Yawning and thermoregulation in budgerigars (*Melopsittacus undulatus*)

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ABSTRACT

Yawning is a widespread behavioural response expressed in all classes of vertebrates. There is however, little agreement on its biological significance. One current hypothesis states that yawning serves as a thermoregulatory mechanism that occurs in response to increases in brain and/or body temperature. The brain cooling hypothesis further stipulates that, as ambient temperature increases and approaches (but does not exceed) body temperature, yawning should increase as a consequence. We tested this hypothesis in a sample of 20 budgerigars (*Melopsittacus undulatus*) through the manipulation of room temperature. Birds were exposed to three separate conditions [control temperature (22^{o}C), increasing temperature (22-34^{o}C), and high temperature (34-38^{o}C)] in a repeated measures design, with each condition lasting 21 minutes. The incidence of yawning differed significantly across conditions (4.20 ± 2.39 yawns per bird in the increasing temperature condition, compared to 2.05 ± 1.90 and 1.25 ± 0.72 yawns per bird, in the high temperature and control condition, respectively). These findings are consistent with the hypothesis that yawning serves a thermoregulatory function.

Keywords: ambient temperature; budgerigar; *Melopsittacus undulatus*; thermoregulation; yawning

INTRODUCTION

Yawning is characterized by a large gaping of the mouth, accompanied by a deep inhalation of air, and a shorter expiration. Although typically studied in humans, yawning is a widely expressed, stereotyped phenomenon occurring in all classes of vertebrates (Baenninger 1987), but little is known about the function of yawning in any species. Research has shown that yawning coincides with a variety of neurochemical interactions in the brain (Ariolas & Melis 1998). While the neurological mechanisms underlying yawning are not entirely clear, research on yawning under laboratory conditions has proven valuable in understanding the physiopathology of certain diseases, as well as the action of new drugs (Danquin et al. 2001). However, numerous attempts at identifying the adaptive or biological significance of the yawn (reviewed by Smith, 1999) have led to little consensus (Provine 2005).

Yawning is under involuntary control, and it cannot be inhibited or elicited by individual command (Provine 2005). Yawning is also contagious in humans and some non-human primates (Anderson et al. 2004; Paukner & Anderson 2006). In humans, attempts to shield a yawn do not prevent its contagion (Provine 2005). The spontaneous and uncontrollable nature of yawning across species lends support for it having adaptive significance. In humans, yawning occurs before birth as early as 20 weeks after conception (Sherer et al. 1991), testifying to its importance postnatally, as many important postnatal behaviours begin to appear prenatally (e.g. breathing movements, swallowing, and eye movements) before they develop any functional significance (Nijhuis 2003).

Throughout the lives of healthy adult humans, yawning occurs in a consistent pattern (Gallup and Gallup 2008), occurring most often during the first hour after wakening and the last hour before sleeping (Baenninger et al. 1996; Provine et al. 1987; Zilli et al. 2007). Similarly, variation in yawning among rats appears to have a circadian pattern (Anias et al. 1984). In addition, stretching has been shown to accompany yawning almost 50% of the time in humans (Provine et al. 1987). Researchers have attributed such findings to an association between yawning and increases in arousal and activity that accompany transitional states (Greco & Baenninger 1991; Greco et al. 1993; Baenninger et al. 1996; Provine et al. 1987). Aside from observational reports, comparative studies investigating yawning in non-humans are few and the ethology of yawning in non-human species remains mysterious. Baenninger (1987) proposed that yawning may actually serve different functions in different species. Nonetheless, the tendency for yawning to correspond with state changes in humans (Baenninger et al. 1996; Greco et al. 1993; Provine et al. 1987) suggests possible adaptive contexts for this behaviour across species.

