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Yawn Duration Predicts Brain Size in Wild Cats (*Felidae*)

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Recently, yawn duration was shown to be a robust predictor of brain size and complexity across a diverse sample of mammalian species. In particular, mammals with larger brains and more cortical neurons have longer yawns on average. Here, we investigated whether this relationship between yawn duration and brain size, which was previously at the taxonomic rank of class, is also present within a more restricted scale: a family of mammals. Using previously published data on brain weight and endocranial volumes among various field species within the family Felidae, we ran correlations with yawn durations obtained from openly accessible videos on the Internet. Consistent with previous findings, we show a strong linear relationship between yawn duration and both brain weight and brain volumes among wild cats. However, yawn duration was not significantly correlated with species body weight. Although limited to a small sample, these results provide convergent evidence for an important and general neurophysiologic function to yawning and highlight the utility of measuring yawn duration in comparative research.

Yawning is characterized by a powerful gaping of the jaw with inspiration, a brief period of peak muscle contraction and a passive closure of the jaw with shorter expiration (Barbizet, 1958). Yawning or yawn-like mandibular gaping patterns have been documented across vertebrate classes (Baenninger, 1987), suggesting it is an evolutionarily conserved behavior with adaptive value. Specifically, the jaw stretching and deep inhalation that accompany yawns alter intracranial circulation (Walusinski, 2014), which supports an important neurophysiological function. Numerous hypotheses have been proposed for why animals yawn (for reviews, see Gallup, 2011; Guggisberg, Mathis, Schnider, & Hess, 2010; Smith, 1999), but comparative research primarily supports a role in promoting cortical arousal, alertness and state change (Baenninger, 1997; Provine, 1986, 2005).

Accumulating research indicates that the arousing and state changing effects of yawns are a result of brain cooling (Gallup & Gallup, 2007). In particular, the brain cooling hypothesis posits that the powerful gaping of the jaw and deep inhalation that categorize yawns functions as a thermoregulatory mechanism by increasing blood flow to the skull and providing counter-current heat exchange between cooled venous return and arterial blood supply (reviewed by Gallup & Eldakar, 2013). Empirical support for this hypothesis comes from correlatonal research showing predicted patterns of brain/skull temperature change surrounding yawns in rats and humans (Eguibar, Uribe, Cortes, Bautista, & Gallup, 2017; Gallup & Gallup, 2010; Shoup-Knox, Gallup, Gallup, & McNay, 2010), and experiments showing that brain cooling manipulations diminish yawn frequency among human participants in the laboratory (Gallup & Gallup, 2007). Further evidence for this hypothesis comes from the repeated demonstration that yawn frequency can be effectively increased or diminished across diverse species as a function of ambient temperature manipulation and variation (reviewed by Gallup, 2016). Moreover, interdisciplinary research shows that medical conditions and drug use which produce changes in brain temperature have predicted effects on yawn frequency; that is, those that increase temperature result in heightened yawning, while those that decrease temperature suppress yawns (Gallup & Gallup, 2008).

The neurophysiologic effects from yawns are likely tied to the magnitude of the response, i.e., longer and more powerful yawns should produce greater circulatory consequences within the skull. Thus, it would be expected that in order to achieve the same functional outcomes, animals with larger and more neuron rich brains would have longer yawns on average. To test this prediction, a recent study examined whether yawn duration varied as function of brain size and complexity in mammals (Gallup, Church, & Pelegrino, 2016). By coupling previously reported brain parameters from a representative sample of taxa across the class Mammalia with yawn durations obtained from openly accessible videos online, it was revealed that yawn duration is a robust predictor of brain weight and cortical neuron number (ρ-values > 0.9). Within-taxon variance in yawn duration was equally correlated with these measures, indicating that mammals with larger and more complex brains have more variable yawn lengths as well. Consistent with these findings, primates within the sample had longer and more variable yawns compared to non-primate species (Gallup et al., 2016).

Here, we investigated whether the relationship between yawn duration and brain size, which was previously at the taxonomic rank of class (Mammalia), is also present within a family of mammals. This more refined approach allows for the determination of whether variability in yawn duration is related specifically to brain size or other features pertaining to phylogenetic history and morphological diversity between species. Since a paper was just recently published documenting the total endocranial and regional brain volumes of 13 field species within the family Felidae (Sakai, Arsznov, Hristova, Yoon, & Lundrigan, 2016), this data set was used as a template for the current report. Comparatively, felines also have a relatively high yawning rate (Baenninger, 1987) and thus serve as an appropriate group to collect archival video footage and explore this relationship. We used the same methods as Gallup et al. (2016) to acquire representative yawn durations of these species from openly accessible videos available online.

