



## Yawning and thermoregulation in budgerigars, *Melopsittacus undulatus*

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### ARTICLE INFO

#### Article history:

Received 15 May 2008

Initial acceptance 15 July 2008

Final acceptance 4 September 2008

Published online 5 November 2008

MS. number: A08-00318R

#### Keywords:

ambient temperature

budgerigar

*Melopsittacus undulatus*

thermoregulation

yawning

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 °C), increasing temperature (22–34 °C), and high temperature (34–38 °C)) in a repeated measures design, with each condition lasting 21 min. The incidence of yawning differed significantly across conditions ( $4.20 \pm 2.39$  yawns per bird in the increasing temperature condition, compared to  $2.05 \pm 1.90$  and  $1.25 \pm 0.72$  yawns per bird, in the high temperature and control conditions, respectively). These findings are consistent with the hypothesis that yawning serves a thermoregulatory function.

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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 (Argiolas & 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 (Daquin 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 nonhuman 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 & Gallup 2008), occurring most often during the first hour after waking and the last hour before sleeping (Provine et al. 1987a; Baenninger et al. 1996; 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. 1987a). Researchers have attributed such findings to an association between yawning and increases in arousal and activity that accompany transitional states (Provine et al. 1987a; Greco & Baenninger 1991; Greco et al. 1993; Baenninger et al. 1996). Aside from observational reports, comparative studies investigating yawning in nonhumans are few and the ethology of yawning in nonhuman species remains mysterious. Baenninger (1987) proposed that yawning may actually serve different functions in different species. Nevertheless, the tendency for yawning to correspond with state changes in humans (Provine et al. 1987a; Greco et al. 1993; Baenninger et al. 1996) suggests possible adaptive contexts for this behaviour across species.

New evidence suggests that yawning may be involved in thermoregulation (Gallup & Gallup 2007, 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

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from specific areas, while introducing cooler blood from the lungs and extremities. Increases in facial blood flow may alter cerebral blood flow as well (Heusner 1946; Barbizet 1958; 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 vasodilation 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 travelling 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<sub>2</sub> and/or CO<sub>2</sub> concentrations has no effect on yawn frequency (Provine et al. 1987b).

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, 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 predictions are that (1) the frequency of yawning should rise as ambient temperature approaches body temperature and (2) yawning 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 should 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 in a laboratory environment while recording yawning, stretching and gular fluttering, a thermoregulatory response that 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. We chose *M. undulatus* as our study species 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 found no evidence for contagious yawning in this species (M. L. Miller, S. M. Vicario & A. B. Clark, 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, Binghamton, NY, U.S.A. These birds are routinely housed outside in the spring and summer months, and are then brought inside during the late autumn and winter. These experiments were conducted indoors during January–March 2008.

During this time, all birds were kept in an aviary (1.8 × 1.8 × 1.8 m) in an animal room maintained at 22 °C, on a 11:13 h light:dark cycle.

### Experimental Conditions

All birds in this study were caught 24 h before being tested, and all experiments occurred during 1200 and 1400 hours. Birds were tested in groups of four in a wire-mesh cage (0.40 × 0.30 × 0.30 m), which was then covered by a wooden box. This arrangement allowed us to adjust the ambient temperature accordingly using heat lamps placed within the box. The box (0.96 × 0.43 × 0.61 m) fully enclosed the cage, and a set of small heat lamps were used to adjust the temperature. A window (0.28 × 0.30 m) covered with Plexiglas allowed viewing and filming of the birds inside the box. A Springfield PreciseTemp digital thermometer (Springfield Precision Instruments, Inc., Wood Ridge, NJ, U.S.A.), which was positioned near the birds (0.5 m from heat lamps) in the upper half of the box, was used to monitor the ambient temperature. Temperature was recorded every 3 min to the nearest 0.1 °C.