New evidence suggests that yawning may be involved in thermoregulation (Gallup & Gallup 2007; Gallup & Gallup 2008) and may act as a brain cooling mechanism. This hypothesis has been developed for humans but suggests one general utility across endotherms. Based on this theory, the yawn serves as a cooling mechanism that keeps the brain and/or body in thermal homeostasis, thus maintaining mental efficiency. Increases in facial blood flow resulting from a yawn may operate like a radiator, removing hyperthermic blood from specific areas, while introducing cooler blood from the lungs and extremities. Increases in facial blood flow may alter cerebral blood flow as well (Barbizet 1958; Heusner 1946; Zajonc 1985). Consistent with the radiator hypothesis of human brain evolution (see Falk 1990), the respiratory and arterial actions that follow the yawn match those required to cool the brain effectively. An increase in cranial blood flow due to yawning may aid in the dissipation of heat via the emissary veins. In humans, increased arousal—as measured by skin conductance—occurs during yawning (Greco &

Baenninger 1991), and vasodialation has been hypothesized to promote further cooling. Gaping of the mouth and deep inhalation of air taken into the lungs during a yawn can also alter the temperature of the blood traveling from the lungs to the brain through convection (Gallup & Gallup 2007). This hypothesis proposes that it is the temperature of the air that gives the yawn its utility, not the air's composition. In fact, variation in O_2 and/or CO_2 concentrations has no impact on yawn frequency (Provine et al. 1987).

The brain cooling hypothesis leads to several testable predictions. First, it predicts that there will be a fairly narrow range of external temperatures—a "thermal window"—over which yawning can be triggered (Gallup & Gallup 2007; Gallup & Gallup 2008). As ambient temperature rises, it becomes increasingly difficult to maintain thermal homeostasis, but it also becomes less effective to lower body temperature by using environmental heat transfer. The model's central prediction is that (a) the frequency of yawning should rise as ambient temperature approaches body temperature, and (b) should not occur when ambient temperature reaches or exceeds body temperature, because its cooling component will no longer occur. Likewise, when temperatures fall below a certain point, yawning would cease to be adaptive and could become maladaptive by sending unusually cool blood to the brain. This hypothesis is intriguing because it applies generally across endotherms and suggests differences in the importance of yawning for different species, dependent on both morphology and environment.

To test the central hypothesis, we manipulated the ambient temperature experienced by budgerigars (*Melopsittacus undulatus*) in a laboratory environment while recording yawning, stretching, and gular fluttering, a thermoregulatory response which promotes evaporative cooling in birds experiencing heat stress (Bartholomew et al. 1968). Body temperature is a balance between heat production and heat dissipation, and raising the ambient temperature would be expected to trigger compensatory thermoregulatory mechanisms. We therefore hypothesized that the frequency of yawning would increase in response to rising ambient temperatures, as opposed to when temperature is held constant. This species was chosen because of its large relative brain size (Iwaniuk & Nelson 2002) as well as the fact that its natural habitats include arid Australia where it would be subject to wide swings in temperature. In addition, a recent study has shown no evidence for contagious yawning in this species (Miller et al. unpublished data). Thus, we were able to investigate the frequency of yawning within small groups with confidence that any individual's yawns would not influence yawning in others.

METHODS

Study Animals

The budgerigars tested in this study included nine females and 11 males, from a research population bred and maintained at Binghamton University. These birds are routinely housed outside in the spring and summer months, and are then brought inside during the late fall and winter. These experiments were conducted indoors during January-March 2008. During this time, all birds were kept in an aviary (1.8x1.8x1.8 m) in an animal room maintained at 22^{o}C, on a constant 11:13 light cycle.

Experimental Conditions

All birds in this study were caught 24 hours prior to being tested, and all experiments occurred during the hours of 12pm and 2pm. Birds were tested in groups of four in a wire-mesh cage (0.40x0.30x0.30 m) which was then covered by a wooden box. This allowed us to adjust the ambient temperature accordingly using heat lamps placed within the box. The box (0.96x0.43x0.61 m) fully enclosed the cage and a set of small heat lamps were used to adjust the temperature. A window (0.28x0.30 m) covered with Plexiglas^{TM} allowed viewing and filming the birds inside the box. A Springfield PreciseTemp^{TM} digital thermometer which was positioned near the birds (0.5 m from heat lamps) in the upper ½ of the box was used to monitor the ambient temperature. Temperature was recorded every three minutes to the nearest tenth degree Celsius.

Three separate thermal conditions, each 21 minutes in length, were tested. A 20 minute acclimation period occurred after the birds were positioned within the box before the start of each testing session. During each session, the birds and temperature were monitored by a researcher and recorded using a video camera. Conditions included a control condition (steady at 22°C), a rapidly increasing temperature condition (22-34°C), and a high temperature condition (held between 34-38°C). A repeated measures design was used in which each testing session lasted a total of 63 minutes and included all three conditions. The experiments were partially counterbalanced, utilizing two trial orders: (a) control condition, increasing condition, then high temperature condition; and (b) increasing condition, high temperature condition, then control condition. Three groups of four were tested in the first trial, and the other two groups were tested in the second trial. Birds were randomly assigned to groups, and two trial procedures were alternated between groups.