Using the list of 13 wild cat species compared within Sakai et al. (2016; Table 1, p. 7), two researchers were instructed to find as many yawns as possible from each species by searching openly accessible videos from the Internet. For each video, the researchers noted the time(s) at which the yawn(s) on the clip occurred and the duration of all yawning events using the operational definition provided by Barbizet (1958) to the nearest 0.01sec using the stopwatch feature on an iPhone. The researchers also noted for each yawn whether the animal was an adult or subadult. As expected, this approach resulted in a significant overlap in the videos scored between raters ($N = 29$), and the total inter-rater reliability for yawn duration was high (intraclass correlation = 0.800). A third researcher then confirmed all yawns from both searches, which occurred during the fall semester of 2016.

The average yawn duration for each species was calculated by summing all the respective durations from that group and then dividing by the number of yawners. To avoid pseudo-replication in cases where the same individual displayed multiple yawns in a given video, the average duration for this animal was used as a single data point when generating the overall average for that species. The maximum yawn duration was also recorded from each species. One video was not included because it was not confirmed as a full yawn, and two videos from subadult bobcats were removed since brain parameters were based on adult averages. Four videos were removed from the analysis because the yawns started prior to the onset of the video (including one lion, jaguar, cougar and bobcat), and seven videos were removed because they did not represent one of the species outlined in the Sakai et al. (2016) paper (e.g., clouded leopard, Euasian lynx, caracal). In total, 66 full yawns were confirmed from 61 individuals across 10 of the 13 species with available neurological data: bobcat (7) Canada lynx (1), cheetah (11), cougar (3), jaguar (4), kodkod (1), leopard (8), lion (12), margay (1), and tiger (13). The supplemental material includes hyperlinks to all videos acquired during the search.

Using the same criterion set within Gallup et al. (2016), analyses were restricted to species with at least three adult yawns (58 individudals from 7 species). The average, maximum, and standard error of mean (*SEM*) yawn durations were then linked to the reported total endocranial and regional (anterior cerebrum, posterior cerebrum, and combined cerebellum + brain stem) brain volumes from each species reported in Sakai et al. (2016). Correlations were also run on previously published measures of average brain (g) and body weight (kg) from each species examined (Gittleman, 1986). Analysis of brain weight provides a more direct test of a neurological function, as endocranial volume includes non-brain tissue. In addition, the inclusion of body weight allows for the determination of whether yawn duration is more related to brain or overall body size. Due to the small sample, Spearman Rank correlations were used to assess the linear relationships. There were perfect rank correlations between the total endocranial and regional brain volumes across species (ρ-values = 1.00), thus only one statistic is provided for brain volume. Analyses were performed in SPSS v.22 with an alpha set at 0.05.

Both average and maximum yawn durations were robustly correlated with measures of brain size across species represented within the family Felidae. In particular, average and maximum yawn durations were positively correlated with brain weight ($\rho = 0.937$, $p = 0.002$; $\rho = 0.847$, $p = 0.016$; Figure 1) and brain volumes ($\rho = 0.893$, $p = 0.007$; $\rho = 0.821$, $p = 0.023$). Although brain and body weight were highly correlated with one another ($\rho = 0.883$, $p = 0.008$), body weight was neither a significant predictor of average nor maximum yawn duration ($\rho = 0.750$, $p = 0.052$; $\rho = 0.643$, $p = 0.119$). Within-species variance in yawn duration was also not correlated with average or maximum yawn duration across species ($\rho = 0.607$, $p = 0.148$; $\rho = 0.750$, $p = 0.052$), neither was it predictive of brain weight nor brain volumes ($\rho = 0.342$, $p = 0.452$; $\rho = 0.286$, $p = 0.535$). Within-species variance was not related to sample size ($\rho = 0.107$, $p = 0.819$), and therefore did not reflect sampling error.
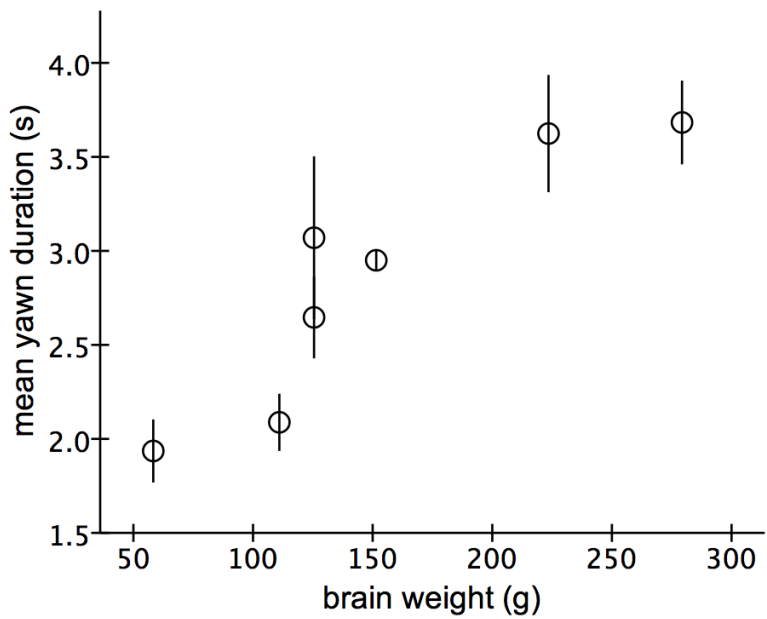

