is commonly associated with yawning and arousal (Provine et al., 1987), was not affected by the direction or range of ambient temperature change. Stretching was also uncorrelated with the incidence of yawning or panting. Therefore, consistent with our previous research (Gallup et al., 2009), stretching does not appear to be involved in thermoregulation in this species. However, because yawning predicts stretching in humans (Provine et al. 1987), and there was a close to significant relationship between yawning and stretching across trials, we are not ruling out the possibility of an association between these two behaviors in budgerigars within normal temperature variation. In fact, we have preliminary evidence to suggest a temporal association between these behaviors in budgerigars under thermally unstressful conditions (Miller et al., 2008, in preparation). Since the physiological consequences of stretching are similar to that of yawning (i.e., increased circulation) the yawn/stretch relationship should be further studied in a naturalistic setting. It should also be noted that although there was a trend towards significance across temperature variation, these effects were driven primarily by only one of the four groups tested, which accounted for over 69% of all stretching across trials. Interestingly, this finding replicates previous results in budgerigars showing that stretching occurs in clusters under natural conditions (Miller et al., 2008, in preparation), and may even be somewhat contagious in this species. However, further research is needed to investigate this phenomenon.

Consistent with previous theories explaining the occurrence of yawning across taxa (Baenninger, 1997), this account also suggests that yawning is a behavior involved in arousal and state change. These findings refine our understanding of the factors that affect yawning, as it occurs primarily in response to high temperature ranges, and in association with other cooling behaviors. Temperature change alone is, however, not sufficient to influence yawning. In this study it occurred most frequently during high and increasing temperatures. This research indicates that yawning is similar to panting and wing venting in this species, in that it is triggered as a part of a combination of behavioral cooling mechanisms during times of heat stress. Before further conclusions can be drawn about its efficiency or exact timing during rising ambient temperatures, more studies of the direct effect of yawning on brain and/or body temperature are needed. Nonetheless, we believe these findings could have important implications not just for the study of yawning per se, but also for the basic understanding of comparative thermoregulation. Because the functionality of yawns in poikilotherms may be fundamentally different from that in homeotherms, future research should examine potential differences between these kinds of animals in yawning in response to thermal stress. At the very least, yawning should be considered as a variable of interest in future studies investigating thermoregulation among vertebrates, especially since it is an easily measured behavior.

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Appendix

Table 1
Pearson correlations between temperature and recorded behaviors

	temperature	panting	stretching	wing venting	yawning
Temperature	-				
Panting	.740**	-			
Stretching	.069	-.059	-		
wing venting	.214*	.166	.182*	-	
Yawning	.333**	.365**	.175	.312*	-

*$p < .05$
**$p < .01$

Table 1. Yawning and stretching represent the number of yawns and stretches recorded during each 2-minute interval, while panting and wing venting indicate the number of birds observed engaging in these behaviors during each interval.

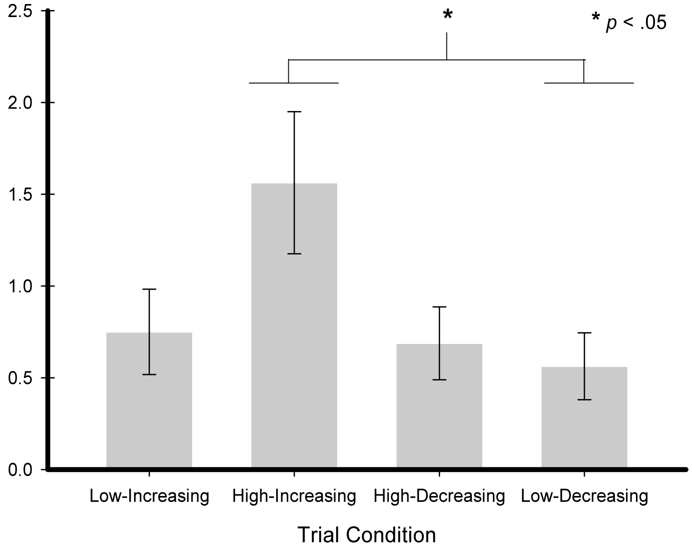

Fig 1. The temperature condition affected the frequency of yawning. Shown here is the number of yawns per subject (Average ± SEM) within each consecutive 10-minute condition. Subjects yawned significantly more during the high increasing condition (23→27^{o}C), as compared to the low decreasing condition (28→24^{o}C).

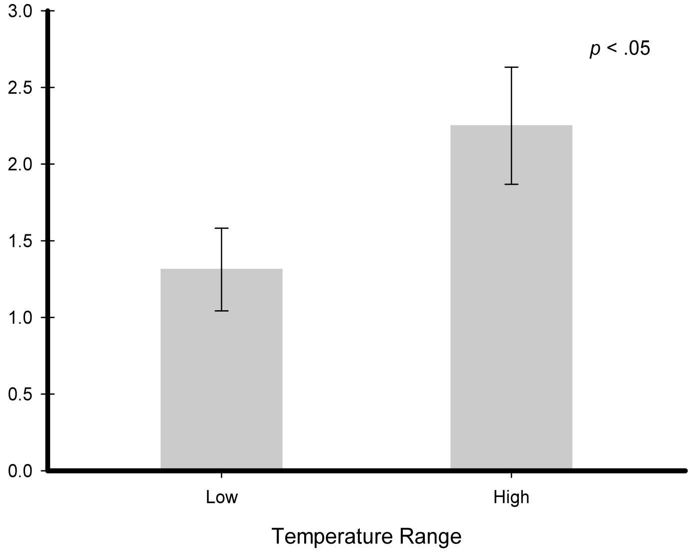

Fig 2. The temperature range significantly influenced the frequency of yawning per bird. Birds yawned significantly more during the high temperature range (~28→34°C), as compared to the low temperature range (~23→28°C), irrespective of the direction of temperature change direction.

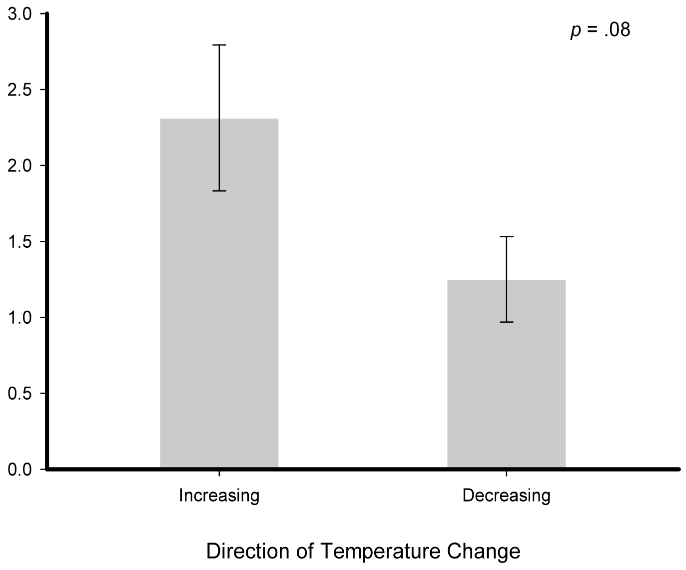

Fig 3. The direction of temperature change alone did not significantly affect yawn frequency. Taken with Fig 2, this trend suggests yawning is more sensitive to temperature range—high versus low—than direction of change.