Analyses

Video recordings were scored after each testing session by two researchers who were unaware of the temperature conditions. Yawns and stretches from each bird were recorded. Yawning was recognized as a wide opening of the beak with slight closing of the eyes, followed by a brief interruption (the acme state) with stretching of the neck. Stretching consisted of an initial posterio-dorsal extension of one leg followed by further posterior extension of one or both wings. Gular flutter, a form of evaporative cooling induced by heat stress in birds (Bartholomew et al., 1968), was also recorded. Gular fluttering was characterized by the rapid and continuous opening and closing of the beak, which acts to flap membranes in the throat and increase evaporation. Gular flutter was charted in two separate instances: (a) when at least one bird within the group began to display this behaviour (first flutter); and (b) when the entire group showed this response (all flutter). The behaviours for each bird in each group were summed for each 21 minute condition. The distribution of behavioural observations was then paired with the appropriate temperature recordings. A repeated-measures ANOVA was used to investigate differences between groups and conditions using SPSS version 15.0. In addition, linear and quadratic regression analyses were conducted between yawning, stretching and ambient temperature across conditions in blocks of three minute intervals. As a result of non-normal distributions between yawning and stretching, these variables were log-transformed before regression analyses.

Ethical Note

The ambient temperatures experienced by the budgerigars in this experiment were within the range of they typically experience in the summers of Binghamton, New York. This species is regularly exposed to even higher fluctuations in ambient temperature in its natural habitat of mainland Australia. In addition, the budgerigars were subjected to only a brief temperature alteration, never exceeding 42 min of increasing or warm temperatures and they were monitored continuously during the tests. Forty-two minutes is a very limited amount of time compared to procedures used by Hoffman et al. (2007), who tested Inca doves (*Columbina inca*) for 2 hours with ambient temperatures ranging from 30°C to 42°C. Upon release, birds in this study showed no signs of stress or dysfunction and resumed normal activities. All aspects of this experiment were approved by the Institutional Animal Care and Use Committee at Binghamton University (Protocol 610-07).

RESULTS

In all, 150 yawns (85 by males, 65 by females) were observed during the five testing sessions. Of these, 84 occurred during the increasing temperature condition (4.20 ± 2.39 yawns per bird), 41 during the high temperature condition (2.05 ± 1.90 yawns per bird), and 25 during the control condition (1.25 ± 0.72 yawns per bird). The yawning rates differed significantly across conditions ($F_{2, 32} = 36.700$, $P < 0.0001$). A paired t-test revealed that the increasing condition was significantly different from both the high temperature ($t_{19} = 4.921$, $P < 0.0001$) and control conditions ($t_{19} = 5.064$, $P < 0.0001$) respectively; however, here was no difference between the high temperature and control conditions ($t_{19} = 1.566$, $P = 0.134$).

A test of between-subjects effects revealed a significant difference between the two trial procedures ($F_{1, 16} = 16.807$, $P = 0.0008$), with yawning occurring more frequently during the increasing and high temperature conditions of the second trial procedure (increase-high-control). There was also a significant interaction within conditions and trials ($F_{2, 32} = 11.863$, $P = 0.0001$). On average, males yawned slightly more than females throughout all three conditions (7.727 ± 3.90 versus 7.222 ± 3.70), but this difference was not significant ($F_{1, 16} = 0.803$, $P = 0.383$). There was also no sex difference in yawning during the two trial procedures ($F_{1, 16} = 0.764$, $P = .395$).

There was a total of 42 observed stretches (24 by males, 18 by females), but this behaviour was not affected by the temperature conditions ($F_{2, 32} = 0.551$, $P = 0.582$). As with yawning, the second trial procedure (increase-high-control) did, however, elicit significantly more stretching than the first procedure ($F_{1, 16} = 13.079$, $P = 0.002$), and this contributed to a significant interaction between temperature condition and trial procedure ($F_{2, 32} = 9.587$, $P = 0.001$). On average, males stretched slightly more than females throughout all three conditions

(2.182 ± 2.44 versus 2.000 ± 2.18), but this difference was not significant ($F_{1,\ 16} = 0.144$, $P = 0.710$). After log transformation, stretching was not correlated with yawning ($r = 0.249$, $N = 13$, $P = 0.412$).