Three separate thermal conditions, each 21 min long, were tested. A 20 min acclimation period occurred after the birds were positioned within the box before the start of each testing session. During each session, the birds and the ambient temperature were monitored by a researcher and recorded using a video camera. Conditions included a control condition (22 °C), a rapidly increasing temperature condition (22–34 °C) and a high temperature condition (34–38 °C). A repeated measures design was used in which each testing session lasted 63 min and included all three conditions. The experiments were partially counterbalanced, utilizing two trial orders: (1) control condition, increasing condition, then high temperature condition; and (2) 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 posterodorsal 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: (1) when at least one bird within the group began to display this behaviour (first flutter) and (2) when the entire group showed this response (all flutter). The behaviours for each bird in each group were summed for each 21 min 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 between conditions using SPSS version 15.0 (SPSS, Inc., Chicago, IL, U.S.A.). In addition, linear and quadratic regression analyses were conducted between yawning, stretching and ambient temperature across conditions in blocks of 3 min 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 temperatures that these birds 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 h with ambient temperatures ranging from 30 °C to 42 °C. Upon their release into the indoor aviary at the end of this study, the birds 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 No. 610-07).

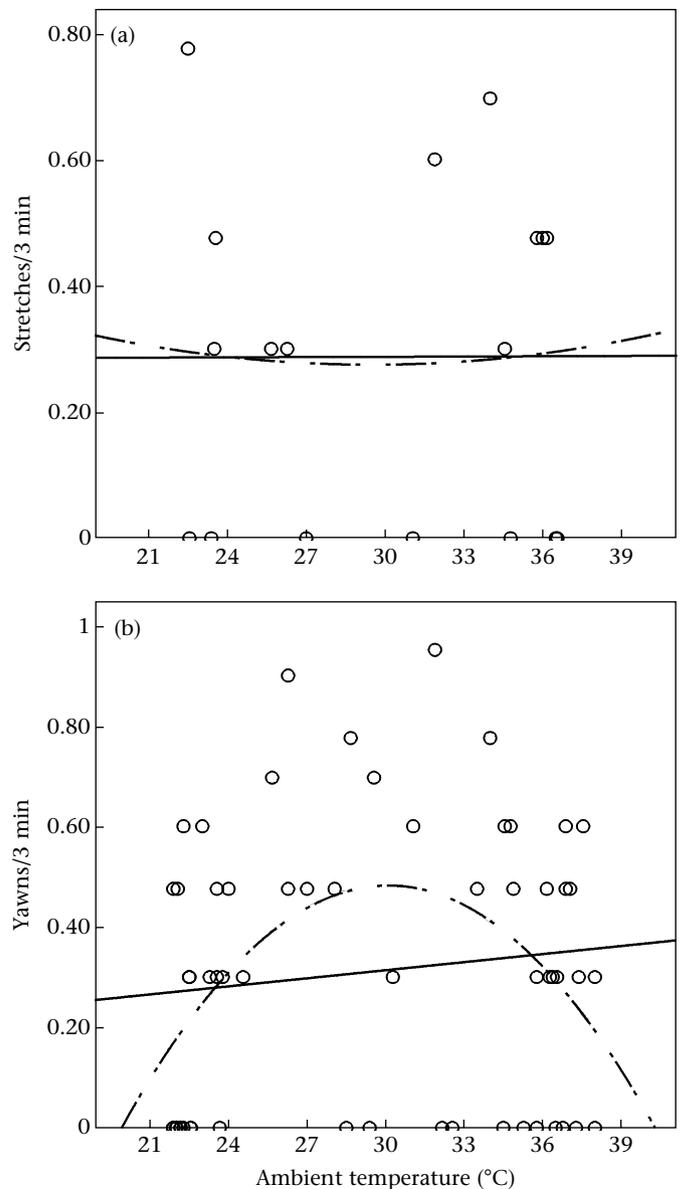
### RESULTS

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 ( $\bar{X} \pm SE = 4.20 \pm 2.39$  yawns per bird), 41 during the high temperature condition ( $2.05 \pm 1.90$  yawns per bird) and 25 during the control condition ( $1.25 \pm 0.72$  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 yawning rate in the increasing condition was significantly different from that in both the high temperature ( $t_{19} = 4.921, P < 0.0001$ ) and control ( $t_{19} = 5.064, P < 0.0001$ ) conditions; however, there was no difference in yawning rate 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 ( $7.727 \pm 3.90$  versus  $7.222 \pm 3.70$ ), 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 ( $F_{1,16} = 0.764, P = 0.395$ ).