Figure 1. **The correlations between mean yawn duration and brain weight and brain volume.** The correlations between mean yawn duration and brain weight and brain volume were highly significant (brain weight depicted above; $M \pm SEM$). Species in order of mean yawn duration: bobcat; cheetah; leopard; jaguar; cougar; lion; tiger.

As an extension of a previous report identifying strong linear relationships between yawn duration and brain weight and cortical neuron number across a diverse sample of species within the class Mammalia (Gallup et al., 2016), we show that interspecies yawn duration is an equally robust predictor of brain size within a more restricted taxonomic scale. In particular, both average and maximum yawn durations were highly correlated with brain weight and brain volumes among wild cat species in the family Felidae. However, unlike these neurological measures, overall body size was not a significant predictor of the yawn durations obtained. Unlike that which was documented in species across the class Mammalia, which included a sample of primates, interspecies variance in yawn duration was not predictive of the available neurological measures in wild cats.

Consistent with previous research (Baenninger, 1997; Gallup & Gallup, 2007; Walusinski, 2014), these results support the view that yawns serve an important neurophysiologic function. Although both brain weight and brain volumes were highly correlated ($\rho > 0.9$), average and maximum yawn duration showed the strongest linear relationship with brain weight. Due to perfect correlations between the total endocranial and regional brain volumes of the species analyzed here, yawn duration was equally correlated with all measures. However, if data were available future research could examine how variation in more specific neuroanatomical structures relates to yawn duration across species. The neural structures necessary for yawning appear to be located in the brain stem (Heusner, 1946), and a recent case study demonstrated that electrical stimulation of the putamen, which has extensive connectivity between the brain stem and cortical regions, induces yawning in humans (Joshi, Bayat, Gagnon, Shields, & Koubeissi, 2017). Given recent comparative research showing that yawns provide widespread cooling across the surface of skull (Eguibar et al., 2017), this newfound evidence on yawn duration implies yawns contribute to large-scale neurophysiologic effects. These findings can be readily interpreted under the functional hypotheses of arousal and state change (Baenninger, 1997; Provine, 1986; 2005), whereby greater neurological volumes and more cortical neurons necessitate longer yawns to achieve these adaptive outcomes. Although social and communicative (i.e., signaling) functions of yawning have been proposed (e.g., Liang, Grace, Tompkins, & Anderson, 2015), empirical tests of this hypothesis are lacking (Gallup & Clark, 2015) and the current findings provide no clear connection between yawn duration and the degree of sociality within the species sampled.

Limitations to this study should be acknowledged. First and foremost, the correlational analyses were restricted to a small sample of wild cats within the family Felidae, with an average of just over eight yawns per species. Furthermore, the method of data collection could be considered a limitation since yawn durations were captured from videos posted to the Internet rather than through naturalistic observations. For example, it remains unknown whether these videos are representative of the true variability in yawn duration for a given species and it is possible that the longest and most robust yawns are disproportionately posted online. While this would not alter our interpretations, since maximum yawn length was equally predictive of brain size, future research could include naturalistic observations to represent all forms of yawn morphology among cats (for discussion of different yawn types in non-human primates, see Leone, Ferrari, & Palagi, 2014; Palagi, Leone, Mancini, & Ferrari, 2009; Vick & Paukner, 2010). The inability to determine the contextual triggers of yawning within the videos also limits our interpretation of the variability in this response between species, but future research could examine these factors.

Overall, these findings provide convergent evidence that yawn duration can be used as a behavioral marker of interspecies differences in brain size within mammals. Among other areas of comparative and clinical research (see Gallup et al., 2016, Table 1, p.3), future studies could investigate whether yawn duration predicts individual differences in neurological parameters within a species, and how yawn duration may relate to cognition and neural processing.

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