Figure 1 depicts the frequency and distribution of stretching and yawning in response to ambient temperature across conditions in three minute intervals. A linear regression of yawning on ambient temperature showed a non-significant relationship ($F_{1,\ 58} = .814$, $P = 0.371$). A quadratic regression however, revealed a significant result ($F_{2,\ 57} = 4.659$, $P = 0.013$), explaining 14% of the variance in yawning behaviour. For stretching, neither linear nor quadratic regressions showed a significant relationship with temperature (linear, $F_{1,\ 16} = 0.000$, $P = 0.991$; quadratic, $F_{2,\ 15} = 0.005$, $P = 0.995$).

The incidence of gular flutter was significantly affected by ambient temperature (first flutter, $t_{103} = 19.376$, $P < 0.0001$; all flutter, $t_{103} = 18.081$, $P < 0.0001$). There was a strong positive correlation between ambient temperature and gular flutter (first flutter, $r = 0.886$, $N = 105$, $P < 0.001$; all flutter, $r = 0.872$, $N = 105$, $P < 0.001$). In every trial, gular flutter began during the increasing temperature condition, and then lasted throughout the entire high temperature condition. The incidence of gular fluttering by at least one of the four birds (first flutter) occurred on average at 25.6^{o}C, while flutter among the entire group (all flutter) occurred at mean temperature of 35.4^{o}C. The incidence of gular flutter within one to three birds was associated with significantly higher rate of yawning ($t_{58} = 2.455$, $P = 0.017$). But when fluttering occurred throughout all four birds, this trend receded and birds yawned less, but not significantly ($t_{58} = -0.096$, $P = 0.923$). The use of gular fluttering for cooling at higher temperatures may partially explain the difference between yawning frequency in the increasing condition (4.20 yawns per bird) and the high temperature condition (2.05 yawns per bird) as the two are complimentary mechanisms that function toward the same end. Stretching showed, however, no such relationship to gular flutters (first flutter, $t_{16} = -0.312$, $P = 0.759$; all flutter, $t_{16} = -0.503$, $P = 0.622$).

DISCUSSION

The frequency of yawning was significantly affected by ambient temperature. As ambient temperature increased, birds were over twice as likely to yawn, compared to when temperatures were held constant (both low and high). Yawning occurred less frequently at low temperatures (1.25 ± 0.72 yawns per bird), slightly more when held at high temperatures (2.05 ± 1.90 yawns per bird), and most frequently with increasing temperatures (4.20 ± 2.39 yawns per bird). Likewise, the strong quadratic correlation between yawning frequency and temperature supports the relationship between yawning and ambient temperature change. These data are consistent with the hypothesis that yawning, like gular fluttering, is connected with thermoregulation. Stretching, although often seen with yawning at control temperatures, was not influenced by ambient temperature manipulation.

Although the rate of yawning peaked around 30^{o}C—during the increasing temperature condition—it began to decrease in frequency as temperature further increased (i.e., 34-38^{o}C during the high temperature condition). This trend appeared to be influenced by the prevalence of gular fluttering; while fluttering was originally positively correlated with the incidence of yawning—at around 25.6^{o}C—this trend was reversed by the time all birds were engaged in this behaviour (i.e., 35.4^{o}C). As gular fluttering is widely associated with thermoregulation (Bartholomew et al. 1968), we argue that this respiratory mechanism may supplant yawning, especially when temperature exceeds some critical point around 35.4^{o}C. That is, yawning may be inhibited when continuous gular fluttering is required to prevent hyperthermia. Yawning appears to be an initial response associated with thermal homeostasis; as temperature increases and heat dissipation becomes more difficult, more effective regulatory mechanisms, such as the gular flutter, are triggered. This corroborates the view that yawning serves as a compensatory rather than primary cooling mechanism (Gallup & Gallup 2007). Furthermore, as ambient temperature approaches body temperature, one would expect yawning to diminish in frequency (Gallup & Gallup 2007). Although the ambient temperature in this study never exceeded budgerigar body temperature (39.5°C), attenuation of yawn frequency at 35.4°C is consistent with this prediction. At this point the cooling capacity of the yawn (i.e., difference between ambient and body temperature) was less relative to lower temperatures.