We observed 42 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 ( $2.182 \pm 2.44$  versus  $2.000 \pm 2.18$ ), but this difference was not significant ( $F_{1,16} = 0.144, P = 0.710$ ). After log transformation, stretching was not correlated with yawning (Pearson correlation:  $r_{11} = 0.249, P = 0.412$ ).

Figure 1 depicts the frequency and distribution of stretching and yawning in response to ambient temperature across conditions in 3 min intervals. A linear regression of yawning on ambient temperature showed a nonsignificant relationship ( $F_{1,58} = 0.814, P = 0.371$ ). 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:  $F_{2,15} = 0.005, P = 0.995$ ).



**Figure 1.** Frequency and distribution of (a) stretching and (b) yawning in budgerigars in response to ambient temperature. ○: observed; —: linear regression; - - -: quadratic regression.

The incidence of gular flutter was significantly affected by ambient temperature (first bird to flutter:  $t_{103} = 19.376, P < 0.0001$ ; all birds fluttered:  $t_{103} = 18.081, P < 0.0001$ ). There was a strong positive correlation between ambient temperature and gular flutter (Pearson correlation: first flutter:  $r_{103} = 0.886, P < 0.001$ ; all fluttered,  $r_{103} = 0.872, P < 0.001$ ). In every trial, gular flutter began during the increasing temperature condition and 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 °C, while flutter among the entire group (all fluttered) occurred at mean temperature of 35.4 °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 complementary mechanisms that function towards 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 ( $1.25 \pm 0.72$  yawns per bird), slightly more when held at high temperatures ( $2.05 \pm 1.90$  yawns per bird), and most frequently with increasing temperatures ( $4.20 \pm 2.39$  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 °C, during the increasing temperature condition, it began to decrease in frequency as temperature further increased (i.e. 34–38 °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 °C, this trend was reversed by the time all birds were engaged in this behaviour (i.e. 35.4 °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 °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 35.4 °C, the cooling capacity of the yawn (i.e. difference between ambient and body temperature) was less than that at 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 temperatures 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 temperature, stretching is accompanied by yawning nearly half of the time (Provine et al. 1987a), with the incidence of yawning predicting stretching, but not vice versa. 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 into yawning as a 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 in 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 (Provine et al. 1987a; Baenninger et al. 1996). 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, subjective ratings of sleepiness are correlated 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 complements 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) proposed 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 in nonhuman 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 our study, it was unclear whether the change in yawn frequency resulted from the increase in ambient temperature or the change in temperature (irrespective of direction). If yawning serves to maintain optimal thermal homeostasis, yawning frequency should increase with temperature change. Thus, a decreasing temperature condition may impose similar effects on yawn frequency. Our results remain consistent with the view that yawning is associated with behavioural state change (Provine et al. 1987a; Greco et al. 1993; Baenninger et al. 1996). 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 & Guillemeute 2001).

Because of 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.

## Acknowledgments

We thank Darien Sutton for helping with data collection.