The incidence of stretching was not affected by ambient temperature. There was no difference in stretching among temperature conditions, and the incidence of stretching did not vary across the range of temperature within this experiment ($P > 0.9$), nor was there a correlation between the incidence of yawning and stretching. Within the increasing and high temperature conditions, there was also no observed relationship between stretching and gular fluttering. Therefore, we propose that unlike yawning, stretching appears to be independent of thermoregulation in this species. In humans at room temperatures, stretching is accompanied by yawning nearly half of the time (Provine et al. 1987); with the incidence of yawning predicting stretching, but stretching not predicting yawning. The yawn/stretch relationship in budgerigars should be studied at lower ambient temperatures before a similar relationship can be dismissed.

This comparative evidence provides novel insight onto yawning as thermoregulatory mechanism, revealing that rising ambient temperature promotes excessive yawning in parakeets. This effect could be tested further among an array of species, including humans. Recent interdisciplinary research has strengthened this connection between yawning and thermoregulation (Gallup & Gallup 2008). A growing body of medical and physiological evidence implicates instances of abnormal thermoregulation and heat stress with symptoms of atypical yawning. For instance, there is a link between the negative symptoms of epilepsy, multiple sclerosis, and migraine headaches and increases in the ambient temperature. More importantly, individuals suffering from these disorders also yawn excessively (Gallup & Gallup 2008). Therefore, applications of this research range from basic physiological understanding to improved health and treatment of patients with thermoregulatory dysfunction.

These findings have significant ramifications regarding the way at which we study yawning in humans and other species. Yawning is widely associated with states of fatigue, frequently occurring when an individual wakes or gets ready for sleep (Baenninger et al. 1996; Provine et al. 1987). Evidence shows that sleep and thermoregulation appear to be interrelated, with prolonged sleep deprivation in rats producing an increase in deep brain temperature (Everson et al. 1994). Likewise, it has been argued that core body temperature and sleep vary inversely (Gilbert et al. 2004). Following this rationale, it has been shown that subjective ratings of sleepiness correlate with increases in body temperature (Krauchi et al. 2005). These results may explain the empirical correlates of yawning with transitional states of fatigue. Moreover, the metabolic activity and locomotor changes associated with awakening may disrupt thermal homeostasis, and this underlying change in thermal homeostasis may trigger the association between yawning and awakening.

The thermoregulatory model compliments and may also help explain models highlighting the association between yawning and other transitional states, such as alertness and arousal (Greco & Baenninger 1991; Walusinski 2006). Gallup & Gallup (2007) propose that the cooling component of yawning may actually facilitate these processes (i.e., mental efficiency and vigilance) by reinstating optimal brain temperature. Moreover, this model has implications for understanding contagious yawning in humans, as well as non-human primates (e.g., see Anderson et al. 2004; Paukner & Anderson 2006), as the infectiousness of the yawn may have evolved to facilitate group vigilance.

In this study it remains unclear as to whether the increase in temperature caused the change in yawn frequency, or whether it was merely the temperature change (irrespective of direction). If the purpose of yawning serves to maintain optimal thermal homeostasis, one would predict the frequency of this behaviour to increase with temperature change. Thus, a decreasing temperature condition may impose similar affects on yawn frequency. It should also be noted that our results remain consistent with the view that yawning is associated with behavioural state change (Baenninger et al. 1996; Greco et al. 1993; Provine et al. 1987). In addition, we propose that the difference in yawning frequency among trial procedures may be due in part to the control condition in the first trial inadvertently lengthening the initial acclimation period. As a result, the second trial procedure (increase-high-control) may have coupled an already mildly stressful situation of environmental change with the manipulation of ambient temperature, increasing the likelihood of hyperthermia in the first two thermal conditions (Cabanac & Guillemente 2001).

Due to the potential multifunctionality of yawning across species (Baenninger 1987), we suggest that further comparative research is necessary to more completely understand the relationship between yawning, ambient temperature and other factors. For instance, the thermoregulatory model suggests that there should be differences in the potential adaptive significance of yawning between endotherms and ectotherms, as well as between endothermic species selected to different degrees for cooling abilities in challenging thermal environments.

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