## References

- Anderson, J. R., Myowa-Yamakoshi, M. & Matsuzawa, T. 2004. Contagious yawning in chimpanzees. *Proceedings of the Royal Society of London, Series B*, **271**, 468–470.
- Anias, J., Holmgren, B., Urba Holmgren, R. & Eguibar, J. R. 1984. Circadian variation in yawning behavior. *Acta Neurobiologiae Experimentalis*, **44**, 179–186.
- Argiolas, A. & Melis, M. R. 1998. The neuropharmacology of yawning. *European Journal of Pharmacology*, **343**, 1–16.
- Baenninger, R. 1987. Some comparative aspects of yawning in *Betta splendens*, *Homo sapiens*, *Panthera leo*, and *Papio sphinx*. *Journal of Comparative Psychology*, **101**, 349–354.
- Baenninger, R., Binkley, S. & Baenninger, M. 1996. Field observations of yawning and activity in humans. *Physiology & Behavior*, **59**, 421–425.
- Barbizet, J. 1958. Yawning. *Journal of Neurology, Neurosurgery and Psychiatry*, **21**, 203–209.
- Bartholomew, G. A., Lasiewski, R. C. & Crawford, U. C. Jr. 1968. Patterns of panting and gular flutter in cormorants, pelicans, owls, and doves. *Condor*, **70**, 31–34.
- Cabanac, A. J. & Guillemeute, M. 2001. Temperature and heart rate as stress indicators of handled common eider. *Physiology & Behavior*, **74**, 475–479.
- Daquin, G., Micallef, J. & Blin, O. 2001. Yawning. *Sleep Medicine Reviews*, **5**, 299–312.
- Everson, C. A., Smith, C. B. & Sokoloff, L. 1994. Effects of prolonged sleep deprivation on local rates of cerebral energy metabolism in freely moving rats. *Journal of Neuroscience*, **14**, 6769–6778.
- Falk, D. 1990. Brain evolution in *Homo*: the “radiator” theory. *Behavioral and Brain Sciences*, **13**, 333–381.
- Gallup, A. C. & Gallup, G. G. Jr. 2007. Yawning as a brain cooling mechanism: nasal breathing and forehead cooling diminish the incidence of contagious yawning. *Evolutionary Psychology*, **5**, 92–101.
- Gallup, A. C. & Gallup, G. G. Jr. 2008. Yawning and thermoregulation. *Physiology & Behavior*, **95**, 10–16.
- Gilbert, S. S., van den Heuvel, C. J., Ferguson, S. A. & Dawson, D. 2004. Thermoregulation as a sleep signaling system. *Sleep Medicine Reviews*, **8**, 81–93.
- Greco, M. & Baenninger, R. 1991. Effects of yawning and related activities on skin conductance and heart rate. *Physiology & Behavior*, **50**, 1067–1069.
- Greco, M., Baenninger, R. & Govern, J. 1993. On the context of yawning: when, where, and why? *Psychological Record*, **43**, 175–183.
- Heusner, A. P. 1946. Yawning and associated phenomena. *Physiological Reviews*, **25**, 156–168.
- Hoffman, T. C. M., Walsberg, G. E. & DeNardo, D. F. 2007. Cloacal evaporation: an important and previously undescribed mechanism for avian thermoregulation. *Journal of Experimental Biology*, **210**, 741–749.
- Iwaniuk, A. N. & Nelson, J. E. 2002. Can endocranial volume be used as an estimate of brain size in birds? *Canadian Journal of Zoology*, **80**, 16–23.
- Krauchi, K., Cajochen, C. & Wirz-Justice, A. 2005. Thermophysiological aspects of the three-process-model of sleepiness regulation. *Clinical Journal of Sport Medicine*, **24**, 287–300.
- Nijhuis, J. G. 2003. Fetal behavior. *Neurology of Aging*, **24**, 41–46.
- Paukner, A. & Anderson, J. R. 2006. Video-induced yawning in stump-tail macaques (*Macaca arctoides*). *Biology Letters*, **2**, 36–38.
- Provine, R. R. 2005. Yawning. *American Scientist*, **93**, 532–539.
- Provine, R. R., Hamernik, H. B. & Curchack, B. B. 1987a. Yawning: relation to sleeping and stretching in humans. *Ethology*, **76**, 152–160.
- Provine, R. R., Tate, B. C. & Geldmacher, L. L. 1987b. Yawning: no effect of 3–5% CO<sub>2</sub>, 100% O<sub>2</sub>, and exercise. *Behavioral and Neural Biology*, **48**, 382–393.
- Sherer, D. M., Smith, S. A. & Abramowicz, J. S. 1991. Fetal yawning in utero at 20 weeks gestation. *Journal of Ultrasound in Medicine*, **10**, 68.
- Smith, E. O. 1999. Yawning: an evolutionary perspective. *Journal of Human Evolution*, **14**, 191–198.
- Walusinski, O. 2006. Yawning: unsuspected avenue for a better understanding of arousal and interoception. *Medical Hypotheses*, **67**, 6–14.
- Zajonc, R. B. 1985. Emotion and facial efference: a theory reclaimed. *Science*, **288**, 15–21.
- Zilli, I., Giganti, F. & Salzarulo, P. 2007. Yawning in morning and evening types. *Physiology & Behavior*, **91**, 218–222.